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Effects of harvester ants on plant species distribution and abundance in a serpentine grassland

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Abstract Seed harvesting ants can have important effects on the composition and structure of plant communities. We investigated two effects of *Messor andrei*, the black seed-harvesting ant, on a serpentine grassland plant community in northern California. First, to determine if selective seed predation by ants affects plant community composition, we excluded harvester ants from 1-mediameter circular plots of grassland. Abundances of all species on these plots and on control plots were measured before and after exclosure. Second, to determine if *M. andrei* nest mounds affect plant community composition, we compared plant species abundances on and off nest mounds. *M. andrei* deposit large amounts of organic matter on their nest mounds over a foraging season, so mounds may alter the edaphic environment. The exclusion of seed-harvesting activity did not cause changes in the plant community. Nest mounds had a strong effect on plant communities: there were many more grasses and fewer forbs on ant mounds, although at least one forb, *Lepidium nitidum*, produced twice as many seeds when it grew on nest mounds. We found that nest mounds formed islands of higher-temperature soil in the serpentine grassland.

Key words Seed-harvesting ants · Ant mounds · Serpentine grassland · Plant abundance · *Messor andrei*

Introduction

Ants influence the structure and composition of plant communities. They can protect plants directly from herbivores or from competition with other plants (Janzen 1966, 1967, 1969; Bentley 1977). Ants also affect plant community composition or dynamics by selective weeding or "gardening" (Kleinfeldt 1978; Jolivet 1990), altering nutrient availability (Gentry and Stiritz 1972; Beattie and Culver 1977; King 1977; Petal 1978; Rissing 1986; Treseder et al. 1995; Wagner 1997), pollinating flowers (Hickman 1974; Wyatt 1981; review in Peakall et al. 1991) or by dispersing and harvesting seeds (Berg 1972; Beattie and Lyons 1975; Brown et al. 1979; Westoby et al. 1982; Bond and Slingsby 1984; Davidson et al. 1984, 1985; Samson et al. 1992).

Seed-harvesting ants can affect plant communities through at least two different processes. Selective harvesting of particular seed species can affect the relative and absolute abundance of plant species (Brown et al. 1979; Carroll and Risch 1984; Davidson et al. 1985; Hobbs 1985; Risch and Carroll 1986; Andersen 1987; Samson et al. 1992), while the production of mounds provides enriched edaphic environments that can support plant communities that differ from the surrounding vegetation (Hobbs 1985; review in Beattie 1989; Danin and Yom-Tov 1990; Nowak et al. 1990). In addition, plants that grow on mounds may enjoy increased seed production (Tevis 1958; Rissing 1986; review in Beattie 1989; Dean and Yeaton 1993).

Messor andrei, the black seed-harvesting ant, is the primary granivore in serpentine grasslands in northern California (Hobbs 1985). *M. andrei* ants harvest seeds selectively (Hobbs 1985; M.J.F. Brown, unpublished work), and hence might influence plant abundances in this community. A study conducted at a site in northern California (Jasper Ridge Biological Preserve) suggested that seed predation by *M. andrei* decreased the abundance of preferred species in areas immediately adjacent to nests (Hobbs 1985). Hobbs suggested that these local effects might be representative of similar reductions across the entire grassland, regardless of proximity to ant nests. In this study, we test this hypothesis and ask whether seed-harvesting affects plant abundances in the serpentine grassland community.

M. andrei produces large nest mounds composed of excavated soil and seed chaff which is deposited throughout the year. Hobbs (1985) demonstrated that

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mounds support plant communities that differ from those on the surrounding serpentine soil. The abundance of different species in the serpentine grassland community has changed significantly over the last decade (Hobbs and Mooney 1995). We repeated Hobbs' study, comparing plant communities on and off ant mounds, to determine if mounds have a consistent effect on plants despite changes in the surrounding grassland community. We also examined how ant mounds affect the seed set of one forb which was consistently present both on and off mounds.

