RESEARCH ARTICLE

Landscape position moderates how ant nests affect hydrology and soil chemistry across a Chihuahuan Desert watershed

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Abstract Ants moderate the supply of critical resources such as water and nutrients in desert environments by changing the physical arrangement of soils during nest construction. We measured water infiltration and soil physical and chemical properties on and off the nests of two ant species (*Pogonomyrmex rugosus*, *Aphaenogaster cockerelli*) across five sites at differing landscape positions within a Chihuahuan Desert watershed. Our aim was to test whether the effects of these long-lived ant nests on water infiltration and soil chemistry varied between ant species or across sites within a watershed. Water flow was generally slowest at the site with the highest silt and clay contents, and fastest at the site with sandy soils. Flow was generally greater through ant nest soils than adjacent non-nest soils, and we attribute this to increases in macropores in the nests. However, the effects of both ant nests and species varied among sites. Despite wide variation in soil chemical properties across all sites, ant nests had a consistent effect on soil chemical properties, with higher levels of carbon, nitrogen, sulphur, phosphorus and electrical conductivity on nests compared with non-nest soils. Our results demonstrate that while we can generalise about the effects of ant nests on water flow and nutrient levels, differences in soil type, nest density and ant species across sites are likely to moderate these effects.

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Introduction

Regional variation in climate and topography exert profound and overriding top-down effects on soil and ecological processes (Paul and Clark 1989; Burke 1989). At landscape or watershed scales, fluvial and aeolian erosion and deposition processes create gradients of soil organic matter and nutrients (Lajtha and Schlesinger 1988; Burke 1989), while at finer

patch-level scales, variations in plant-inter-plant distribution result in changes in the availability of nutrients. In arid ecosystems, many soil and ecological processes are moderated by water availability, which is an important driver of ecosystem productivity and diversity across a range of spatial scales (Noy-Meir 1972). Water infiltration capacity affects rates of erosion and deposition, soil physical and chemical properties, litter decomposition and nutrient cycling, and plant germination and establishment (Snyder et al. 2002). The patchy distribution of soil moisture across all scales eventually results in stable patterns in community assemblages, and governs primary productivity (Burke 1989).

Within deserts, runoff is generally greater on the steeper, upper slopes, with water redistributed as runon to positions lower in the watershed (Snyder et al. 2002). Lower landscape positions tend to have deeper soil profiles with greater clay content and therefore greater soil carbon and nitrogen pools. This results in an enhanced water holding capacity, greater levels of infiltration, higher mineralisation rates and greater concentrations of available nutrients (Burke 1989). Within landscapes, variation in productivity is largely determined by the distribution of soil, water and nutrients at smaller spatial scales, with patches of higher productivity (sinks, islands of fertility or fertile patches) separated by more or less unvegetated and infertile interspaces (Schlesinger and Jones 1984; Montana 1992; Tongway and Ludwig 1994).

While the distribution of water and nutrients is driven by differences in geomorphology and landscape position at watershed scales, changes at finer spatial scales may moderate these effects. In many desert systems, the physical activity of animals dramatically alters soil ecological processes across fine spatial scales (Huntley and Inouye 1988), and invertebrates such as ants may affect ecosystem processes primarily by their effect on soil properties (Whitford 2000, 2002; Jouquet et al. 2006). For example, a study in the Negev Desert showed that the effect of harvester ants on vegetation was influenced more by their physical effect on the soil through the creation of nest structures, than through their role as seed harvesters (Wilby et al. 2001). In the Chihuahuan Desert, redistribution of water is a dominant factor structuring the environment, and feedbacks moderated by animals influence

nutrient availability and plant demography through several direct and indirect pathways (Whitford and Bestelmeyer 2006).

Ants modify soil by creating nest structures that alter soil hydrology, organic matter and nutrients, thus modulating flows of limiting resources and increasing habitat complexity within ecosystems (Crist and Wiens 1996). The transport of soil by ants is a form of fine-scale disturbance that has profound bottom-up effects by inducing landscape-level changes in infiltration through the creation of macropores (Eldridge 1994; Whitford 2000), by the redistribution of nutrients (Nkem et al. 2000), and by creating substantial soil biomantles (Whitford and DiMarco 1995). Because of the nature of the soil substrate, ecosystem engineers such as ants typically create structures that far outlive the organisms that created them (Hastings et al. 2007). The functional significance of these structures is likely to vary and the same type of soil disturbance may produce variable effects at different watershed locations, within different seasons, or through time (Steinberger and Whitford 1984; Whitford and DiMarco 1995; Snyder et al. 2002). Few studies, however, have considered the effects of ant-created structures across different landscapes (though see Whitford and DiMarco 1995; Snyder et al. 2002), despite the fact that spatial variability within landscapes is an important determinant of many ecosystem processes in deserts (Peters and Havstad 2006). Studies in these systems that do not encompass landscape-, patch- and species-level scales are unlikely to capture the true nature of the effects of biota on a range of ecosystem processes.

This paper reports on a study of how nests of two ant species (*Aphaenogaster cockerelli*, *Pogonomyrmex rugosus*) affect both the infiltration of water and soil chemical properties in the northern Chihuahuan Desert in New Mexico. The study was conducted at two spatial scales: (1) across five different landscape positions (sites) distributed along a catenary sequence from the top to the bottom of a watershed, and (2) between nests of two different ant species as patches within a matrix of non-nest soils in each of the five landscape positions.

Our aim was to determine whether the effects of ants on water movement and soil chemistry can be generalised, both between ant species and among landscape positions. Specifically, we hypothesised

that (1) water infiltration and levels of carbon, nitrogen, sulphur and phosphorus would be consistently greater on ant nest soils compared with adjacent non-nest soils, irrespective of ant species or landscape position, (2) differences in infiltration would be due to differences in macroporosity between nest and non-nest locations, which we assessed using disc permeameters at two different supply potentials, and (3) any differences among sites would result from differences in soil physical properties, particularly soil texture, which consistently changed down the watershed.

