

Effects of three species of Chihuahuan Desert ants on annual plants and soil properties

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Abstract

We tested the hypothesis that ant species, which occupy the same nest for a decade or longer, would modify nest soils by increasing soil nutrients and microorganisms resulting in increased biomass, density, cover and species richness of annual plants. We measured soil properties and annual plants on nest soils of three species of Chihuahuan Desert ants (*Pogonomyrmex rugosus*—seed harvester, *Aphaenogaster cockerelli*—generalist forager, and *Myrmecocystus depilis*—liquid collector-insect scavenger) in comparison to paired reference soils at several locations. There were no differences in nest and reference total soil nitrogen of *M. depilis* and of *P. rugosus* on three catena soils. Total soil nitrogen of nest-modified soils was higher than of reference soils of *A. cockerelli* and *P. rugosus* in a desert grassland site. Soil microbial biomass and respiration were not significantly different among ant species at most locations with the exception of *P. rugosus* at the base of the catena. Annual plant biomass was higher on *M. depilis* and *A. cockerelli* nest soils than on the reference soils. Annual plant biomass was higher on *P. rugosus* nest soils than on reference soils at the base of the catena and in the grassland but not at the mid-slope and top of the catena. The effects of long-lived ant colony nests on soil properties and vegetation vary in time and space but are independent of the feeding behavior of the ant species.

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1. Introduction

Animals are important in ecosystems primarily as agents that affect the processes and properties of ecosystems (Whitford, 2002a). In desert ecosystems, invertebrates affect ecosystem processes primarily by their effects on soil properties (Whitford, 2000, 2001, 2002b). Ants are abundant and conspicuous components of arid ecosystems and are known to contribute to heterogeneity or patchiness of landscapes and to pedogenesis (Whitford, 2002a). In order to generalize about the role of ants in arid ecosystems, it is necessary to understand the spatial and temporal variability of the processes or properties affected by ants and to understand differences related to the trophic behaviors and life history characteristics of the individual species.

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A number of studies have documented the effects of seed harvesting ants on the soils associated with the nests and on the corona of vegetation around the margins of the nests (Boulton et al., 2003; Carlson and Whitford, 1991; Coffin and Lauenroth, 1990; Hobbs, 1985; MacMahon et al., 2000; Rissing, 1986; Wagner and Jones, 2004; Wagner et al., 1997; Whitford, 1988). Most of these published studies have focused on one species of seed-harvesting ant at a single location. Higher density and biomass of plants associated with harvester ant nests have been attributed to organic matter enrichment of soils as a result of accumulation of chaff around the nests of seed harvesters. Several recent studies reported increased diversity and abundance of soil biota (bacteria, fungi, nematodes, protozoans and microarthropods) in soils associated with harvester ant nests (Boulton et al., 2003; Wagner and Jones, 2004; Wagner et al., 1997). These studies have focused on large body-size seed-harvesting ants because they produce large nests (> 1 m in diameter), are central place foragers, and accumulate organic matter in the vicinity of the nests (Wagner and Jones, 2004). One exception to the generalization that nests of large seed-harvesting ants represent nutrient rich, soil biota rich patches was reported in a study of the effects of harvester ant (*Pogonomyrmex rugosus*) nests on corona vegetation and soil properties on a Chihuahuan Desert watershed (Whitford and DiMarco, 1995). They documented that the soil and vegetation patterns were significantly different between nests and reference areas only in some locations on the watershed.

Wagner (1997) reported that the nests of *Formica perpilosa*, a honey-dew feeder—predator/scavenger (Schumacher and Whitford, 1974) increased the concentration of soil nitrogen and phosphorous. The study of *F. perpilosa* suggests that central place forager ant species that build and occupy large subterranean nests for several decades may affect soil properties in ways similar to seed-harvesting ants. In order to test this hypothesis, we designed a study to compare the effects of nests of a seed-harvesting ant (*P. rugosus*) known to affect soil properties with the effects on soils of the nests of two species of ants that are not seed harvesters (*Aphaenogaster (Novomessor) cockerelli*), a collector of detritus, seeds, and insects (Whitford et al., 1980) and a honey-pot ant, *Myrmecocystus depilis*, a species that collects plant exudates, honey dew, and small insects. Chew (1995) documented that *A. cockerelli* and *M. depilis* produce subterranean nests that persist for a decade or more.