Methods

Study Site

Our study took place between 1994 and 1996 on a serpentine grassland site at Jasper Ridge Biological Preserve, a 450-ha reserve in San Mateo County, northern California (122°12′W, 36°25′N, elevation *c.* 180 m). Serpentine soils are shallow and nutrient poor, and plant communities are spatially and temporally heterogeneous (Hobbs and Mooney 1985). The plant community consists primarily of native annual forbs, a few native perennial bunch-grasses, and some native and exotic annual grasses (McNaughton 1968).

Ant exclosures

To determine the effect of ant exclusion on the plant community, we set up three types of experimental plot in March 1994: (1) ant exclosure plots, (2) pseudo-exclosure plots, and (3) open plots. Pseudo-exclosure plots and open plots were controls for the effects of exclosures and the effects of harvesting respectively. Ant exclosure plots were ringed with painted tin cylinders, 20 cm high and 1 m in diameter, sunk 2.5 cm into the soil. Cylinders were slippery and tall enough that harvester ants could not climb over them. Pseudo-exclosure plots were surrounded by similar cylinders, except that semi-circles were cut from the bottom edges, so that ants could pass through easily. Occasional observations confirmed that harvester ants did indeed forage within pseudo-exclosure plots. This treatment enabled us to investigate the effects of the cylinders on the plant community. Open plots were of the same size and shape as the other treatments but were not ringed with cylinders.

We set up seven replicates of each of the three types of experimental plot, for a total of 21 plots, in an area of serpentine grassland. After excluding areas with large rocks, recent gopher disturbances, or ant mounds, plot positions and treatments were assigned randomly. All plots were separated by at least 10 m. As a measure of potential seed-harvesting activity, we counted the number of active *M. andrei* nests within 10 m of each plot in April 1994, September 1994, and April 1996. Nests within 10 m of more than one plot were counted once for each plot. The density of active nests was similar for all treatments; an ANOVA revealed no significant association between treatment type and local density of ant nests ($P = 0.66$ for April 1994, $P = 0.08$ for September 1994, $P = 0.93$ for April 1996).

Exclosures might change the plant community, by altering the abiotic environment or disrupting normal patterns of seed dispersal and germination. Though pseudo-exclosure plots were used to identify such effects, we also designed our sampling regime to minimize these effects.

Abiotic effects

To determine if exclosures affected soil temperature through shading, we recorded soil temperatures at 1 cm depth in three areas around each ant exclosure and pseudo-exclosure plot: (1) center, (2) inside, 2 cm from the shaded inside edge, and (3) outside, 10 cm from the edge. Soil temperatures were measured in April 1996 with a Licor soil probe thermocouple (model 6000-09TC) and an Omega digital readout (model 450-AET). We took measurements early in the morning of a clear day to maximize the likelihood of discovering differences between the shaded interior edges of exclosures and the unshaded centers and outside edges. To determine if soil temperatures differed among the locations, we used a one-way ANOVA, with a priori contrasts between center and outside, and interior edge and outside (Sokal and Rohlf 1981). In addition, to minimize the impact of potential microclimatic effects, plant community censuses were taken at the center of plots where they were least likely to be shaded by the exclosure cylinder.

Biotic effects

The serpentine plant community is dependent upon the annual seed rain for next year's seedlings. There is no carry-over in the seed bank from one year to the next (Hobbs and Mooney 1985). Furthermore, though ants harvest seeds, they rarely drop seeds anywhere other than on their mounds (M. Brown, personal observation). Thus the distribution of next year's seedlings on the open grassland depends on the present year's plant distribution and corresponding seed rain shadow. Hobbs and Mooney (1985) showed that the seed rain shadows of most species on the serpentine grassland are extremely local. Most plants drop seeds within 12.5 cm of the stem. Those few grass species that have a larger seed rain shadow (up to 25 cm) are tall enough to disperse seeds over the exclosures. Thus, exclosure cylinders are unlikely to interfere with seed dispersal patterns, except possibly by increasing seed densities at the inside edge of cylinders. To avoid this problem, plant communities were sampled in the centers of the plots, away from the edges.