Methods

Study area

Our study was conducted in September 2005 within a small watershed in the Jornada Basin, southern New Mexico, USA. The watershed is on the Chihuahuan Desert Rangeland Research Centre (CDRRC) of New Mexico State University, approximately 40 km NW of Las Cruces, Dona Ana County, N.M (Fig. 1). The watershed is approximately 5 km in length, extending from the base of Mt Summerford downslope to an active alluvial basin adjacent to an ancient riverbed, which grades gently upslope to a sandy rise. The slope on the watershed ranged from approximately 5% at the mountain base to <1% on the sandy rises,
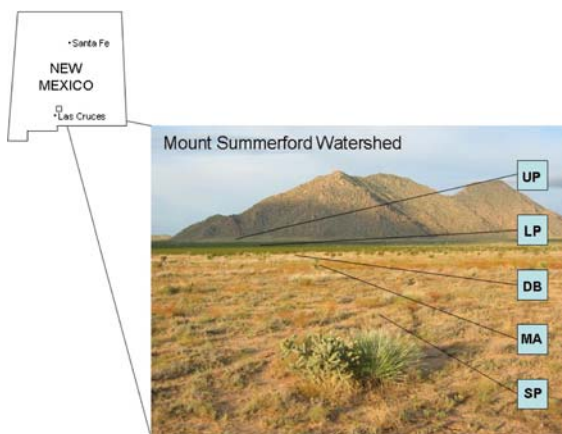

Fig. 1 Location of the study site in southern New Mexico and the five landscape positions in the Mount Summerford watershed. UP = Upper piedmont, LP = Lower piedmont, DB = Drainage basin, MA = Midslope alluvium, S = Sandplain

and elevation varied from 2000 to 1300 m (Whitford and DiMarco 1995). Mean annual rainfall during the last century has been 211 mm, with a standard deviation of 77 mm (Houghton 1972). More than half the annual rainfall occurs between July and early October in the form of intense convectional storms (Whitford and DiMarco 1995). Potential evapotranspiration exceeds precipitation, with summer maxima reaching 40°C and winter minima ranging from 0 to −10°C.

We conducted our study at five sites within the watershed, along a SW-NE-trending transect about 6 km long from Mt Summerford in the south-west to a sandy rise in the north-east near South Well (Fig. 1). Two of the sites at the western end of the transect (Upper Piedmont and Lower Piedmont) were on a steep catena on the flanks of Mt Summerford, with slopes up to 8%. The other three sites (Drainage Basin, Midslope Alluvium, Sandplain) were located on a second gently sloping catena (<2% slope) at the north-eastern end of the transect.

(1) The Upper Piedmont (UP) site, at the base of Mt Summerford, was characterised by shallow loamy-skeletal Argic Petrocalcids overlain by a lag stone pavement (Hachita-Casito complex, Gile et al. 1981). The soil at this site is typically shallow (<0.3 m), shows signs of extensive surface erosion over the past 150 years, and is intersected by numerous arroyos and deep rills less than 50 m apart. The vegetation is dominated by creosotebush (*Larrea tridentata*) (Fig. 1). (2) The Lower Piedmont (LP) site is located at the base of the western catena with slopes to 3%. It is characterised by sandy-loam Typic Calciargid soils (Berino complex, Gile et al. 1981), and supports a mixed bunchgrass grassland of black grama (*Bouteloua eriopoda*), dropseed (*Sporobolus* spp.) and three awns (*Aristida* sp.), with scattered honey mesquite (*Prosopis glandulosa*), soaptree yucca (*Yucca elata*) and creosote bush. (3) Drainage Basin (DB), the lowest site on the NE catena, receives runon water from the Midslope Alluvium (MA) site, and is characterised by sandy loam to clay loam Vertic Calciargid and Ustic Calciargid soils (Stellar-Continental complex, Gile et al. 1981). It is dominated by burro grass (*Scleropogon brevifolia*) and tobosa grass (*Pleuraphis mutica*). (4) The Midslope Alluvium site is an active alluvial fan derived from volcanic material. The soils are Typic Haplocalid, overlain by coarse-grained decomposed

granite. It is dominated by tobosa grass, burro grass and the annual forb *Erodium texanum*, and receives run-off water from the upslope Sandplain (SP). The Midslope Alluvium is separated from the Sandplain by a 0.5 m escarpment. (5) The highest point in the NE catena is the Sandplain site, which comprises low sandy rises to 0.3 m interspersed with finer-textured clay Ustic Calciargids and Vertic Calciargids (Stellar Continental complex). It is dominated by the grasses *Crypthantha angustifolia*, tobosa grass and three awns.

Nests of the seed harvester *Pogonomyrmex rugosus* (Fig. 2a) and the generalist forager *Aphaenogaster cockerelli* (Fig. 2b) were sampled at each site, except for the Upper Piedmont site where *Pogonomyrmex* colonies were absent. *P. rugosus* nests generally have a single entrance, with numerous burrows in the upper levels, and one or two main tunnels that may extend to between 300 and 400 cm deep (MacKay 1981).
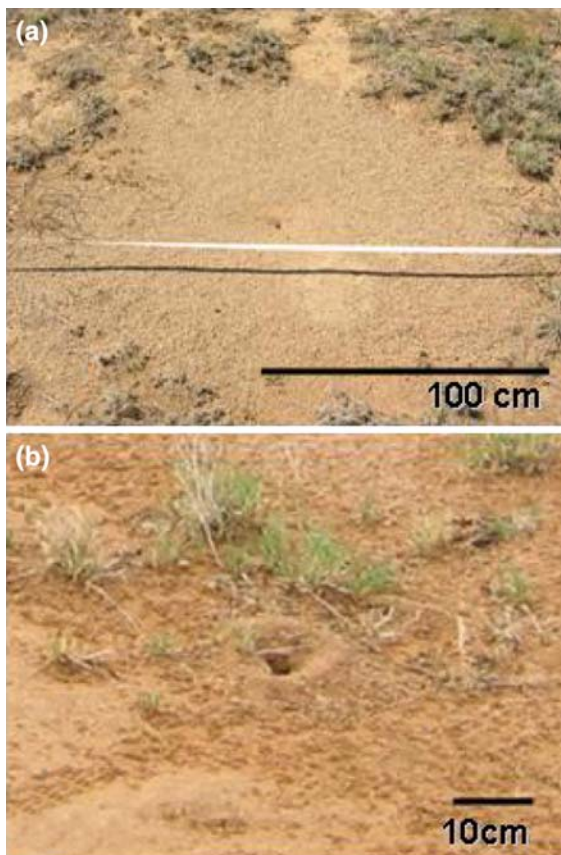

Fig. 2 Nests of (**a**) *Pogonomyrmex rugosus* and (**b**) *Aphenogaster cockerelli*. Note the different scales in each plate

A. cockerelli can form polydomous colonies of 1–5 nests (Barton et al. 2002), with tunnels extending to depths of at least 1 m (Whitford 1973).

