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Effect of Ants on Sandy Soils in Semi-arid Eastern Australia: Local Distribution of Nest Entrances and their Effect on Infiltration of Water

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Abstract

The influence of the funnel ant (*Aphaenogaster barbigula*) on water infiltration was studied on an aeolian soil in a semi-arid *Callitris glaucophylla* woodland in eastern Australia. At the study site at Yathong Nature Reserve, densities of up to 37 nest entrances m^{-2} were recorded in some areas, equivalent to a density of 88 000 entrances ha^{-1} over small areas or 0·9% of the surface area of the landscape. Seventy-two per cent of the entrances were actively being used by the ants. Steady-state water infiltration on soils with entrances averaged 23·3 mm min^{-1} which was about four times that on entrance-free soils. As the diameter of the nest entrance increased, water penetrated deeper into the soil. The results provide further evidence that ants have a marked influence on redistribution of water in semi-arid environments.

Keywords: *Aphaenogaster barbigula*, soil biota, ant nests, infiltration, semi-arid woodland, aeolian soil.

Introduction

Soil surface conditions have a major influence on runoff and erosion processes, particularly in arid and semi-arid areas where vegetation cover is often low (Scoging 1989). In these semi-arid environments, soil invertebrates such as termites and ants play an important role in infiltration, bioturbation and the movement of soil material (Lee and Wood 1971). More recently, the role of invertebrates has received renewed attention, particularly in relation to soil modification (Lobry de Bruyn and Conacher 1990) and soil structure (Lee and Foster 1991).

Although there is a large body of literature on the influence of termites on soil processes in semi-arid areas, little has been documented on the role of ants in water infiltration. Ants could affect water infiltration by their influence on soil macroporosity and through nest openings at the surface. Increasing porosity through construction of channels, particularly those with openings at the surface, would be expected to enhance water movement through the soil (Lobry de Bruyn and Conacher 1990). Alternatively, repacking of the soil through bioturbation might decrease water infiltration by increasing the soil bulk density.

Funnel ants (*Aphaenogaster* spp.) are found throughout eastern and southern Australia where their colonies have conspicuously large (10–20 mm diameter) and often multiple entrances, each surrounded by a raised crater of soil (torus) up

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to 150 mm high (Anderson 1990). Construction of the tori appears to be more pronounced where the soils are aeolian in origin. In these aeolian environments, the ants and their associated entrances occur as either scattered individuals or in massive subterranean colonies occurring over many hundreds of square metres.

At Yathong Nature Reserve in semi-arid eastern Australia, nest openings of the funnel ant (*Aphaenogaster barbigula*) are common on grazed and ungrazed rangeland dominated by white cypress pine (*Callitris glaucophylla*) or mallees (*Eucalyptus* spp.). Field observations suggested that where these ants occur in large subterranean colonies, they play an important role in altering both the physical properties of the soil and its hydrology.

The presence of a massive colony at Yathong Nature Reserve presented an ideal opportunity to study the dynamics of ant nest entrances and their effects on the physical and hydrological properties of an aeolian soil. The objectives of the study were twofold: (i) to determine the distribution and morphology of nest entrances on the Nature Reserve, and (ii) to quantify the effect of the entrances on soil hydrological properties. Specifically, it was intended to determine the spatial variability in density of nest entrances and the relationship between nest entrance size and nest volume. A disc permeameter was used to determine the relationship between nest entrance size and ponded water infiltration, to determine whether these distinctive structures had a significant effect on the infiltration and depth to penetration of water on a semi-arid aeolian soil.