Desert annual plants make up an important but variable component of the vegetation. In the Chihuahuan Desert, there are two distinct annual plant communities: winter-spring annuals and summer annuals. Winter-spring annuals are present infrequently and occur only when there is sufficient rainfall from mid-November through February for the germinants to survive (Kemp, 1983). Nests of the seed harvester, *P. rugosus* were reported to support higher biomass of a spring annual than soils several meters from the nest (Whitford, 1988). In order to test the hypothesis that temporally persistent ant nests would support larger populations and/or biomass of annuals, we measured biomass production, density, cover and species richness of winter annuals associated with the nests of three species of ants in addition to the measurements of selected soil properties.

2. Methods

Three species of ants that build nests that persist for decades (Chew, 1995; MacMahon et al., 2000) (*P. rugosus*, *A. cockerelli*, and *M. depilis*) were selected for study on a watershed of the Dona Ana Mountains that terminates on the Jornada Basin and one watershed on the east slopes of the Black Range Mountains in Luna County, NM. We selected sites on three geomorphic surfaces of a catena on the Jornada Basin to evaluate spatial variability in soils and vegetation associated with *P. rugosus* nests. A soil/geomorphic catena is the cumulative result of natural downslope interactions between pedogenic and geomorphic processes including drainage conditions, differential transport of eroded materials, and leaching. The Dona Ana Mountains watersheds are approximately 40 km NNE of Las Cruces, NM, in the Chihuahuan Desert Rangeland Research Center of New Mexico State University (CDRRC) on the Jornada plain. The Black Range watershed site was located in the Nutt grasslands approximately 60 km WNW of Hatch, NM. We selected sampling sites based on the criterion of a minimum density of five colonies of the species of interest per hectare. *P. rugosus* are abundant in the low elevation grasslands on the Jornada plain. *M. depilis* is relatively abundant on creostebush (*Larrea tridentata*) upper piedmonts but sparse in the low elevation grasslands. Because of the low density of *A. cockerelli* colonies on the Jornada plain, we sampled the Nutt

Table 1
Soil, vegetation, and topographic locations of study sites sampled for persistent ant colonies

Ant species	Location/slope	Vegetation	Soil
<i>P. rugosus</i>	Nutt grassland <1% slope	Tabosa grass (<i>Pleuraphis mutica</i>) and Burro grass (<i>Scleropogon brevifolia</i>)	Silty loam
<i>P. rugosus</i>	Jornada plain catena (top) <1% slope	Tabosa grass (<i>Pleuraphis mutica</i>) and three awn (<i>Aristida</i> spp.)	Sandy loam
<i>P. rugosus</i>	Jornada plain catena (mid-slope) <2%	Burro grass (<i>Scleropogon brevifolia</i>) and Tabosa grass (<i>Pleuraphis mutica</i>)	Silty loam
<i>P. rugosus</i>	Jornada plain catena (basin) <0.5% slope	Burro grass (<i>Scleropogon brevifolia</i>) and Tabosa grass (<i>Pleuraphis mutica</i>)	Clay loam
<i>A. cockerelli</i>	Nutt grassland <1% slope	Tabosa grass (<i>Pleuraphis mutica</i>) and Burro grass (<i>Scleropogon brevifolia</i>)	Silty loam
<i>M. depilis</i>	Montane piedmont	Creosotebush (<i>Larrea tridentata</i>)	Sand

grasslands in order to find relatively dense colonies of *A. cockerelli*. *A. cockerelli* and *P. rugosus* were equally abundant in the Nutt grasslands. Because the study sites were located in different topographic positions and geomorphic surfaces on the landscape, the soils and dominant vegetation were different among sites (Table 1).

Soils and annual plants were sampled in early May. At each site, annual plants were sampled at the edges of five ant nests (discs or craters) and at five reference points, 5 m from the edge of the nest disc or crater, using a 0.5 m² frame (divided into 10 cm square grids) designed to estimate density and cover (Whitford, 1988). Soil cores (10 cm diameter by 20 cm deep) were collected from the edge of five ant nest mounds or discs and five reference points located in a random direction, 5 m from the ant nest. Soil cores were thoroughly mixed and passed through a 2.0 mm sieve prior to sub-sampling.

Five-gram subsamples were weighed, dried at 105 °C and re-weighed to obtain gravimetric soil moisture. Soil organic matter was obtained by placing samples of known mass in a muffle furnace at 490 °C for 8 h and the ash content measured (Parker et al., 1984; Whitford et al., 1986).

Total soluble nitrogen (TSN) was measured in a subsample of 10.0 g from each sample. TSN was extracted with 25 mL of 0.01 N CaCl₂ solution by shaking for 90 min. The amounts of TSN in the soil extract were measured with a Skalar Autoanalyzer System.