Nest densities and profiles

We counted the number of nests of both *Aphaenogaster* and *Pogonomyrmex* located within one 30-m radius plot at each of the five sites. For each nest we recorded two diameters perpendicular to each other through the centre, and calculated the surface area of the nests using the equation for the area of a circle. The cross-sectional profile of one nest of each species was also recorded at each site by using a 2-m steel bar suspended over the nest parallel to the soil surface and through the centre of the nest. The vertical distance to the surface was then measured every centimeter across the entire nest surface and including an area of adjacent non-nest surface either side of the nest.

Measurement of soil hydrological properties

We measured both sorptivity (mm $h^{-0.5}$) and steady-state infiltration (mm h^{-1}) through nest and non-nest soils at two water supply potentials using a disc permeameter. The supply potentials were −40 mm tension, which measures flow only through matrix pores and +10 mm tension, which measures flow through both matrix pores and macropores (Perroux and White 1988). At each of the five sites we measured water infiltration at five nest and five non-nest locations for each of the two ant species, but only for *Aphaenogaster* at the Upper Piedmont site ($n = 90$). Nests were selected by sweeping the area with three observers spaced 25 m apart until five nests were located. Nest activity was determined by blowing air into the nest to ensure that they were occupied by ants. Only active nests were used. The permeameters were placed at the edge of the nest, within the circumference of the corona, and the non-nest location was an unvegetated surface within 5 m of the nest. Both ponded (+10 mm tension) and unsaturated (−40 mm tension) permeameters were placed about 70 cm apart. The unsaturated permeameter was placed on a thin bed of sand to provide a uniform contact with the soil surface and the ponded permeameter placed on a steel ring and sealed along the outside edge to prevent leakage of water. The

permeameters were run until steady-state had been achieved (approximately 30 min). At each supply potential, sorptivity was calculated according to the method of Cook and Broeren (1994), and steady-state infiltration according to White (1988).

Sorptivity is the early phase of infiltration, lasting up to about 10 min after water is applied. Over this period water enters the soil in response to gradients in water potential influenced by soil dryness and capillary (pore) structure (White 1988). The sorptivity phase is largely governed by the forces of attraction between soil and water molecules. As the soil wets up, gravitational forces become more important (White 1988) and, over time, a steady-state is reached when the flow rate from the disc permeameter stabilises. This steady-state flow rate, or steady-state infiltration, is governed by capillarity, gravity, the area of the disc permeameter in contact with the soil, and the pressure at which the water is supplied to the soil surface.

Water flow through the soil depends on the combination of matrix pores (also called micropores) and macropores. Matrix pores occur between individual mineral grains and between soil particles, and are not biogenic. Macropores are larger pores, generally >0.7 mm or more in diameter, are biogenic and formed by plant roots and soil fauna. Macropores are extremely important for transferring water, oxygen and nutrients through soil (Bouma 1992). We were particularly interested in macropore effects because we hypothesised that ant nests would alter soil macroporosity and thus its ability to conduct water. When a negative pressure is applied to the soil with the disc permeameter, water is prevented from entering macropores pores larger than about 0.74 mm (Coughlan et al. 1991), and thus the influence of micropores on sorptivity and steady-state infiltration can be assessed independent of the effect of macropores. Conversely, when a positive pressure is applied to the soil, flow through both macropores and micropores is assessed. Therefore it is possible to isolate water flow through either micropores only or both micropores and macropores by varying the tension (pressure) applied to the disc permeameter. Whilst macroporosity is not directly measured, infiltration theory indicates that the ratio of sorptivity under ponding (+10 mm) to sorptivity under tension (−40 mm) is a measure of the relative contribution of macropores to total water flow (White 1988). This

measure is called the macropore index and is derived from the Eq. 1:

Macropore index

$$
= (\text{sorptivity} + 10\ \text{mm} + \text{sorptivity} - 40\ \text{mm})
$$
$$
/\text{sorptivity} - 40\ \text{mm} \tag{1}
$$

This measure enables an assessment of the relative importance of animals in producing macropores that increase conductivity in soils.

Soil physical and chemical properties

We sampled three of the five nest (and inter-nest) locations of both ant species at each site (except for *Pogonomyrmex* at the Upper Piedmont site). Samples were taken from within 20 cm of the infiltration measurement locations and at the same distance from the nest entrance. Soil bulk density was measured in duplicate using a core 58-mm diameter by 100-mm deep. Total carbon (C), nitrogen (N) and sulphur (S) from two depths (0–1 cm, 1–5 cm) were measured using high temperature combustion in an oxygen stream using a LECO CNS-2000 CNS Analyser (LECO Corporation, St Joseph, MI, USA). Particle size analysis of the <2.0 mm fraction was undertaken on dispersed samples using the hydrometer method (Day 1965). Electrical conductivity (EC) and pH were measured in 1:5 soil–water extracts. Available phosphorus (P) was measured using the Bray 1 method (Rayment and Higginson 1992).

Statistical analyses

Two analyses were performed using a mixed-models ANOVA approach within the GenStat (2007) statistical package. The first analysis explored differences in soil nutrient concentrations and percentage of silt-, clay- and sand-sized particles at four levels: (1) landscape-level (sites within watershed), (2) species-level (*Aphaenogaster, Pogonomyrmex* within sites), (3) patch-level (nest versus non-nest within species and sites), and (4) depth-level (topsoil versus subsoil within patches). Due to different spatial scales of observation, the ANOVA model required three error terms (see structure in "Results" below); the main-plot stratum considered site and ant species effects (and their interaction); the sub-plot stratum nest effects (i.e. the pairing of nest versus non-nest) and

its interaction with ant species and site; and the sub-sub-plot stratum depth effects and its two-, three- and four-way interactions with site, ant species and the nest factor. The second analysis examined changes in water flow using a similar model structure, but did not require the depth effect of the third strata. For all analyses, the site by ant species interaction had only three degrees of freedom as *Pogonomyrmex* nests were absent from the Upper Piedmont site. One-way ANOVA was used to examine possible differences in nest size among sites. For all ANOVA analyses, data were transformed, where necessary, prior to analyses, based on diagnostic tests (e.g. residual and normal plots) (GenStat 2007). Significant differences between means were examined using Fisher's protected least significant difference (LSD) testing. Simple linear regression was used to examine relationships between particle size and measures of water flow.