Harvesting effects on the plant community

The serpentine grassland community is extremely heterogeneous. Because most plants in the community are small, it is difficult to sample a large enough area to account for spatial heterogeneity and still obtain an accurate count of plants within the area. To increase the likelihood of discovering differences due to ant exclosure, we used two sampling methods, percent cover and density. Percent cover, which incorporates both spatial distribution and abundance, was measured by counting the number of 5 cm by 5 cm squares in a 50 cm by 50 cm grid in which plants of a species were present (Hobbs and Mooney 1995). Density, a smaller-scale measure of abundance, was measured by counting the number of plants of each species in three 10 cm by 10 cm squares in each plot. Density measurements served as both an independent measure of the plant community and a check for percent cover results.

In 1994 we sampled the percent cover and density of all plant species within the 21 plots in April, May, June and September, using the 50 cm by 50 cm sampling grid placed in the center of each plot. Squares were oriented north-south and centered within the plot so that the same plot of grassland was always sampled. The three density measurements were taken on the north, east and south edges of the percent cover sample area. The 1994 data showed that all plants could be identified and counted accurately by May, so in 1995 and 1996 we sampled in April and May only. There was no association between treatment type and percent cover for any species in 1994 (arcsin-transformed data, one-way ANOVA, all P-values > 0.05).

To compare changes across years in the percent cover and density of plant species in ant exclosure, pseudo-exclosure, and open plots, we used a repeated-measures ANOVA on data from 1995 and 1996. Percent cover data were arcsin-transformed prior to analysis. Grass data were collected only in open plots in 1995. We used a one-way ANOVA to analyze 1996 grass data. We tested each plant species independently and used the step-up sequential Bonferroni correction (Hochberg 1988) for multiple comparisons.

Mound-building effects on the plant community, seed production and soil temperatures

In April 1995 we compared the plant community growing on and off ant mounds. We chose seven harvester ant mounds that were inhabited by colonies throughout the previous summer and compared the plants sampled on these sites to plants sampled in our open sites. As in experimental plots, we sampled the percent cover of all species in a 50 cm by 50 cm area, and plant density in three 10 cm by 10 cm areas. For each plant species, we compared percent cover and density on and off ant mounds using the Mann-Whitney *U*-test (Sokal and Rohlf 1981) and the step-up sequential Bonferroni correction (Hochberg 1988).

In April 1996 we investigated seed set of *Lepidium nitidum* plants on and off ant mounds. *L. nitidum* grows both on and off mounds, and, unlike other native forbs, it is possible to measure seed set of this species non-destructively. We measured the seed set of all *L. nitidum* plants on each of seven ant mounds and compared it to the seed set of *L. nitidum* plants in open grassland using a two-tailed *t*-test (Sokal and Rohlf 1981).

Ant mounds might affect the plant community by changing the soil temperature. To examine this possibility, we measured soil temperatures in the centers of seven active ant mounds, on the edges of these mounds, and on open ground 50 cm away. Soil temperatures were taken in April 1996 at depths of 1 cm and 5 cm. We compared soil temperatures on and off mounds using a two-way ANOVA with planned contrasts between center and edge temperatures and mound vs. off-mound temperatures (Sokal and Rohlf 1981).

Results

Harvesting effects on the plant community

Neither ant foraging activity nor exclosures affected the plant community over the two year study. There were no significant treatment effects on either percent cover or density (repeated-measures ANOVAs and one-way ANOVAs, for *F* values see Tables 1 and 2, no significant treatment effects after step-up sequential Bonferroni correction).

The percent cover and density of only one species changed during the study period. There was a significant decline in the percent cover and density of *Brodiaea* sp. (a lily) in all treatments across the study period (see Tables 1a and 2a; repeated-measures ANOVAs, percent cover $F = 34.3$, $P < 0.0001$, density $F = 13.2$, $P < 0.001$). There were no other significant time effects (repeated-measures ANOVAs, for *F* values see Tables 1 and 2, no significant time effects after step-up sequential Bonferroni correction).