Soil microbial biomass (C_{mic}) and CO₂ evolution was measured by a chloroform-fumigation incubation assay described by Jenkinson and Powelson (1976) and Sparling and West (1990). Five-gram soil samples were adjusted to 40% water-holding capacity and fumigated in a CHCl₃-saturated atmosphere in a desiccator for 24 h. Then the fumigated and corresponding non-fumigated (control) samples were transferred to 0.5-L glass jars and incubated for 10 days at 25 °C in the dark. CO₂ concentrations were measured in the headspace of the glass jars using a gas chromatograph and soil microbial biomass was calculated as

$$C_{mic} = \frac{(\text{CO}_2\text{-C from fumigated soil}) - (\text{CO}_2\text{-C from control sample})}{kc}$$

A kc of 0.41 was used, as proposed by Anderson and Domsch (1990).

Differences in biomass, cover, density, and species richness of annual plants at ant nests and reference sites were assessed by Students “*t*” tests (Sokal and Rohlf, 1981).

The effects of ant nests on soil properties were analyzed by analysis of variance (ANOVA) using a statistical analysis system (SAS). Multiple comparisons made by Duncan’s multiple range tests. Differences at the $p < 0.05$ were considered significant.

3. Results

3.1. Soil properties

Soil moisture was significantly higher in the *P. rugosus* nest disk soil than the reference soils of the mid-elevation site on the Jornada catena ($F_{5,4} = 51.7$, $p < 0.003$) (Fig. 1A). There were no significant differences in

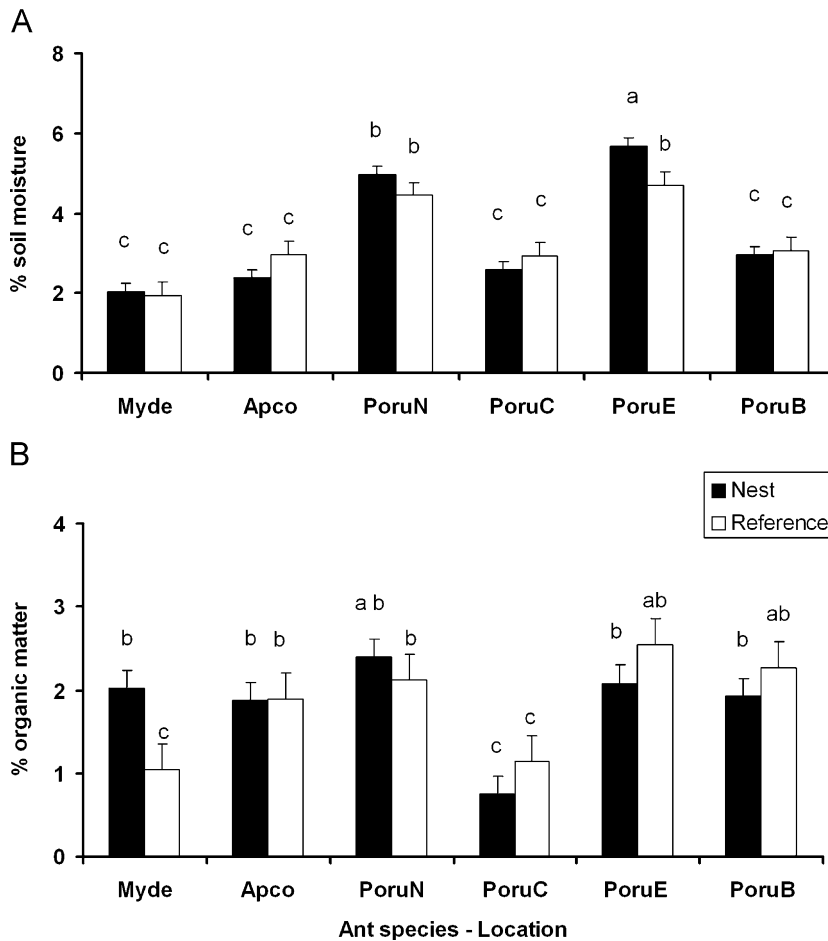


Fig. 1. Percent soil moisture (A) and percent organic matter (B) in ant nest soils and reference soils. Myde, *Myrmecocystus depilis*; Apco, *Aphaenogaster cockerelli*; PoruN, *Pogonomyrmex rugosus* in the Nutt grasslands; PoruC, *P. rugosus* on sandy loam soils at the top of a catena; PoruE, *P. rugosus* on fine loam soils mid-slope of a catena; and PoruB, *P. rugosus* at the bottom of a catena (■: nest; □: control).

