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Harvester ant nests, soil biota and soil chemistry

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Abstract Many ant species accumulate organic debris in the vicinity of their nests. These organic materials should provide a rich resource base for the soil biota. We examined the effect of harvester ant nests (*Pogonomyrmex barbatus*) on the soil community and soil chemistry. Ant nest soils supported 30-fold higher densities of microarthropods and 5-fold higher densities of protozoa than surrounding, control soils. The relative abundances of the major groups of protozoa differed as well: amoebae and ciliates were relatively overrepresented, and flagellates underrepresented, in ant nest versus control soils. Densities of bacteria and fungi were similar in the two soil types. Concentrations of nitrate, ammonium, phosphorus, and potassium were significantly higher in ant nest soils, while concentrations of magnesium, calcium, and water were similar in nest and control soils. Ant nest soils were marginally more acidic than controls. The results demonstrate that *P. barbatus* nests constitute a significant source of spatial heterogeneity in soil biota and soil chemistry in arid grasslands.

Key words Formicidae · *Pogonomyrmex* · Soil · Community · Spatial heterogeneity

Introduction

Ants that form large, stable nests can concentrate the organic materials they collect as forage in the vicinity of the nest, in the form of inedible debris, stored food, and waste products. Consequently, ant nest soils are often rich in both organic matter and the mineral products of organic decomposition, such as ammonium, nitrate, and phosphorus (reviewed by Petal 1978; Beattie 1985, 1989). Nutrient cycling rates may also be higher in ant nests than in surrounding soils; for example, nitrogen mineralization rates are significantly higher in nest soils of the ant species *Formica perpilosa* than in nearby, control soils (Wagner 1997).

The soil biota is primarily responsible for chemical transformations in the soil. High mineralization rates and concentrations of mineral nutrients in ant nests suggest that ants alter the abundance, and perhaps the taxonomic identity, of the biotic agents of nutrient cycling. Bacteria and fungi typically occur at high densities in ant nest soils (Czerwinski et al. 1969, 1971; Petal 1980; Friese and Allen 1993). To our knowledge no previous study has addressed the effects of ant nests on other components of the soil community, such as protozoa and microarthropods, although these taxa are also important to decomposition and nutrient cycling (Santos and Whitford 1981; Parker et al. 1984; Beare et al. 1995). Both protozoa and microarthropods can enhance the mineralization of nutrients by feeding on bacteria and fungi (Seastedt 1984; Kuikman and van Veen 1989). Microarthropods can also contribute to decomposition by increasing litter surface area and dispersing fungal spores (Moore et al. 1988; Seastedt 1984).

The nesting activities of seed harvesting ants in the genus *Pogonomyrmex* alter the physical and chemical characteristics of soil. *Pogonomyrmex* nests have been associated with altered soil particle size and high soil moisture (Rogers and Lavigne 1974; Whitford 1988; Laundré 1990), as well as high concentrations of organic matter (Whitford 1988; McGinley et al. 1994). All of these factors – pore size, moisture, and organic matter – help to maintain an active and diverse soil microflora and fauna in arid environments (reviewed by Whitford 1996). The purpose of this study was to characterize the effects of nests of the harvester ant *P. barbatus* on the soil community and soil chemistry.

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Methods

Study site and natural history

The study area was located in arid grassland near Rodeo, New Mexico (elevation *c*. 1200 m), at the intersection of the Chihuahuan and Sonoran deserts. This area receives most of its annual precipitation from summer rains. Vegetation at the site was described in Gordon (1993). The site was grazed by cattle, and vegetation was sparse over most of the area. The density of *P. barbatus* was approximately 30 nests per ha^{-1} (Gordon and Kulig 1996).

P. barbatus colonies live 15–20 years (Gordon 1991) and rarely move from their natal nests (Gordon 1992). The entrances to mature (more than 5 years old) *P. barbatus* nests are surrounded by large, gravel-covered discs 1–1.5 m in diameter. Workers mill seeds within the nest, and deposit considerable amounts of chaff on the surface in midden piles located within about 1 m of the nest entrance. A related species with similar dietary habits, *P. rugosus*, discards over 60% of the total energy collected by foragers onto the midden (MacKay 1985). Clipped vegetation and dead ants are sometimes also deposited on the midden, but ant carcasses are usually removed by other arthropod scavengers. The location of the midden pile shifts from week to week. Workers collect small pebbles and place them onto the nest disc (Gordon 1984a,b), covering and eventually burying the piles of chaff and debris. Ant feces, deposited both inside and outside the nest, probably also contribute organic matter to nest soils.