Treatments did not affect the percent cover or density of plant species differently in different years (repeated-

Table 1a,b Mean percent cover (± SEs) for plant species in the three plot types during the study. *F* ratios are given for main effects in statistical analyses. **a** Data for non-grass species and *F* ratios from repeated-measures ANOVA for treatment and time effects. **b** Data for grass species and *F* ratios from one-way ANOVA for treatment effects. Significant results after correction for multiple comparisons are indicated by *asterisks*

a	1995			1996			$F_{2,15}$ Treatment	$F_{1,15}$ Time
Plant species	Ant exclosure	Pseudo-exclosure	Open	Ant exclosure	Pseudo-exclosure	Open		
Plantago erecta	76.1 ± 10.30	63.3 ± 7.40	90.4 ± 5.56	55.9 ± 14.24	75.9 ± 7.07	85.7 ± 6.67	3.9	1.2
Lasthenia californica	54.5 ± 11.91	63.4 ± 11.66	74.2 ± 11.56	83.7 ± 12.14	77.2 ± 14.21	89.6 ± 2.91	0.3	7.3
Castilleja densiflora	18.2 ± 5.97	11.1 ± 4.81	29.2 ± 8.55	16.9 ± 6.02	12.6 ± 3.41	11.2 ± 4.31	1.6	0.8
Hemizonia congesta	33.1 ± 7.34	18.0 ± 5.41	18.8 ± 4.03	12.8 ± 5.79	7.1 ± 4.81	8.2 ± 1.78	0.8	11.2
Lotus subpinnatus	10.2 ± 1.80	10.4 ± 2.09	7.7 ± 1.96	10.2 ± 3.24	7.7 ± 2.42	9.8 ± 2.27	0.1	0.6
Microseris douglasii	8.8 ± 7.68	0.3 ± 0.18	0.7 ± 0.57	0.5 ± 0.51	1.0 ± 0.55	0.3 ± 0.18	1.0	1.0
Hesperevax sparsiflora	9.2 ± 3.96	3.7 ± 2.01	8.4 ± 6.79	5.2 ± 2.14	3.8 ± 2.87	11.9 ± 6.24	0.4	0.3
Brodiaea sp.	13.8 ± 3.24	11.1 ± 3.18	19.7 ± 4.11	5.1 ± 2.45	10.1 ± 3.26	8.4 ± 2.84	0.3	34.3*
Astragalus gambelianus	2.4 ± 1.09	2.3 ± 0.68	5.2 ± 3.00	3.1 ± 1.05	2.5 ± 1.07	4.3 ± 1.31	0.2	0.3
Lepidium nitidum	2.0 ± 1.17	0.6 ± 0.37	3.0 ± 1.20	1.0 ± 0.64	0.2 ± 0.20	0.9 ± 0.51	2.1	0.5
Tillaea erecta	4.7 ± 3.27	7.0 ± 3.59	10.6 ± 7.57	1.6 ± 1.04	3.0 ± 2.32	8.6 ± 7.27	0.3	5.6
Agoseris heterophylla	5.6 ± 2.12	2.9 ± 1.45	4.9 ± 3.56	5.5 ± 1.95	2.1 ± 0.88	3.4 ± 1.93	0.3	0.7
Eschaltzia californica	0.7 ± 0.57	0.9 ± 0.46	0.0 ± 0.00	1.0 ± 0.64	0.6 ± 0.40	0.3 ± 0.29	1.1	1.5
Gilia tricolor	1.3 ± 1.29	3.0 ± 1.07	6.3 ± 4.62	3.1 ± 2.01	1.7 ± 1.23	1.1 ± 0.58	0.1	0.5
Epilobium sp.	5.6 ± 3.88	0.1 ± 0.14	0.0 ± 0.00	4.9 ± 2.81	0.4 ± 0.40	0.4 ± 0.30	2.0	1.1
Trifolium sp.	0.4 ± 0.31	0.4 ± 0.30	0.9 ± 0.86	0.4 ± 0.23	0.2 ± 0.20	0.1 ± 0.14	0.1	0.5
Alchemilla occidentalis	6.1 ± 3.14	3.0 ± 2.52	2.0 ± 2.01	2.7 ± 2.49	3.0 ± 1.55	3.3 ± 2.42	0.3	0.1
Calandrinia ciliata	0.9 ± 0.70	1.7 ± 1.13	1.2 ± 0.87	0.0 ± 0.00	0.0 ± 0.00	0.2 ± 0.25	0.6	3.0
Plagiobothrys nothofulvus	0.3 ± 0.29	0.7 ± 0.57	1.7 ± 1.71	1.9 ± 1.49	3.3 ± 2.29	0.0 ± 0.00	0.7	0.5