soil moisture between nest soils and reference soils in the remaining sites on the catena ($F_{5,4} = 0.1$, $p > 0.05$). Soil organic matter content was significantly higher on the two lowest elevation sites on the basin catena than the higher catena site soil and the piedmont soils (Fig. 1B). Reference soils had significantly higher organic matter content than nest soils of the *P. rugosus* sites on the low elevation catena ($F_{5,4} = 3.7$, $p < 0.002$) (Fig. 1B). Soil organic matter content was significantly higher in soils adjacent to *M. depilis* nests than in the reference soils on the *L. tridentata* piedmont ($F_{5,4} = 51.7$, $p < 0.003$). There were no significant differences in soil moisture or soil organic matter with nests of either species or reference points at the Nutt grasslands sites (Fig. 1A and B).

There were no significant differences ($F_{5,4} = 0.09$, $p > 0.05$) in total soil nitrogen in *P. rugosus* nest soils and reference soils at any of the locations on the catena (TSN ranged from 2.8 to 4.2 ppm). However, TSN was significantly higher in soils from *A. cockerelli* nests (14.8 ppm) and *P. rugosus* nests (9.4 ppm) in the Nutt grassland than in the paired reference soils (Fig. 2). There were no significant differences in TSN in *M. depilis* nest soils and paired reference soils (Fig. 2).

Soil microbial biomass was slightly higher in nest soils than in paired reference soils but was significantly higher only in the *P. rugosus* nest soils at the bottom of the catena ($F_{5,4} = 6.2$, $p < 0.05$) (Fig. 3A). There was no consistent pattern in the soil respiration values and soil respiration was significantly higher in *P. rugosus* nest soils at the base of the catena than in the paired reference soils ($F_{5,4} = 6.3$, $p < 0.05$) (Fig. 3B).

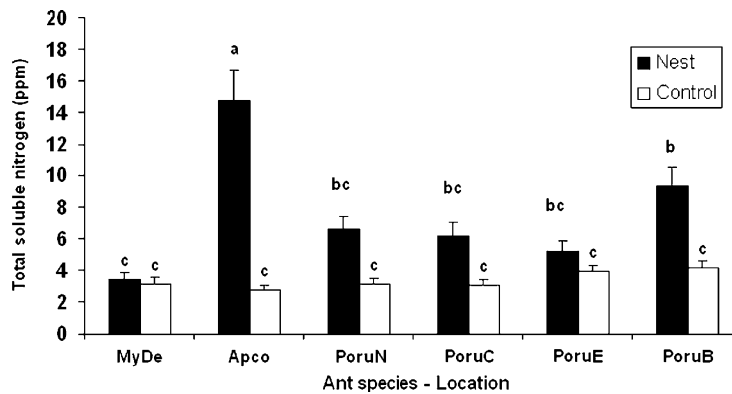


Fig. 2. Comparison of the soluble nitrogen content of soils associated with ant nests and reference soils. Myde, *Myrmecocystus depilis* on sandy piedmont; Apco, *Aphaenogaster cockerelli* in the Nutt grasslands; PoruN, *Pogonomyrmex rugosus* in the Nutt grasslands; PoruC, *P. rugosus* on sandy loam soils at the top of a catena; PoruE, *P. rugosus* on fine loam soils mid-slope of a catena; and PoruB, *P. rugosus* on clay loam soils at the bottom of a catena (■: nest; □: control).

3.2. Annual plants

Annual plant biomass associated with the *P. rugosus* nests was significantly higher than at reference plots at the base of the Jornada catena but not at the higher elevation areas on the catena (Table 2). There were no significant differences in annual plant biomass, cover, density or species richness at *M. depilis* nest mounds and the reference plots. Annual plant biomass at the margins of *P. rugosus* and *A. cockerelli* nests in the Nutt grasslands was significantly higher than biomass at the reference plots. The only significant differences in cover percent were with winter annuals associated with the nests of *P. rugosus* and *A. cockerelli* at the Nutt grassland area. The winter annual plant density and species richness was significantly higher at the margins of *A. cockerelli* nests than at the reference plots in the Nutt grassland (Table 2).