We studied the contents of soil from six *P. barbatus* nests located within an area of approximately 1.5 ha. The nests were at least 20 m apart. All nest mounds were at least 1 m in width and the colonies were estimated to be at least 5 years old.

Soil biota

Populations of soil microarthropods, protozoa, bacteria, and fungi were measured in July 1996. The 1996 rains began in late June, so at the time of soil collection the site had received intermittent rain for 3–4 weeks. Four soil samples (7 cm diameter by 10 cm depth) were removed from each ant nest, and from control sites located 3 m east of each nest. Replicate samples at each site were taken from an area approximately 0.5 m diameter. The four replicate samples from each site were mixed together and a subsample was removed, weighed, and dried to constant mass to determine water content. Microarthropods were extracted from 500 ml (500–600 g fresh mass) subsamples of soil using Tullgren funnels suspended over water (Santos et al. 1978). Numbers of extracted Acari and Collembola were counted daily for 14 days, after which no more microarthropods emerged.

Protozoan, bacterial, and fungal densities were measured by Soil Foodweb, Inc. (Corvallis, Or., USA). Soil subsamples of approximately 150 g were sealed in zip-lock bags and shipped immediately by overnight mail to the laboratory. Samples were refrigerated upon receipt and processed within 24 h of arrival. Numbers of protozoa were estimated by the most probable number method (Darbyshire et al. 1974). Protozoan biomass was calculated assuming dry masses of 1.0, 1.4, and 0.26 ng for amoebae, ciliates, and flagellates, respectively (Beare et al. 1992). Total bacterial numbers, including dormant, senescent, and active bacteria, were determined using the fluorescein isothiocyanate method of Babiuk and Paul (1970). Numbers of active bacteria were assessed by observation after staining with fluorescein diacetate, using epifluorescent microscopy. Diameters of bacteria were measured and biomass calculated following estimates by van Veen and Paul (1979). Lengths and widths of fungal hyphae were used to determine total fungal biomass; lengths and widths of hyphae stained with fluorescein diacetate were used to determine active fungal biomass (Ingham and Klein 1984). Abundance and biomass data for all taxa were normalized per kilogram (microarthropods) or gram (all other taxa) of dry soil.

Soil chemistry

The pH and concentrations of nitrate, ammonium, phosphorus, potassium, calcium, and magnesium were determined for samples collected in May 1996. At the time of collection the weather was hot and the soil appeared very dry. Three soil samples (5 cm diameter by 10 cm depth) were taken from each ant nest and control site. The three replicate samples were well mixed, sieved through a 2-mm mesh, and dried. Available mineral nitrogen and phosphorus were extracted in Morgan's solution (Morgan 1941) and concentrations measured colorimetrically: ammonium concentration was determined using the Nessler method (American Public Health Association 1980), nitrate concentration using the brucine method (Baker 1969), and phosphorus concentration using an ammonium molybdate method (Bray and Kurtz 1945). Potassium, calcium, and magnesium concentrations were measured using atomic absorption spectrophotometry (Baker and Suhr 1982). Soil moisture was not measured in this May sampling period. The concentrations of all soil nutrients were calculated as micrograms per gram of dry soil.

Data analysis

Data were tested for normality and equality of variances, and log-transformed when necessary to meet parametric assumptions. Ant nest and control soils were compared with paired *t*-tests, or with Wilcoxon signed-rank tests where data violated parametric assumptions (Sokal and Rohlf 1981). The proportion of flagellates, ciliates and amoebae in the protozoan communities of ant nest and control soils were compared with a *G*-test (Sokal and Rohlf 1981).

Results

Soil biota

Ant nest soils contained much higher abundances of microarthropods and protozoa than control soils. The density of microarthropods (Acari and Collembola) was 30–40 times higher in ant nest soils than in control soils (Table 1). Total microarthropod abundances per 500 ml of soil averaged 337 ± 111 (mean ± SE) in ant nest soils and only 11 ± 3 in control soils. Other arthropods were rare in both soil types (beetle larvae, 1.0 ± 0.8 in ant nest soil, 0.5 ± 0.5 in control soil; diplopods, 0.2 ± 0.2 in both ant nest and control soil; no termites in either soil type).