b	1996			*F*
Plant species	Ant exclosure	Pseudo-exclosure	Open	
Bromus mollis	51.3 ± 16.43	36.0 ± 18.13	21.0 ± 15.08	0.8
Gastridium ventricosum	33.2 ± 20.83	19.2 ± 15.32	46.4 ± 17.75	0.7
Lolium perenne	2.7 ± 2.50	1.6 ± 1.36	1.0 ± 1.06	0.1
Vulpia microstachys	4.1 ± 2.91	25.0 ± 12.54	8.4 ± 3.71	2.9
Nassella pulchra	0.8 ± 0.37	0.9 ± 0.64	1.0 ± 0.46	0.2
Elymus elymoides	0.2 ± 0.20	1.0 ± 0.63	0.3 ± 0.31	0.8

Table 2a, b Mean density (±SEs) for plant species in the three plot types during the study. F ratios are given for main effects in statistical analyses. **a** Data for non-grass species and F ratios from repeated-measures ANOVA for treatment and time effects. **b** Data for grass species and F ratios from one-way ANOVA for treatment effects. Significant results after correction for multiple comparisons are indicated by *asterisks*

a	1995			1996			$F_{2,48}$ Treatment	$F_{1,48}$ Time
Plant species	Ant exclosure	Pseudo-exclosure	Open	Ant exclosure	Pseudo-exclosure	Open		
Plantago erecta	36.3 ± 9.62	19.8 ± 4.87	47.2 ± 6.94	13.8 ± 5.90	24.7 ± 5.12	32.7 ± 6.35	3.2	8.6
Lasthenia californica	30.6 ± 14.84	15.9 ± 5.21	15.2 ± 3.02	28.6 ± 10.10	15.6 ± 4.70	23.1 ± 3.37	1.7	0.1
Castilleja densiflora	1.3 ± 0.64	1.2 ± 0.65	1.7 ± 0.55	0.7 ± 0.28	0.8 ± 0.25	0.8 ± 0.32	0.3	2.3
Hemizonia congesta	1.3 ± 0.43	0.9 ± 0.26	2.2 ± 0.44	0.6 ± 0.26	1.6 ± 0.47	1.1 ± 0.33	1.5	1.2
Lotus subpinnatus	0.7 ± 0.26	1.0 ± 0.20	0.5 ± 0.16	1.3 ± 0.35	0.9 ± 0.21	0.8 ± 0.25	0.9	1.8
Microseris douglasii	0.2 ± 0.17	0.0 ± 0.00	0.2 ± 0.10	0.2 ± 0.17	0.0 ± 0.00	0.0 ± 0.00	1.2	3.6
Hesperevax sparsiflora	0.8 ± 0.43	0.5 ± 0.17	1.8 ± 0.88	1.6 ± 1.18	0.2 ± 0.12	2.05 ± 1.27	1.4	0.4
Brodiaea sp.	1.8 ± 0.64	2.3 ± 0.71	2.6 ± 0.85	0.5 ± 0.26	0.5 ± 0.24	1.2 ± 0.51	0.5	13.2*
Astragalus gambelianus	0.3 ± 0.18	0.2 ± 0.09	0.5 ± 0.26	0.2 ± 0.11	0.5 ± 0.17	0.1 ± 0.05	0.3	0.3
Lepidium nitidum	0.2 ± 0.11	0.1 ± 0.05	0.4 ± 0.19	0.1 ± 0.08	0.1 ± 0.07	0.0 ± 0.00	0.9	3.2
Tillaea erecta	3.6 ± 1.58	1.6 ± 0.64	5.0 ± 3.84	0.0 ± 0.00	3.2 ± 2.07	1.7 ± 0.98	0.2	1.1
Agoseris heterophylla	0.3 ± 0.18	0.1 ± 0.05	0.5 ± 0.23	0.2 ± 0.11	0.5 ± 0.17	0.1 ± 0.05	0.5	0.0
Eschaltzia californica	0.1 ± 0.08	0.2 ± 0.11	0.1 ± 0.05	0.2 ± 0.11	0.0 ± 0.00	0.0 ± 0.00	0.9	0.4
Gilia tricolor	0.1 ± 0.08	0.2 ± 0.16	0.6 ± 0.30	1.2 ± 0.44	0.2 ± 0.12	0.2 ± 0.09	1.7	1.4
Epilobium sp.	0.2 ± 0.17	0.1 ± 0.07	0.0 ± 0.00	0.3 ± 0.25	0.1 ± 0.05	0.0 ± 0.00	2.3	0.0
Trifolium sp.	0.0 ± 0.00	0.0 ± 0.00	0.1 ± 0.07	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	1.8	1.6
Alchemilla occidentalis	1.6 ± 0.72	1.8 ± 1.31	0.5 ± 0.29	1.4 ± 1.33	0.5 ± 0.2	0.6 ± 0.35	0.5	0.7
Calandrinia ciliata	0.0 ± 0.00	0.2 ± 0.08	0.2 ± 0.10	0.0 ± 0.00	0.1 ± 0.05	0.0 ± 0.00	1.1	5.0
Plagiobothrys nothofulvus	0.1 ± 0.08	0.1 ± 0.07	0.1 ± 0.07	0.0 ± 0.00	0.2 ± 0.08	0.0 ± 0.00	0.8	0.9