4. Discussion

In contrast to several studies that reported increased soil nutrients and/or diversity and abundance of soil biota (Boulton et al., 2003; Snyder et al., 2002; Wagner, 1997; Wagner and Jones, 2004), our study found that differences among nest soils and paired reference soils were not the same in all locations. In addition, ant nest modified soils were not always higher in soil biota or soil microbial activity than paired reference soils. The importance of topographic position as a factor affecting the variability of the effects of *P. rugosus* nests on soil properties was documented by Whitford and DiMarco (1995).

Position on the landscape with respect to run-off appeared to be the most important factor affecting both microbial biomass and soil respiration. Soil microbes contribute approximately 71% of the CO₂ flux from soils (Edwards and Sollins, 1973; Macfadyen, 1971; Parker et al., 1983). Therefore, the higher soil respiration in *P. rugosus* nest modified soils at the base of the catena in comparison to paired reference soils were the result of the higher microbial biomass at that location. This also suggests that material deposited by overland flow during large rains in the months preceding this study may have increased available substrates for soil microbes. Substrate availability was the most important factor affecting the diversity, abundance and activity of soil microbes in the Chihuahuan Desert (Liu et al., 2000).

Our hypothesis that nests of ant species that persist in the environment for 5–10 years will exhibit enriched nutrients and higher annual plant biomass in the nest modified soils was partially supported by the data. The ant species that did not support this hypothesis was *P. rugosus*, a seed-harvesting species. Seed-harvesting ants have been reported to affect soil properties and vegetation in a number of papers (MacMahon et al., 2000). This effect was recorded in two of four *P. rugosus* locations sampled in this study. Topographic position with respect to run-off appears to be the primary factor affecting the development of annual plant biomass in the nest modified soils. This study presents evidence that conclusions based on data from a single season at one

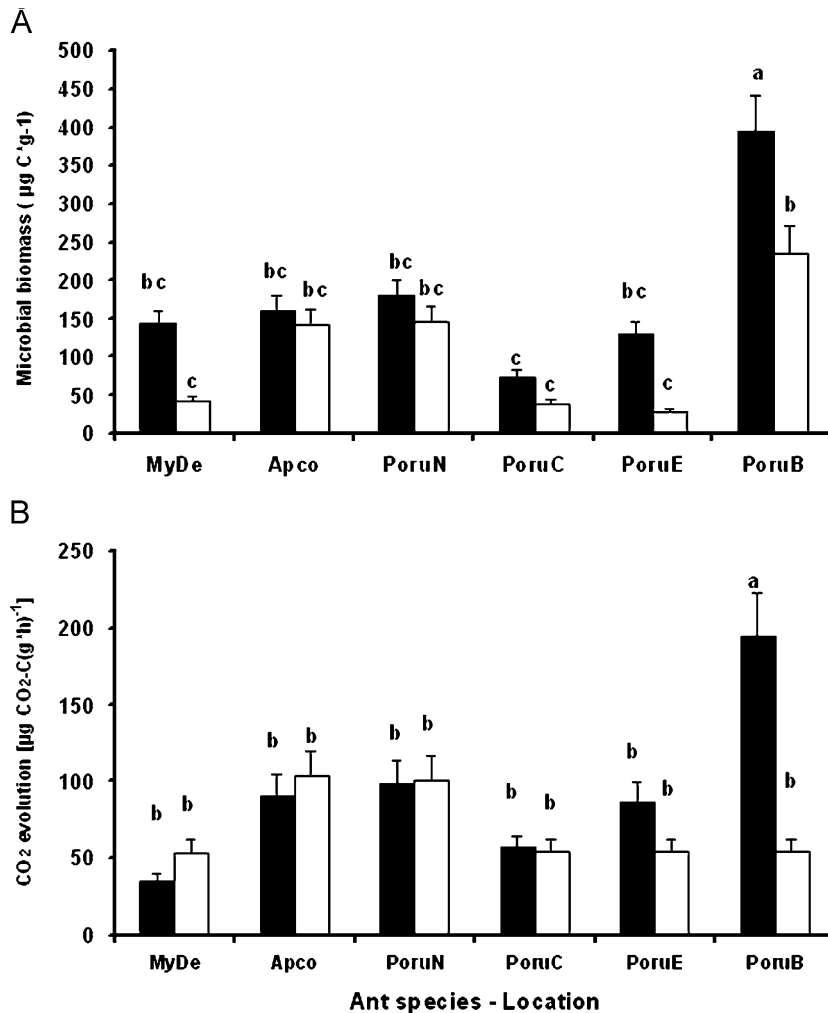


Fig. 3. Comparisons of microbial biomass (A) and CO₂ evolution (B) of ant nests soils and reference soils. Myde, *Myrmecocystus depilis* on sandy piedmont; Apco, *Aphaenogaster cockerelli* on loam soils in the Nutt grasslands; PoruN, *Pogonomyrmex rugosus* on loam soils in the Nutt grasslands; PoruC, *P. rugosus* on sandy loam soils at the top of a catena; PoruE, *P. rugosus* on fine loam soils mid-slope of a catena; and PoruB, *P. rugosus* on clay loam soils at the bottom of a catena (■: nest; □: control).