Results

Nest densities across the watershed

Nest density varied markedly among sites with 10–88 nests ha^{-1} for *Aphaenogaster* and 17–56 nests ha^{-1} for *Pogonomyrmex* (Table 1). The nest density of the two species was negatively correlated, and *Aphaenogaster* was dominant or co-dominant over *Pogonomyrmex* at all landscape positions except the Sandplain site. Nests had similar profiles at the different sites; *Pogonomyrmex* nests were gently broadly concave while *Aphaenogaster*

nests were strongly concave to hemispherical (Fig. 2). The surface area of *Pogonomyrmex* nests was on average more than six times that of *Aphaenogaster* nests (Table 1). *Aphaenogaster* nests in the Lower Piedmont location had more than double the surface area of those in the Upper Piedmont, Drainage Basin and Sandplain sites ($F_{4,59} = 6.26$, $P < 0.001$ on log$_{10}$ transformed data). *Pogonomyrmex* nests at the Midslope Alluvium and Lower Piedmont sites were larger in surface area than those at the Drainage Basin and Sandplain sites ($F_{3,34} = 4.73$, $P = 0.007$ on $\sqrt{}$-transformed data, Table 1).

Measures of water flow: sorptivity and steady-state infiltration

In general, all measures of water flow were greatest in the Lower Piedmont and Sandplain sites and least at the Midslope Alluvium site ($P < 0.001$, Tables 2 and 4, Fig. 3). The macropore index suggests that the Sandplain site had fewer macropores than the other sites ($P = 0.004$, Fig. 4a).

All measures of water flow were significantly greater through nest compared with non-nest soils ($P < 0.022$, Tables 3 and 4, Fig. 3), except for sorptivity under tension, which only showed a weak trend towards higher flow through ant nests ($P = 0.064$). Relative differences in water flow between nest and non-nest soils were greater (almost double) under ponding compared with under tension (<8% increase). The magnitude of nest effects on water infiltration differed, however, across the watershed. Ponded steady-state infiltration was

Table 1 Density (nests ha^{-1}) and mean surface area (m^2) (±SD) of nests of *Pogonomyrmex rugosus* and *Aphaenogaster cockerelli* in relation to geomorphic position

			Landscape position					
			Sandplain	Midslope alluvium	Drainage basin	Lower piedmont	Upper piedmont	Average
Nest density (ha^{-1})	*P. rugosus*		56.6	21.2	38.9	17.7	0	26.9
	A. cockerelli		21.3	63.7	42.5	88.5	10.6	47.3
Nest area (m^2)	*P. rugosus*	Mean	0.79[b]	1.76[a]	1.04[b]	1.84[a]	–	1.36
		SD	0.21	0.33	0.12	0.42	n.a.	0.27
	A. cockerelli	Mean	0.12[a]	0.23[c]	0.14a	0.43[b]	0.15	0.21
		SD	0.02	0.04	0.03	0.06	0.01	0.03

For nest area data within a species, differences in superscripts indicate a significant difference in means across landscape positions at $P < 0.05$. –, no nests found. Data for nest densities were collected from one large plot per landscape position and are therefore not mean values

Table 2 Mean values of water flow and soil properties in relation to landscape position, and corresponding *F*-statistics and *P*-values

Attributes	Landscape position					*F*-statistic	*P*-value
	Sandplain	Midslope alluvium	Drainage basin	Lower piedmont	Upper piedmont		
Sorptivity (−40 mm) mm h$^{-0.5\#}$	62.9^a	12.7^b	28.9^c	48.5^c	22.9^c	17.48	<0.001
Sorptivity (+10 mm) mm h$^{-0.5\#}$	108.2^b	61.7^a	91.1^b	139.4^b	82.6^b	10.69	<0.001
Steady-state infiltration (−40 mm) mm h$^{-1\#}$	17.8^a	2.6^b	6.6^c	12.6^a	5.8^c	18.86	<0.001
Steady-state infiltration (+10 mm) mm h$^{-1\#}$	25.4^b	18.2^a	23.4^b	42.8^c	24.3^b	12.43	<0.001
Total C (%)$^\#$	0.53^a	0.90^b	0.60^a	0.42^a	1.39^c	13.50	<0.001
Total N (%)	0.04^a	0.07^b	0.05^a	0.03^c	0.06^b	12.40	<0.001
Total S (%)$^\#$	0.002^a	0.002^a	0.002^a	0.002^a	0.002^a	0.53	0.715
Available P (mg kg^{-1})	16.0^{ac}	15.3^{ac}	20.1^a	17.7^{ac}	13.2^{bc}	3.10	0.042
EC (dS m^{-1})	0.09^a	0.13^b	0.10^a	0.08^a	0.09^a	13.40	<0.001
pH	8.5^a	8.6^a	8.4^a	8.6^a	8.7^a	1.44	0.262

Within an attribute, different superscripts indicate significant differences in means between landscape positions. $^\#$ log$_{10}$ transformed

eight-times greater on the nests compared with non-nests at the Midslope Alluvium site, but at the other sites the increase was only up to three-times greater ($P < 0.001$, Fig. 3). Other significant site by nest interactions were found for ponded sorptivity ($P = 0.008$) and steady-state infiltration under tension ($P < 0.043$, Fig. 3). All these interactions resulted from much greater differences between nests and non-nests at the Midslope Alluvium site compared with the other sites.

Increases in both ponded sorptivity ($F_{1,3} = 19.6$, $P = 0.021$) and ponded steady-state infiltration ($F_{1,3} = 11.6$, $P = 0.042$) on nest soils were associated with increases in the percentage of coarse plus medium sand. However, there were no significant relationships for non-nest soils ($P > 0.14$). When we explored the presence of a similar relationship for soils under tension (i.e. when macropores are bypassed and prevented from conducting water), differences in water flow could not be explained by changes in sand content ($P > 0.55$).