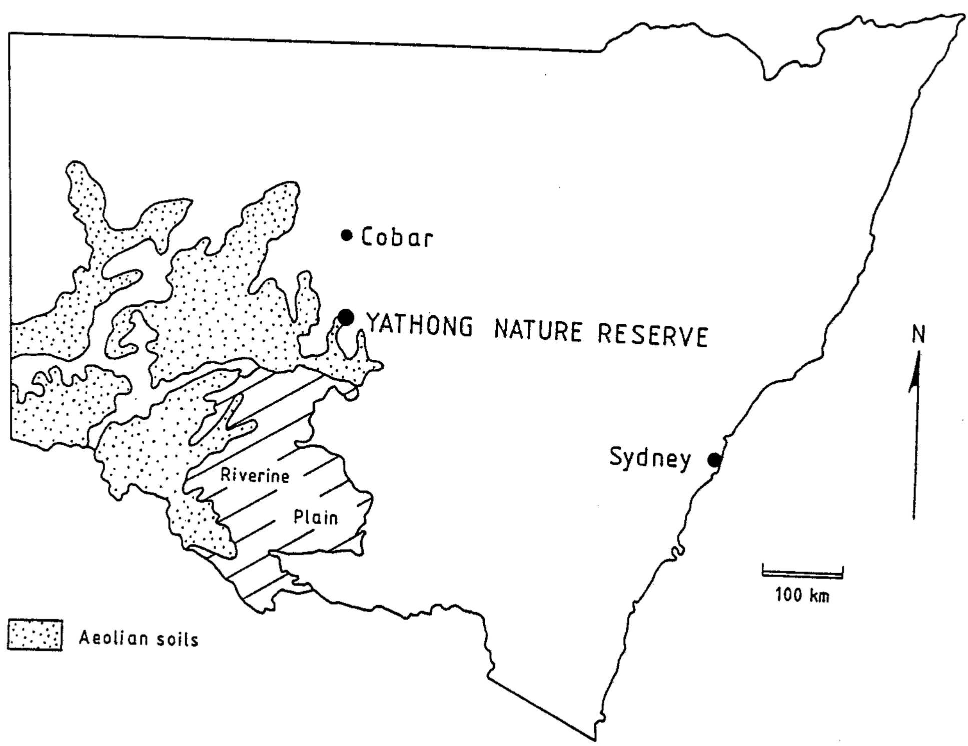

Fig. 1. Location of the study area in semi-arid western New South Wales.

Methods

The Study Area

The study area was Yathong Nature Reserve (32° 56′ S., 145° 35′ E.), which covers an area of 107 000 ha and is located approximately 140 km south-west of Cobar in western New South Wales (Fig. 1). Sheep grazing on native pastures is the principal land use in the region but the Nature Reserve has not been grazed by sheep or cattle since 1977. It is currently grazed, however, by large populations of rabbits (*Oryctolagus cuniculus*), Grey and Red kangaroos (*Macropus giganteus*, *M. fuliginosus* and *M. rufus*) and feral goats (*Capra hircus*; Leigh *et al.* 1989).

The vegetation at the study area is an open woodland dominated by white cypress pine (*Callitris glaucophylla*) and scattered red box (*Eucalyptus intertexta*). Small ephemeral forbs form a sparse understory. Cryptogamic crusts of mosses, blue-green algae (cyanobacteria) and some lichen were present on some surfaces. The soil type is a brownish or calcareous sand (Stace *et al.* 1968) or an Entisol (Soil Survey Staff 1975). Surface textures are sandy loams. Slopes at the study site vary between 1 and 2%.

Measurements

Density and size distribution of ant holes

In May 1991, two transects were established and permanently marked within an area encompassing a large colony of *Aphaenogaster barbigula*. The transects were positioned in such a way as to pass through both open areas and areas under trees. A total of 70 quadrats each 1 m^2 were positioned along the transects. On the first transect, which ran up a 2% slope for a distance of 100 m, 50 quadrats were measured at every second metre. On a second transect, which was approximately 80 m long and ran perpendicular to the slope, 20 quadrats were sampled at approximately 4 m intervals. Transect two was established to study another aspect of the ecology of *Aphaenogaster barbigula*, namely the rate of relocation of nest entrances. For the purpose of this paper, however, data from transect 2 have been included, as measurements were made at the same time as transect 1. This allowed analyses to be made using a larger data set.