location must be treated with caution. Whitford (1988) reported higher biomass of the annual, *Erodium texanum*, associated with the nests of *P. rugosus* at the same location as the mid-slope catena in the present study. In the present study, the biomass of annuals on the *P. rugosus* modified soils at the mid-slope catena was not higher than in the reference locations. One similarity was the lack of difference in soluble nitrogen in the nest and reference soils in both studies. The absence of differences in soluble nitrogen suggests differences in rates of nitrogen mineralization may be masked by different rates of nitrogen uptake by the plants. Whitford (1988) reported higher total soil nitrogen in nest soils at this location. He suggested soil nitrogen as the factor producing higher *E. texanum* biomass in the nest soils. The pattern of nitrogen dynamics reported in the current study may be the result of microbial immobilization of nitrogen as a function of the decomposition of perennial grass roots or roots of ephemeral plants (Whitford and Herrick, 1995).

It has been suggested that central place foraging ants like *M. depilis* that scavenge arthropod carrion can be important agents of nutrient redistribution in grasslands (Bestelmeyer and Wiens, 2003). This hypothesis was supported in part by the higher soil organic matter and annual plant biomass on *M. depilis* nest modified soils in comparison to reference soils. A significant percentage of the materials brought to the nest by *A. cockerelli* foragers are insects and most of those insects appear to be carrion (Whitford et al., 1980) which can contribute

Table 2

Comparison of biomass, cover, density, and species richness of winter annual plants associated with the nests of ants and paired reference sites

	Nest	Reference	Significance
<i>Pogonomyrmex rugosus</i> —base of catena			
Biomass (g/0.04 m ⁻²)	52.07 ± 23.34	9.13 ± 10.40	$t = 3.7, p = 0.02$
Cover (%)	33.16 ± 19.65	10.96 ± 9.90	$t = 2.3, p = 0.08$
Density no. (m ⁻²)	23.6 ± 21.8	24.0 ± 8.4	$t = 0.04, p = 0.97$
Species richness	3.0 ± 0.71	3.0 ± 0.89	$t = 0.00, p = 1.0$
<i>Pogonomyrmex rugosus</i> —mid-slope catena			
Biomass g/0.04 m ⁻²	40.55 ± 24.01	35.45 ± 22.18	$t = 0.57, p = 0.59$
Cover (%)	76.0 ± 20.68	34.1 ± 22.53	$t = 2.43, p = 0.07$
Density no. (m ⁻²)	20.0 ± 7.06	28.0 ± 13.34	$t = 0.92, p = 0.40$
Species richness	2.75 ± 1.25	2.5 ± 1.29	$t = 0.20, p = 0.85$
<i>Pogonomyrmex rugosus</i> —top of catena			
Biomass (g/0.04 m ⁻²)	58.07 ± 30.24	28.96 ± 10.85	$t = 1.83, p = 0.14$
Cover (%)	48.34 ± 12.26	23.48 ± 7.60	$t = 2.95, p = 0.04$
Density no. (m ⁻²)	27.2 ± 6.72	35.2 ± 20.90	$t = 0.78, p = 0.47$
Species richness	4.6 ± 0.89	5.8 ± 0.84	$t = 3.21, p = 0.03$
<i>Pogonomyrmex rugosus</i> —Nutt grassland			
Biomass (g/0.04 m ⁻²)	62.63 ± 17.27	17.17 ± 6.63	$t = 6.37, p = 0.00$
Cover (%)	36.64 ± 4.35	25.06 ± 7.84	$t = 3.38, p = 0.02$
Density no. (m ⁻²)	71.2 ± 26.32	58.0 ± 17.02	$t = 1.00, p = 0.37$
Species richness	8.4 ± 1.14	6.4 ± 2.5	$t = 1.75, p = 0.15$
<i>Aphaenogaster cockerelli</i> —Nutt grassland			
Biomass (g/0.04 m ⁻²)	32.57 ± 5.36	7.8 ± 2.62	$t = 9.3, p = 0.001$
Cover (%)	43.8 ± 22.5	13.3 ± 4.8	$t = 3.2, p = 0.03$
Density no. (m ⁻²)	72.8 ± 26.4	23.2 ± 12.1	$t = 4.9, p = 0.008$
Species richness	7.0 ± 0.63	5.2 ± 0.83	$t = 3.6, p = 0.02$
<i>Myrmecocystus depilis</i> —Piedmont			
Biomass (g/0.04 m ⁻²)	6.6 ± 5.5	1.8 ± 2.1	$t = 2.7, p = 0.05$
Cover (%)	12.8 ± 12.6	5.6 ± 5.4	$t = 2.1, p = 0.11$
Density no. (m ⁻²)	78.0 ± 58.4	34.4 ± 33.8	$t = 1.35, p = 0.25$
Species richness	7.4 ± 3.8	4.4 ± 3.0	$t = 2.86, p = 0.04$