The significant ant species by nest interaction ($P = 0.033$) indicated an 85% increase in macropore status in nest soils compared with non-nest soils for *Pogonomyrmex* nests, but no significant difference between nest and non-nests for *Aphaenogaster* (Fig. 4b). Water flow under tension was about 78% greater through *Aphaenogaster* nests compared with *Pogonomyrmex* nests ($P < 0.008$), but there were no
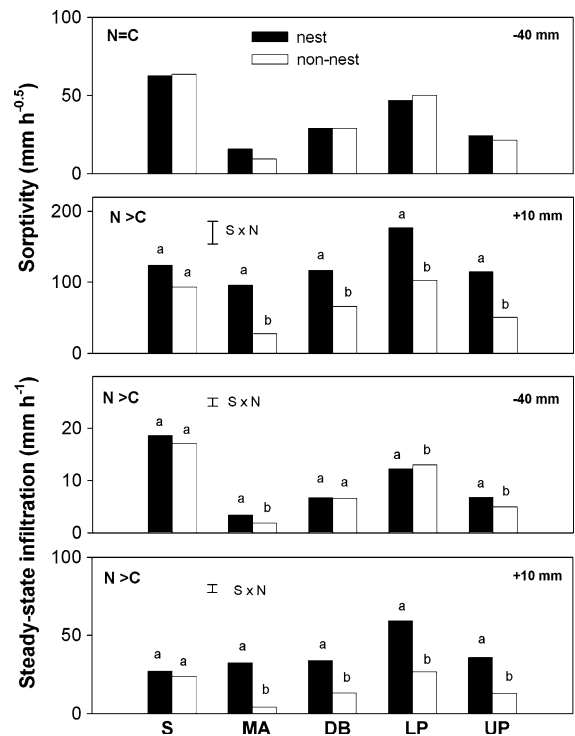

Fig. 3 Mean rates of sorptivity (mm h$^{-0.5}$) and steady-state infiltration (mm h^{-1}) under tension (−40 mm) and ponding (+10 mm) on nest and non-nest soils at the five landscape positions. N = nest, C = non-nest (control). Within a site, different superscripts indicate a significant difference between nest and non-nest at $P < 0.05$. The 5% LSD bar for the site (S) by nest (N) interaction is given
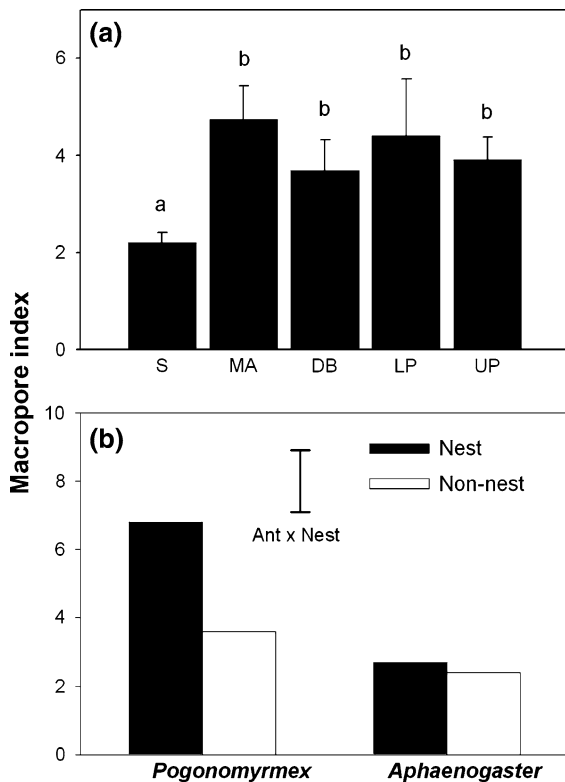
Fig. 4 Macropore index for (**a**) the five watershed positions, and (**b**) nest and species. The 5% LSD bar for ant species by nest location is shown. Different letters in relation to site indicate a significant difference among sites at $P < 0.05$

effect of nests on water infiltration under tension was greater for *Aphaenogaster* than *Pogonomyrmex* (Table 3).

Soil physical and chemical properties

There was almost twice the percentage of clay- and silt-sized particles, and half the percentage of sand-sized particles at the Midslope Alluvium site compared with the other sites ($P < 0.001$, Fig. 5). There were no significant differences in bulk density between nests and non-nests ($P = 0.24$) or among sites ($P = 0.16$, Table 5). The silt content was greater on *Pogonomyrmex* nests compared with *Aphaenogaster* nests at all sites except the Midslope Alluvium, which followed the opposite trend (site × ant: $P = 0.023$). Increases in percentage of both silt-sized and clay-sized particles with depth were most strongly pronounced at the Sandplain site (site × depth: $P = 0.003$ for silt; $P = 0.007$ for clay). The decline in sand-sized particles with depth was greatest at the Midslope Alluvium site compared with the other sites (site × depth: $P < 0.001$). Percentages of sand-sized particles were generally greater in the nests compared with non-nests ($P = 0.042$).

Total C values were about 2.5-times greater on the Upper Piedmont (1.4% C) and double at the Midslope Alluvium sites (0.9% C) compared with the other sites (mean = 0.5%, $P < 0.001$, Tables 2 and 5). Total N concentration followed a similar trend, with

differences between the species under ponding (Tables 3 and 4). A significant ant species by nest interaction ($P = 0.023$) indicated that the relative

Table 3 Water flow and soil nutrients in relation to nest location and ant species, and corresponding *F*-statistics and *P*-values

Attribute	Nest location				Ant species			
	Nest	Non-nest	*F*	*P*	*A. cockerelli*	*P. rugosus*	*F*	*P*
Sorptivity (−40 mm) mm h$^{-0.5}$[#]	37.0[a]	36.1[a]	3.64	0.064	43.2[a]	28.2[b]	9.65	0.004
Sorptivity (+10 mm) mm h$^{-0.5}$[#]	126.6[a]	69.7[b]	68.31	<0.001	93.5[a]	104.0[b]	0.03	0.873
Steady-state infiltration (−40 mm) mm h^{-1}[#]	9.8[a]	9.1[b]	5.74	0.022	11.4[a]	7.0[b]	7.94	0.008
Steady-state infiltration (+10 mm) mm h^{-1}[#]	37.8[a]	16.5[b]	80.56	<0.001	24.7[a]	30.2[a]	0.03	0.859
Total C (%)[#]	0.77[a]	0.63[b]	25.32	0.001	0.75[a]	0.63[a]	0.16	0.697
Total N (%)	0.05[a]	0.04[b]	13.78	0.002	0.05[a]	0.05[a]	0	0.996
Total S (%)[#]	0.001[a]	0.002[b]	6.92	0.017	0.002[a]	0.002[a]	1.37	0.715
Available P (mg kg^{-1})	19.7[a]	14.0[b]	27.93	<0.001	16.7[a]	17.0[a]	0.24	0.627
EC (dS m^{-1})	0.11[a]	0.08[b]	48.99	<0.001	0.10[a]	0.10[a]	0.62	0.442
pH	8.5[a]	8.6[a]	2.67	0.12	8.6[a]	8.5[a]	1.38	0.255