Protozoan abundance and biomass were significantly (5–6 fold) greater in ant nest soils than in control soils (Table 2). Ciliates, amoebae and flagellates made up different proportions of the total protozoan population in the two soil types ($G = 125$, $df = 2$, $P < 0.001$). Ant

Table 1 Microarthropod abundance (per kg dry soil) in paired *Pogonomyrmex barbatus* nest and control soils. Values presented are means ± SE; $n = 6$ pairs. Total microarthropod densities were compared with a Wilcoxon signed-rank test

Microarthropod	Ant nest	Control	T_s
Acari	583 ± 199	18 ± 5	
Collembola	44 ± 23	1 ± 1	
Total	626 ± 214	19 ± 6	10.5 *

* $P < 0.05$

Table 2 Protozoan abundance and estimated dry biomass in soil from *P. barbatus* nest and control soils ($n = 6$ pairs). Values are means ± SE

	Protozoan abundance (n/g)			
	Ant Nest	Control	Paired difference	Paired t
Amoebae	5094 ± 875	817 ± 443		
Ciliates	261 ± 94	8 ± 5		
Flagellates	1074 ± 312	337 ± 150		
Total	6429 ± 835	1162 ± 585	5268 ± 1050	5.0 **
	Protozoan biomass (µg/g)			
	Ant nest	Control	Paired difference	Paired t
Amoebae	5.09 ± 0.88	0.82 ± 0.44		
Ciliates	0.36 ± 0.13	0.01 ± 0.01		
Flagellates	0.28 ± 0.08	0.09 ± 0.04		
Total	5.74 ± 0.93	0.92 ± 0.48	4.82 ± 1.08	4.8 **

** $P < 0.01$

Table 3 Microbial biomass (µg/g dry soil) in soil from *Pogonomyrmex barbatus* nest and control soils. Values are means ± SE; $n = 6$ pairs

Organism	Ant nest	Control	Paired difference	Paired t
Bacteria				
Active[a]	2.2 ± 0.8	3.4 ± 0.7	−1.2 ± 1.1	−1.6 n.s
Total[a]	27.4 ± 3.3	51.2 ± 9.7	−23.8 ± 11.5	−1.6 n.s.
Fungi				
Active	6.9 ± 0.8	9.8 ± 1.5	−2.9 ± 1.6	−1.9 n.s.
Total	45.7 ± 12.2	68.5 ± 9.4	−22.8 ± 19.6	−1.2 n.s.

n.s. $P > 0.1$

[a] Data were log-transformed prior to analysis

nest soils contained a greater proportion of amoebae and ciliates, and a smaller proportion of flagellates, than surrounding soils (ant nests: amoebae 79%, ciliates 4%, and flagellates 17%, $n = 38{,}575$; controls: amoebae 70%, ciliates 1%, and flagellates 29%, $n = 6969$).

The biomass of bacteria and fungi in ant nest and control soils did not differ (Table 3). The two soil types also contained similar ratios of active to total microbial biomass (bacteria: paired $t = 1.0$, $df = 5$, $P = 0.4$, overall mean ± SE = 0.17 ± 0.02; fungi: paired $t = 0.2$, $df = 5$, $P = 0.8$, overall mean ± SE = 0.08 ± 0.02).

Soil chemistry

P. barbatus nest soils contained significantly higher concentrations of nitrate, ammonium, phosphorus, and potassium than control soils (Table 4). Magnesium concentrations were slightly, but not significantly, higher in ant nest soils; calcium concentrations did not differ (Table 4). Ant nest soils were marginally more acidic than control soils (Table 4). Nest and control soils contained similar amounts of water (Table 4).

Table 4 Chemical characteristics of soil from *Pogonomyrmex* mounds and control sites. Soil samples were collected in May 1996 except were noted. Values are means ± SE; $n = 6$ pairs

Component	Ant nest	Control	Paired difference	Paired t
NO_3 (µg/g)[a]	68 ± 14	7 ± 2	50 ± 6	24.8 ***
NH_4 (µg/g)[a]	98 ± 27	6 ± 1	93 ± 26	10.8 ***
P (µg/g)[a]	64 ± 6	14 ± 3	50 ± 6	8.8 ***
K (µg/g)	434 ± 25	337 ± 16	98 ± 17	6.6 ***
Mg (µg/g)	322 ± 10	308 ± 12	13 ± 6	2.3 *
Ca (µg/g)	2917 ± 158	2717 ± 247	200 ± 155	1.5 n.s.
pH	6.1 ± 0.1	6.4 ± 0.1	−0.3 ± 0.1	−2.3 *
Water (%)[b]	4.7 ± 0.5	4.7 ± 0.3	−0.0 ± 0.5	1.0 n.s.