to nutrient redistribution. However, *A. cockerelli* also transports quantities of plant materials and even animal feces to the nest location. The *A. cockerelli* nest modified soils not only supported higher biomass of annuals than reference soils; they were the only ant modified soils where cover, density, and species richness were higher than reference soil.

This study demonstrates that the length of time ants occupy a nest in a location is more important than the feeding behavior of the ant species as the primary factor affecting soil properties and vegetation. The effects of ants on annual plant communities are not restricted to seed-harvesting ants but also occur with generalist foragers (*A. cockerelli*) and liquid—insect feeders (*M. depilis*). The species of ants included in this study occupy the same nest for close to a decade or more (Chew, 1995; MacMahon et al., 2000). For example, long-term studies of Chihuahuan Desert ants reported average and maximum life spans of nests of *M. depilis* of 8.6 and 35 years and of *A. cockerelli* of 5.2 and 23 years (Chew, 1995). Nest construction and maintenance of tunnels and chambers gradually change soil properties by modifying soil aeration, enhancing bulk flow of water into the soil, enhancing water percolation and evaporation (Lei, 2000; Snyder et al., 2002). These physical modifications of the soil column in which the nest is constructed are separate from effects of materials transported to the nests by foragers that are either stored in shallow chambers or deposited around the nest entrance (Whitford et al., 1976). Nest construction and maintenance activities plus deposition of materials transported to the nest location by foragers contribute to soil modifications that stimulate growth of annual

plants. However, as demonstrated by this study, the effects of ant nests, that persist for up to a decade or longer, on soil properties and vegetation is temporally and spatially variable.