Within an attribute, different superscripts indicate significant differences between nest and non-nest, or ant species. [#] log$_{10}$ transformed data

Table 4 ANOVA structure and significance levels for measures of water infiltration

Source by stratum	df	Steady-state infiltration		Sorptivity		Macropore index
		Ponding	Tension	Ponding	Tension	
Rep × Site × Species						
Site	4	<0.001	<0.001	<0.001	<0.001	0.004
Species	1		0.008		0.004	0.002
Site × Species	3					
Residual	36					
Rep × Site × Nest						
Nest (nest versus non-nest)	1	<0.001	0.002	<0.001		<0.001
Site × Nest	4	<0.001	0.043	0.008		
Species × Nest	1		0.023			0.033
Site × Species × Nest	3					0.010
Residual	36					
Total	89					

All data, except macropore index were $\log_{10}$-transformed. Only tests significant at $P < 0.05$ are shown

levels greatest in the Midslope Alluvium and Upper Piedmont sites (mean = 0.06%, $P < 0.001$, Tables 2 and 5). Available P levels were lower at the Upper Piedmont sites ($P = 0.042$), while EC was about 40% greater in the Midslope Alluvium site compared with the other sites (mean = 0.10 dS m^{-1}, $P < 0.001$). There were no differences in total S or soil pH among sites (S mean = 0.002, pH mean = 8.6, $P > 0.05$).

In general, levels of total C, N and S, available P and EC were greater on nest soils compared with non-nest soils ($P < 0.017$, Table 3), and these effects were consistent across sites (site × nest interaction: $P > 0.05$, Table 5). There were no significant differences in any soil chemical properties between *Aphaenogaster* or *Pogonomyrmex* (Table 3), and the results were consistent among sites (ant × site interaction: $P > 0.20$, Table 5).

There were significant declines in total S and available P, a slight increase in pH, an increase in EC ($P < 0.005$), but no changes in total C or N with depth (Tables 5 and 6). There was 75% less total C in the surface compared with the subsoil at the Upper Piedmont sites. This contrasted with about 5% more total C in the surface than at depth at the other sites (site × depth: $P < 0.001$). Thus, for example, while there was no difference in total C in non-nest soils between surface and sub-surface, there was almost 60% more total C in nest soil at the surface (0.81%) compared with sub-surface nest soil (0.51%; nest × depth: $P < 0.001$, Fig. 6). There was a significant site

by nest by depth effect on EC ($P = 0.025$, Table 5). On Sandplain soils, EC changed relatively little with depth on the nests, but doubled with depth off the nests. However, at the Drainage Basin site, EC was significantly higher in the topsoil on the nest, but higher in the subsoil off the nest. There were no other significant three- or four-way effects (Table 5).

Discussion

Despite the variation in soil type across the Mt Summerford watershed and the different nest morphologies of the two ant species, broad trends emerged in the effects of ants nests on water infiltration and soil nutrients. These trends have implications for how we view the effects of ants on soil processes in arid environments. First, water infiltration was generally faster through nest soils than non-nest soils. Second, there were generally greater nutrient concentrations on nests compared with non-nests despite the fact that soil chemical properties varied markedly among the different sites. While broad trends emerged, the magnitude of ant nest effects on soil were both species-specific and landscape position-specific, thus our results also highlight the complexity of generalising about the effects of ant nests on water movement and soil properties. Our study also provides strong evidence for a top-down, landscape-level control on ant distribution, which manifests itself in the

Fig. 5 Mean percentage sand, silt and clay for nest and non-nest soils for each of the five landscape positions. UP = Upper piedmont, LP = Lower piedmont, DB = Drainage basin, MA = Midslope alluvium, S = Sandplain
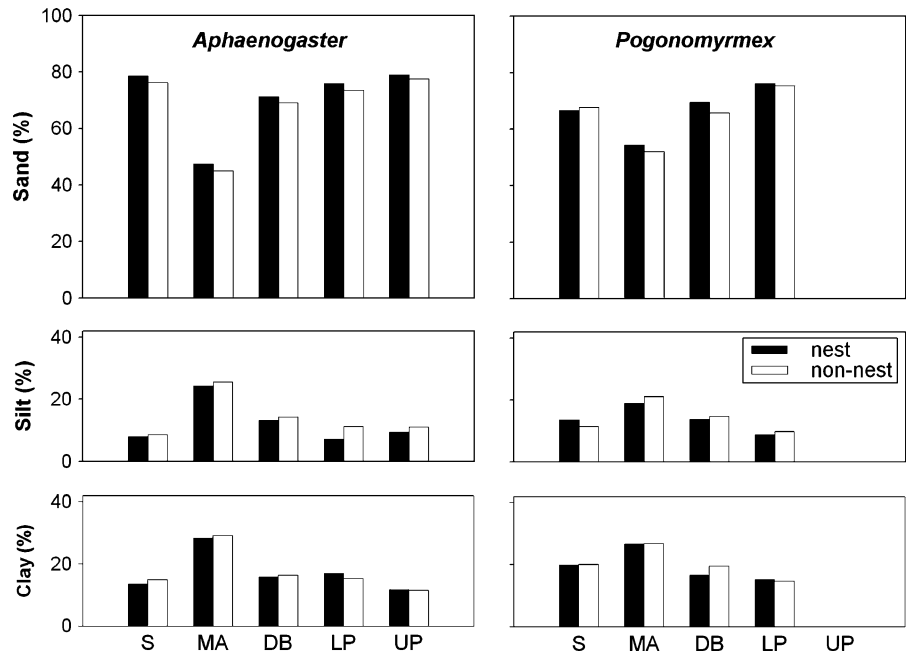