b	1996			F
Plant species	Ant exclosure	Pseudo-exclosure	Open	
Bromus mollis	1.3 ± 0.94	6.2 ± 3.34	3.3 ± 1.33	0.9
Gastridium ventricosum	2.1 ± 1.59	1.6 ± 0.61	10.8 ± 3.98	4.0
Lolium perenne	0.4 ± 0.34	1.2 ± 1.01	0.0 ± 0.00	0.9
Vulpia microstachys	0.0 ± 0.00	1.2 ± 0.56	1.0 ± 0.32	1.6
Nassella pulchra	0.0 ± 0.00	0.0 ± 0.00	0.1 ± 0.05	0.8
Elymus elymoides	0.0 ± 0.00	0.0 ± 0.00	0.1 ± 0.05	0.8

measures ANOVA, interaction effects, all $F_{2,15} < 4.7$, all P values non-significant after step-up sequential Bonferroni correction).

Exclosure cylinders affected soil temperatures at the edges, but not the centers, of experimental exclosures. There was a significant effect of location (one-way ANOVA, $df = 2$, $F = 3.8$, $P < 0.05$), but temperatures in the center of exclosures, where plant communities were sampled, did not differ from temperatures outside exclosures ($df = 1$, $F = 0.9$, $P = 0.35$). Shaded edges were significantly cooler than areas outside the exclosures ($df = 1$, $F = 7.3$, $P = 0.01$).

Mound-building effects on the plant community, seed production and soil temperature

Plant communities on and off mounds were significantly different from each other (Fig. 1). Overall, there were fewer forbs on ant mounds; the density of forbs on undisturbed grassland was 5.6 times their density on ant mounds. The forbs *Brodiaea* sp., *Hemizonia congesta*, *Castilleja densiflora* (a hemi-parasite), and *Plantago erecta* (the most abundant species in the serpentine community) all had significantly lower percent cover on ant mounds than in open grassland plots (Mann-Whitney U-test with step-up Bonferroni correction for multiple tests; all $P < 0.005$). In contrast, the exotic grass *Bromus mollis* had significantly higher percent cover on ant mounds ($P < 0.002$). Results from density data mirrored those from percent cover measurements. Again, *Brodiaea* sp., *H. congesta*, *C. densiflora*, and *P. erecta* were all significantly less dense on mounds (all $P < 0.001$), and exotic grasses *Bromus mollis* and *Lolium perenne*, were significantly denser on mounds ($P = 0.0001$ for both species).