[a] Data were log-transformed prior to analysis

[b] Soil collected in July 1996

*** $P \leq 0.001$; * $P = 0.07$, n.s. $P > 0.1$

Discussion

P. barbatus nests in this study were associated with high densities of some soil taxa. Ant nest soils contained significantly greater numbers of Protozoa, Acari, and Collembola than control soils. Ant nests also contained significantly different relative abundances of ciliates, amoebae, and flagellates, suggesting that the composition of the soil communities might differ in the two soil types as well. High densities of microarthropods and protozoa were probably due at least in part to greater resource availability in ant nest soils relative to control soils, itself a result of the deposition of organic debris near the nest by ants.

We expected that, like the larger soil fauna, microbial decomposers would be more abundant in ant nest soils relative to surrounding soils. However, in contrast to previous studies (reviewed by Petal 1980), we did not find higher bacterial and fungal biomass or activity in ant nest soils than in control soils. Large populations of protozoans and microarthropods may have depressed microbial populations in ant nest soils. In addition, microbial populations may have been generally depressed at the time of sampling due to dry soil conditions. Although it had rained intermittently for several weeks before we sampled the soil biota, soil moisture at the time of sampling was low (Table 4). More information about microbial population dynamics at this site is needed in order to understand the effect of ant nests on microbial populations.

Abiotic factors can play an important role in the abundance and diversity of the soil fauna (Whitford 1996), and may have contributed to differences in ant nest and control soils detected in this study. In contrast to McGinley et al. (1994), we did not find higher water content in *P. barbatus* nest soils than in surrounding soils; however, the effect of ants on soil moisture could vary with rainfall and temperature, and should be evaluated over time. Soil excavation by ants may have increased average soil pore size, improving soil texture

for some components of the soil fauna (Hassink et al. 1993).

Our soil chemistry results are typical of the nest soils of many ant species. Concentrations of phosphorus, potassium, and magnesium are often elevated in ant nest soils relative to surrounding soils (reviewed by Petal 1978; Beattie 1989). Studies comparing mineral nitrogen have yielded more variable results, but mineral nitrogen is often higher in ant nests than in surrounding soils (Czerwinski et al. 1971; Rogers and Lavigne 1974; Davidson and Morton 1981; Ofer et al. 1982; Carlson and Whitford 1991; McGinley et al. 1994; Wagner 1997; but see Whitford 1988; Culver and Beattie 1983). Predation by microarthropods and protozoans can mobilize nutrients held in biomass (Seastedt 1984; Ingham et al. 1986; Kuikman and van Veen 1989; Griffiths 1994). Nutrient mobilization by predacious soil fauna may have contributed to the high concentrations of mineral nutrients found in *P. barbatus* nest soils. Once mobilized, soil nutrients are generally not subject to intense leaching in desert soils of the southwestern United States, although they may be lost to volatilization or to runoff after heavy rains (West and Skujins 1978 and references therein).

Do ant colonies track areas with high concentrations of soil nutrients and soil organisms, rather than cause them? Three lines of evidence suggest that ants are responsible for changes in soil composition. First, concentration of organic materials onto the nest surface is apparent in many ant species, including *P. barbatus*. Second, soil nutrient enrichment has been detected more frequently in ant populations that form large, long-lived, stable nests than in populations that relocate their nests frequently (Hughes 1990), suggesting that ants actively accumulate organic debris over time. Third, the reverse is also true: when ant nests are abandoned, previously high concentrations of soil nutrients dwindle, eventually reaching background levels (Czerwinski et al. 1971). At a larger spatial scale, there is little evidence that *P. barbatus* colonies recruit to particular locations within a 10-ha area adjacent to the plot we sampled, hence there is no indication that ants prefer particular soil types at this site (Gordon and Kulig 1996).

The role of shrubs in creating "islands of fertility" in deserts has been widely recognized (e.g., Garcia-Moya and McKell 1970; Romney et al. 1980). Soil organisms tend to occur at high density in the rhizosphere and in the litter that accumulates under shrubs (Santos et al. 1978; Franco et al. 1979), whereas intershrub spaces are characterized by lower biological activity (Charley and West 1977). Decomposition of accumulated litter leads to high concentrations of mineral nutrients and nitrogen mineralization rates at shrub bases (Garcia-Moya and McKell 1970; Charley and West 1977). The results of this study suggest that *P. barbatus* nests are an additional source of spatial heterogeneity in both community composition and chemistry of arid soils. When ant colonies die, these nutrient-rich microsites can be colonized by plants. Heterogeneity in the soil biota and soil nutrient content caused by ant activities could contribute to the maintenance of plant species diversity (Grubb 1977; McGinley et al. 1994).

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