Table 5 ANOVA structure and significance levels for a range of soil physico-chemical tests

Source by stratum	df	BD	EC	pH	C%	N%	S%	P	%Clay	%Silt	%Sand
Rep × Site × Species											
Site	4		<0.001		<0.001	<0.001		0.042	<0.001	<0.001	<0.001
Species	1										
Site × Species	3									0.023	0.045
Residual	18										
Rep × Site × Species × Nest											
Nest (nest versus control)	1		<0.001		<0.001	0.002	0.017	<0.001			0.042
Site × Nest	4										
Species × Nest	1										
Site × Species × Nest	3										
Residual	18										
Rep × Site × Species × Nest × Depth											
Depth	1		<0.001	0.005			<0.001	<0.001	<0.001	<0.001	<0.001
Site × Depth	4			0.050	<0.001			<0.001	0.003	0.007	<0.001
Species × Depth	1										
Nest × Depth	1		0.006	0.031	<0.001		0.045	0.022			
Site × Species × Depth	3		0.006								
Site × Nest × Depth	4		0.025								
Species × Nest × Depth	1										
Site × Species × Nest × Depth	3										
Residual	36										
Total	107										

Only tests significant at $P < 0.05$ are shown. BD = bulk density, C and S were $\log_e$ transformed

Table 6 Trends in soil nutrient concentrations with depth, and corresponding F-statistics and P-values

Attribute	Depth			
	0–1 cm	1–5 cm	F	P
Total C (%)[#]	0.66[a]	0.73[a]	2.21	0.146
Total N (%)	0.05[a]	0.04[a]	2.27	0.141
Total S (%)[#]	0.002[a]	0.001[b]	22.43	<0.001
Available P (mg kg^{-1})	25.7[a]	8.0[b]	431.78	<0.001
EC (dS m^{-1})	0.09[a]	0.11[b]	42.50	<0.001
pH	8.5[a]	8.6[b]	9.11	<0.001

Within an attribute, different superscripts indicate significant differences between nest and control, ant species or depths.
[#] log$_{10}$ transformed

differences in altered nest densities of both species across the watershed.

We recorded densities of between 0 and 89 ant nests ha^{-1}, close to the reported range of 20–150 nests ha^{-1} (e.g. Whitford 1978; Whitford and Bryant 1979; Whitford et al. 1976; Chew 1995; MacMahon et al. 2000). Although nests occupied only 1.5–1.9% of the surface area across the Mt Summerford watershed, in other western United States deserts they have been known to occupy more than 20% of the soil surface (Willard and Crowell 1965). The distribution of ants across a watershed often reflects small-scale changes in resource availability, habitat quality, or competitive interactions with other ants (Chew and DeVita 1980), with a mosaic of different

ant species occurring within a given landscape location. Given the importance of seed in the diet of the two ant species we studied, nest densities are likely to reflect differences in the spatial pattern of vegetation at both landscape (e.g. shrubland versus grassland) and patch (individual plant or shrub hummock) scales (Wagner et al. 2004). Competition may also be a factor, as apart from the Upper Piedmont site, low densities of *Aphaenogaster* nests were associated with high densities of *Pogonomymex* nests and *vice versa*. This is interesting, given that other studies have shown *P. rugosus* indirectly facilitates *A. cockerelli* through its interference with, and local exclusion of *Pogonomyrmex desertorum* that competes with *A. cockerelli* (Davidson 1985). The size and persistence of nests over decadal time scales, up to 30 years (Chew 1995; Whitford personal observations), suggest that any landscape-level effects of these ants are likely to be substantial and long-lived.

Water infiltration in relation to nest and landscape position

Water flow through both macropores and micropores was faster through nest soils compared with non-nest soils at all sites with the exception of the Sandplain site, and this effect was consistent for both the early (sorptivity) and later (steady-state infiltration) phases of water infiltration. This result is consistent with

Fig. 6 Mean (±SEM) values for electrical conductivity (EC), pH, total carbon (C) and available phosphorus (P) on nests and non-nests for surface and sub-surface soils
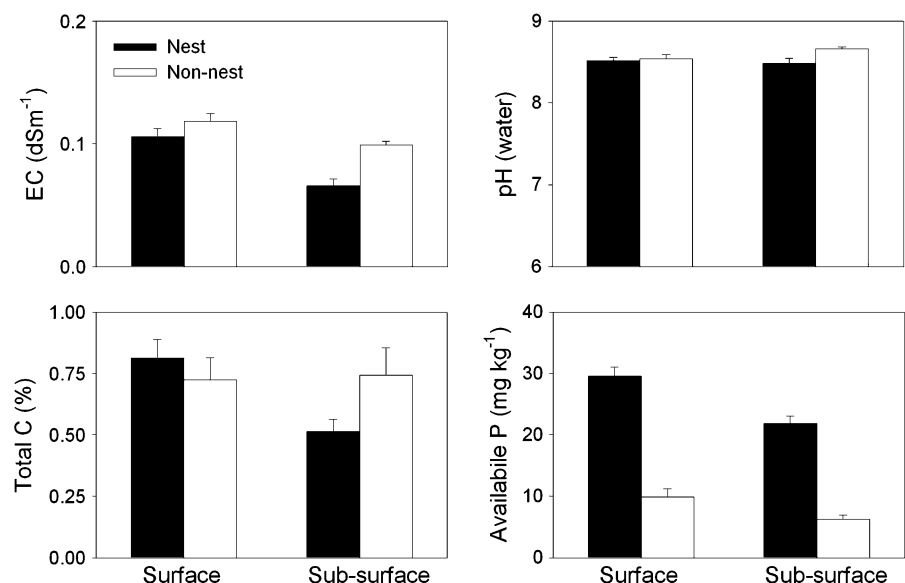
other studies which generally show increased infiltration on ant nests (Lobry de Bruyn and Conacher 1990; Eldridge 1994; Green et al. 1999; Lei 2000), with the exceptions of Wang et al. (1996), who found decreased infiltration on nests due to ants closing the nest entrances, and Cammeraat et al. (2002) who demonstrated that infiltration through nests depended on initial soil water content and the amount of organic debris present. In our study, the lack of a clear nest effect under ponded conditions at the Sandplain site was probably due to the sandy soil type, which showed rapid infiltration of water through both nest and non-nest soils. The overriding effect of soil type on infiltration would be due to the much larger micropores in sandy soils compared with those in soils with a greater silt and clay content. We would expect high rates of saturated hydraulic conductivity in sandy, freely draining soils, even in the absence of macropores (McAuliffe et al. 2007). Further, low clay levels in Sandplain soils (7–10%, Gile et al. 1981) mitigate against the formation of soil aggregates, further restricting the formation of stable macropore channels. Differences could also be due to the presence of complex phenomena in the soil such as coarse sand lenses, vesicular pores near the surface or even slight differences in texture which could force large volumes of water flow laterally rather than horizontally (Ribolzi et al. 2006). At the other sites the influence of ant nests on infiltration differed, with water flowing eight times faster into nests than non-nests at the Midslope Alluvium site, while there was only a three-fold increase in water infiltration at the other sites. We believe that the differences in particle size of the Midslope Alluvium soils compared with other sites may explain the low levels of infiltration through non-nest soils at this site.