L. nitidum plants growing on ant mounds produced almost twice as many seeds as those growing off mounds. On ant mounds, *L. nitidum* produced an average of 10.2 seeds (±0.68), while off mounds they produced 5.4 (±0.32) ($t = 5.9, df = 235, P < 0.001$, 2-tailed test).

Soil temperatures in mounds were higher than those in nearby open, undisturbed grassland (two-way ANOVA, $F = 26.1$, $P < 0.0001$). Temperatures did not differ between the two sites on the mounds ($F = 0.5$, $P = 0.47$) but did differ between the mound and the open sites

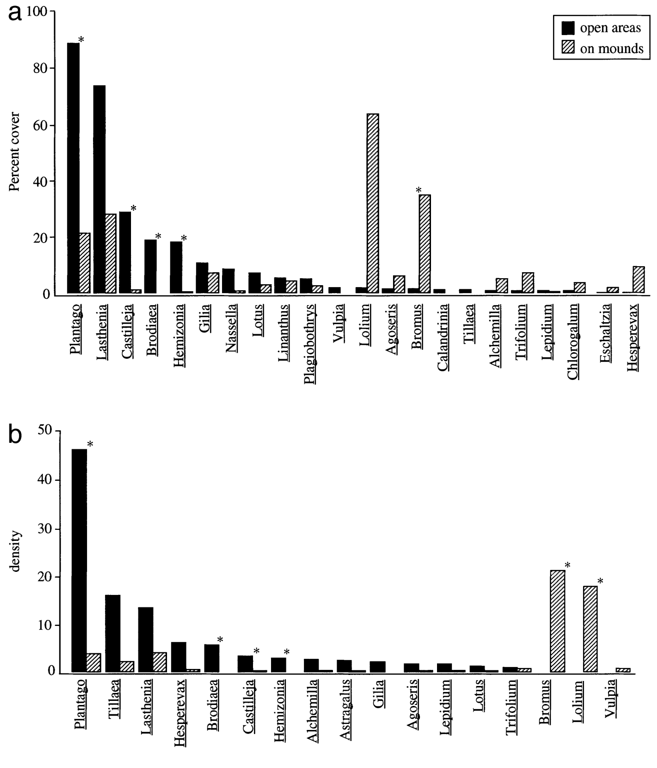

Fig. 1 Differences in **a** the percent cover and **b** the density of plants found on and off ant mounds. *Asterisks* mark significant differences after the step-up sequential Bonferroni correction technique. Plants are ordered by decreasing abundance off mounds. For full species names, see Table 1

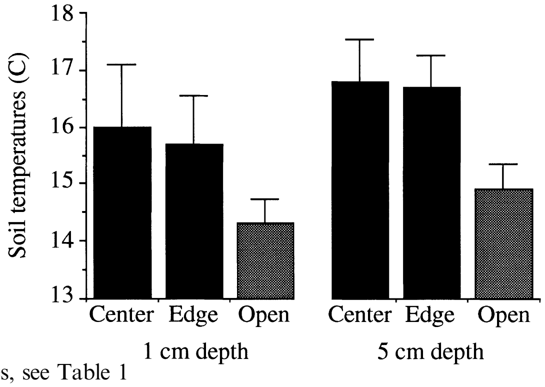

Fig. 2 Soil temperatures measured at two depths in the center and edge of ant mounds and in open grassland sites. *Bars* show mean values with standard deviations. *Black bars* show data for mound sites. *Grey bars* show data for open grassland sites. Soil temperatures were significantly higher at 5 cm depth, and in ant mounds at both depths (for statistical details, see text)

($F = 12.1$, $P < 0.002$) (Fig. 2). Soil temperatures were significantly higher at 5 cm depth than 1 cm depth (two-way ANOVA, $F = 12.1$, $P < 0.002$) (Fig. 2). There was no statistically significant interaction between site and depth ($F = 0.3$, $P > 0.05$); soil temperatures increased similarly with depth in all sites.