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References

- Anderson, T.H., Domsch, K.H., 1990. Application of eco-physiological quotients (qCO₂ and qD) on microbial biomass from soils of different cropping histories. *Soil Biology and Biochemistry* 22, 251–255.
- Bestelmeyer, B.T., Wiens, J.A., 2003. Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands. *Journal of Arid Environments* 53, 373–386.
- Boulton, A.M., Jaffee, B.A., Scow, K.M., 2003. Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota. *Applied Soil Ecology* 23, 257–265.
- Carlson, S.R., Whitford, W.G., 1991. Ant mound influence on vegetation and soils in a semiarid mountain ecosystem. *American Midland Naturalist* 126, 125–139.
- Chew, R.M., 1995. Aspects of the ecology of 3 species of ants (*Myrmecocystus* spp., *Aphaenogaster* sp.) in desertified grassland in Southeastern Arizona, 1958–1993. *American Midland Naturalist* 134, 75–83.
- Coffin, D.P., Lauenroth, W.K., 1990. Vegetation associated with nest sites of western harvester ants (*Pogonomyrex occidentalis* Cresson) in a semiarid grassland. *American Midland Naturalist* 123, 226–235.
- Edwards, N.T., Sollins, P., 1973. Continuous measurement of carbon dioxide evolution from partitioned forest floor components. *Ecology* 54, 406–412.
- Hobbs, R.J., 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* 67, 519–523.
- Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in soil. V. A method for measuring soil biomass. *Soil Biology and Biochemistry* 8, 209–213.
- Kemp, P.R., 1983. Phenological patterns of Chihuahuan Desert plants in relation to the timing of water availability. *Journal of Ecology* 71, 427–436.
- Lei, S.A., 2000. Ecological impacts of seed harvester ants on soil attributes in a *Larrea*-dominated shrubland. *Western North American Naturalist* 60, 439–444.
- Liu, X.Y., Lindemann, W.C., Whitford, W.G., Steinber, R.L., 2000. Microbial diversity and activity of disturbed soil in the northern Chihuahuan Desert. *Biology and Fertility of Soils* 32, 243–249.
- Macfadyen, A., 1971. The soil and its total metabolism. In: Phillipson, J. (Ed.), *Methods of Study of Quantitative Soil Ecology: Population, Production, and Energy Flow*. Blackwell, Oxford, pp. 1–13.
- MacMahon, J.A., Mull, J.F., Crist, T.O., 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* 31, 265–291.
- Parker, L.W., Miller, J., Steinberger, Y., Whitford, W.G., 1983. Soil respiration in a Chihuahuan Desert rangeland. *Soil Biology and Biochemistry* 15, 303–309.
- Parker, L.W., Santos, P.F., Phillips, J., Whitford, W.G., 1984. Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan Desert annual, *Leupedium lasiocarpum*. *Ecological Monographs* 54, 339–360.
- Rissing, S.W., 1986. Indirect effects of granivory by harvester ants—plant species composition and reproductive increase near ant nests. *Oecologia* 68, 231–234.
- Schumacher, A., Whitford, W.G., 1974. Foraging ecology of 2 species of Chihuahuan Desert ants—*Formica perpilosa* and *Trachymyrmex smithi neomexicanus* (Hymenoptera: Formicidae). *Insectes Sociaux* 21, 317–330.
- Snyder, S.R., Crist, T.O., Friese, C.F., 2002. Variability in soil chemistry and arbuscular mycorrhizal fungi in harvester ant nests: the influence of topography, grazing and region. *Biology and Fertility of Soils* 35, 406–413.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry, Principles, Practices and Statistics in Biological Research*, second ed. W.H. Freeman and Co., San Francisco, CA.
- Sparling, G.P., West, A.W., 1990. A comparison of gas chromatography and differential respirometer methods to measure soil respiration and to estimate the soil microbial biomass. *Pedobiologia* 34, 103–112.
- Wagner, D., 1997. The influence of ant nests on *Acacia* seed production, herbivory and soil nutrients. *Journal of Ecology* 85, 83–93.
- Wagner, D., Jones, J.B., 2004. The contribution of harvester the ant nests, *Pogonomyrmex rugosus* (Hymenoptera: Formicidae), to soil nutrient stocks and microbial biomass in the Mojave Desert. *Environmental Entomology* 33, 599–607.
- Wagner, D., Brown, M.J.F., Gordon, D.M., 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia* 112, 232–236.
- Whitford, W.G., 1988. Effects of harvester ant (*Pogonomyrmex rugosus*) nests on soils and a spring annual, *Erodium texanum*. *Southwestern Naturalist* 33, 482–485.

- Whitford, W.G., 2000. Keystone arthropods as webmasters in desert ecosystems (336pp). In: Coleman, D.C., Hendrix, P.F. (Eds.), *Invertebrates as Webmasters in Ecosystems*. CABI Publishing, New York, pp. 25–41.
- Whitford, W.G., 2001. Invertebrates: their effects on the properties and processes of desert ecosystems. In: Prakash, I. (Ed.), *Ecology of Desert Environments*. Scientific Publishers, Jodhpur, India, pp. 333–356.
- Whitford, W.G., 2002a. Ants. In: Lal, R. (Ed.), *Encyclopedia of Soil Science*. Marcel Dekker, Inc., New York, pp. 76–79.
- Whitford, W.G., 2002b. *Ecology of Desert Systems*. Academic Press, London.
- Whitford, W.G., DiMarco, R., 1995. Variability in soils and vegetation associated with harvester ants (*Pogonomyrmex rugosus*) nests on a Chihuahuan Desert watershed. *Biology and Fertility of Soils* 20, 169–173.
- Whitford, W.G., Herrick, J.E., 1995. Maintaining soil processes for plant production and community dynamics. In: West, N.E. (Ed.), *Proceedings of the Fifth International Rangeland Congress*, vol. II. Society for Range Management, Denver, CO, pp. 33–37.
- Whitford, W.G., Johnson, P., Ramirez, J., 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Insectes Sociaux* 23, 117–132.
- Whitford, W.G., Depree, E., Johnson, P., 1980. Foraging ecology of two Chihuahuan Desert ant species: *Novomessor cockerelli* and *Novomessor albigulosus*. *Insectes Sociaux* 27, 148–156.
- Whitford, W.G., Steinberger, Y., Mackay, W., Parker, L.W., Freckman, D., Wallwork, J.A., Weems, D., 1986. Rainfall and decomposition in the Chihuahuan Desert. *Oecologia* 68, 512–515.