The differences in infiltration between nest and non-nest soils were driven by the greater number of macropores on ant nests. This is confirmed by the large macropore index we recorded across all sites except the Sandplain site. This result is consistent with those from other studies that largely attribute increased infiltration on ant nests to macropore flow (e.g. Laundre 1990; Eldridge 1994; Lei 2000). On ant nests, both sorptivity and steady-state infiltration under ponding were faster at landscape positions with coarser soils. A doubling of the coarse and medium sand-sized fraction in nest soils from 25 to 50% corresponded with 170% increases in sorptivity and 60% increases in

steady-state infiltration under ponding. However, the correlation between this coarse fraction and water infiltration was not significant under tension, where macropores were bypassed, or in inter-nest soils. We conclude therefore that water infiltration through nests and non-nests is influenced more by the macropore status of the soil than the texture of nest soil, and that coarser-textured soils may be associated with a propensity to form macropores.

The macropore index for *Pogonomyrmex* was greater than that of *Aphaenogaster* at all sites. *P. rugosus* builds large disc-shaped nests which are level to slightly convex (Fig. 2a), while *A. cockerelli* nests are much smaller (<15 cm across and 10 cm tall) constructed around the base of shrubs or grasses (Fig. 2b). The nests of both species contain a central tunnel that extends to a depth of at least 300 cm (Whitford 1973; MacKay 1981). Generally across all sites, sorptivity under ponding was significantly faster on *Pogonomyrmex* than *Aphaenogaster* nests, but the opposite was observed under tension, when macropores were prevented from conducting water. Greater sorptivity through matrix pores on *Aphaenogaster* nests could be due to differences in the physical arrangement of surface soils such as compaction of soil particles. Equally, *Aphaenogaster* nests could have been constructed on soils with inherently greater levels of microporosity. Our observations of similar values of sorptivity under tension between nest and non-nest for both species suggest similar levels of micropore structure between nest and non-nests at all sites, and suggests that instead of altering arrangement of soil particles, ants may be selecting nest sites with soils of a particular matrix pore structure. Clearly, however, additional information is required such as thin-section analysis of surface soils at nest and non-nest sites of both ant species before we can account for differences in matrix pore flow in the early phase of infiltration. Notwithstanding these observation, the higher rates of infiltration under tension through nest soil of *Aphaenogaster* may explain the lack of a significant macropore effect on *Aphaenogaster* nests as the macropore index can be strongly influenced by high rates of sorptivity, i.e. the magnitude of the denominator in Eq. 1.

Soil nutrients in relation to landscape,
nest and species

We found higher concentrations of N, S and P, and increased soil C in nest soil compared with non-nest

soil. This is consistent with studies that have found that *Pogonomyrmex* nests contain higher amounts of nutrients and organic matter (Whitford 1988; Carlson and Whitford 1991; Friese and Allen 1993; Whitford and DiMarco 1995; Friese et al. 1997; Wagner et al. 1997, 2004; Lei 2000; Snyder et al. 2002; Wagner and Jones 2006; Whitford et al. 2008). This suggests an abundant community of soil microbes in *Pogonomyrmex* nest soils which would encourage greater rates of litter decomposition and N mineralisation (Wagner and Jones 2006). Harvester ants are known to discard protein-rich material around the corona of their nests (Mackay 1985), store material below-ground, and deposit faeces directly onto the soil surface (Whitford et al. 1976; Wagner et al. 2004). Their activities, which directly affect nutrient and microbial processes, may be as important as the effect that they have on the flow of water through soils (MacMahon et al. 2000).

We expected differences in the effects of nests across sites, as landscape-level processes also affect the distribution of nutrients around ant nests. Flooding from intense convection storms during summer frequently deposits rabbit faeces, litter and woody debris onto ant nests at lower watershed positions (Nash and Whitford 1995; Snyder et al. 2002). In this study however, although C, N and available P levels varied greatly among sites, the relative effects of nests on C, N and available P remained consistent across sites and between ant species. This result differs from other studies of multiple landscapes that have generally found a differential landscape-level effect of ants. For example, Folgarait (1998) demonstrated that the differences between nest and non-nest soils tended to be more pronounced in soils of low organic matter content. Similarly, Whitford and DiMarco (1995) demonstrated large landscape-level effects of ants in the Jornada Basin, with *P. rugosus* nest soil more nutrient-enriched at mid-slope positions than at the lower locations in a watershed. Although our study and most others (Lobry de Bruyn and Conacher 1990) show a consistent increase in nutrients on ant nests, generalisations about nutrient enrichment should be made with caution. Sometimes increases are small or negligible (Lobry de Bruyn and Conacher 1990) and the magnitude of the effect may be determined by landscape-level factors (Folgarait 1998; Whitford and DiMarco 1995).

Despite the many studies of the effects of ants on ecosystem processes (Lobry de Bruyn and Conacher 1990; Decaëns et al. 2002; MacMahon et al. 2000; Folgarait et al. 2002), few studies have questioned the universality of their effects. The general trends arising from our study in the Jornada Basin support the results of previous research that water infiltration is greater on ant nests due to greater levels of macroporosity, and that C, N and P levels are greater on ant nests compared with surrounding soils. However, our study has also shown that the magnitude of these effects may differ across landscapes due to differences in soil types. Major differences in ant effects among sites are also likely to result from substantial variation in nest densities across the watershed.

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