Discussion

Excluding *M. andrei* foragers from plots of serpentine grassland did not result in changes to the plant community within these plots over a 2-year period. However, *M. andrei* does affect serpentine grassland dynamics through its mounds, which support an assemblage of plants that is quite different from the surrounding grassland. Results from density measurements mirrored those of percent cover, suggesting that percent cover measured changes in abundance, and not simply changes in spatial distributions.

M. andrei ants forage more intensely on the seeds of particular, preferred species, and they appear to harvest these preferred species until seeds are very rare (Hobbs 1985; M.J.F. Brown unpublished work). We observed that ants foraged within both open and pseudo-exclosure plots. Why were preferred forage species not more abundant in ant-exclosed plots? There are at least three plausible explanations for this unexpected result. First, and most parsimoniously, ants do not harvest enough seeds to change plant abundance from one year to the next. Second, the effects of granivory might be discernible only across many years, with the accumulation of small, statistically insignificant annual effects. Third, variation in other factors that affect plant community dynamics, e.g., soil disturbance by gophers, temperature and rainfall, may have overwhelmed the effects of ant-harvesting in the years of our study.

In a previous study at Jasper Ridge, Hobbs (1985) showed that the annual forbs *Agoseris heterophylla* and *Microseris douglasii* were present at higher densities in small plots adjacent to nests when ants were excluded from foraging and suggested that these results were representative of the whole grassland. Our results suggest that such an extrapolation cannot be made; ant harvesting may have a local effect that does not extend across the whole serpentine grassland. Alternatively, exclosure effects on soil temperature may have caused Hobbs' results (Hobbs 1985); our finding that exclosures alter soil temperatures near the exclosure wall supports this idea.

M. andrei mounds do affect plant communities. Measurements of soil temperatures suggest that the entire mound presents a significantly different microhabitat to the plant community. Abrupt changes in soil temperature at the edges of mounds may help to explain similarly abrupt changes in the plant community. We found that there are more exotic annual grasses on ant mounds than in surrounding areas, and fewer native forbs. Our results are quite similar to those found by Hobbs more than a decade ago, despite significant differences in plant abundances in the surrounding grassland community between the two study periods (Hobbs and Mooney 1995). In both studies, *Bromus mollis*, an exotic annual grass, was one of the most abundant plants found on ant mounds, and most native forbs were less abundant on mounds. Annual grasses appear to colonize both ant and gopher mounds more easily than undisturbed serpentine soils (Hobbs 1985; Hobbs and Mooney 1985, 1995) and thus these mounds are important in maintaining the spatial and temporal patchiness that characterizes the serpentine grassland (Hobbs and Mooney 1995).

One forb that grows both on and off ant mounds, *Lepidium nitidum*, produced almost twice as many seeds when growing on ant mounds than when growing on undisturbed serpentine soil. Other studies have shown similar effects of ant nests on seed set (Rissing 1986; Dean and Yeaton 1993; Wagner 1997). This may result from nutrient-enrichment, soil structural changes, and enhanced microbial activity, indicated by higher temperatures in the soil of ant mounds.

At Jasper Ridge Biological Preserve, *M. andrei* is one of the many native ant species threatened with displacement by the invasive Argentine ant, *Linepithema humile* (Human and Gordon 1996; Human 1996). *L. humile* does not build mounds, although the effect of its nests on the edaphic environment remains unknown. Ironically, the displacement of *M. andrei* from the serpentine grassland by the invasive Argentine ant could inhibit the invasion of the grassland by exotic plant species that utilize *M. andrei* mounds. This possibility deserves further investigation.

In this study, we found that seed-harvesting by ants did not affect overall plant community dynamics in a grassland system. This contrasts with results from desert studies (Brown et al. 1979; Davidson et al. 1985; Samson et al. 1992), and suggests that effects of seed-harvesting ants on plant communities cannot be assumed to be significant simply because the ants selectively harvest large numbers of seeds (Andersen 1991). Increased soil temperatures in ant mounds may affect plant growth and development; the cause and effects of these increased temperatures deserve further investigation.

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