For every nest entrance the following variables were noted: internal diameter of the nest entrance, diameter of the torus surrounding the nest entrance (Fig. 2) and, whether the nest entrance was active or inactive at the time. Active nest entrances were defined as those where ants were actually seen in the holes or where the torus around the entrance of the nests showed evidence of recent activity. Spider webs over the nest entrances indicated an inactive state. The optimum time to make nest measurements was mid-morning. This avoided periods when ant activity was low and avoided difficulties in determining the state of activity of the nests. Transects were measured once only.

Nest volume measurements

To determine the relationship between the nest entrance diameter and nest volume, 14 entrance holes spanning the range of sizes found in the general area were chosen randomly in the study area. After measuring the diameters of the nest entrances, wet plaster of Paris was poured into the holes. After hardening, the plaster casts including the central nest section and associated lateral channels were carefully excavated from the soil. The plaster casts and channels were transported to the laboratory and carefully washed and dried. Nest volumes were determined by measuring the displacement after immersing the plaster casts and anastomosing lateral channels in a water-filled measuring cylinder. These measurements formed the basis for developing the relationship between nest entrance size and nest volume.

Infiltration measurements

In November 1992, a disc permeameter was used with a 10 mm head of water and a total disc area of 353 cm^2 to measure ponded infiltration (Perroux and White 1988) on soil surfaces with and without nest entrances. Water infiltration was measured at 29 locations on soil surfaces with nest openings ranging from 5 to 43 mm in diameter, and at 10 control sites

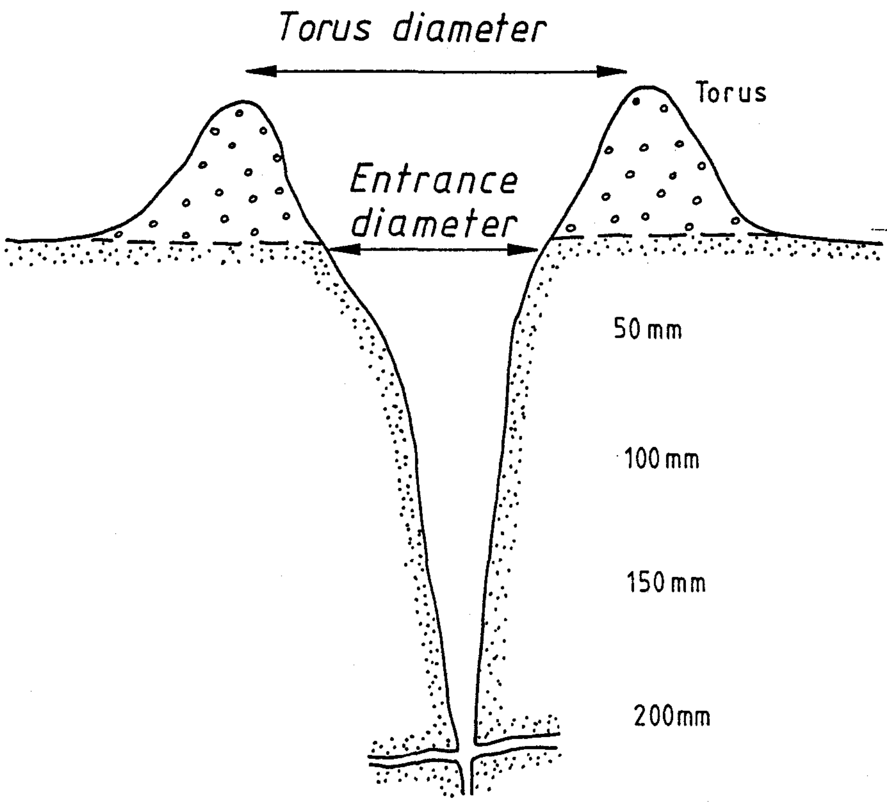

Fig. 2. Vertical cross section of a typical nest of *Aphaenogaster barbigula* based on plaster cast measurements.

with no nest openings. Nest entrances were selected to encompass the full range of entrance sizes found in the study area. A steel ring was pushed gently into the soil around single nest entrances of variable size after the torus had been gently brushed away from around the entrance.

At each location, water infiltration was measured for 30 min. By this time, steady-state infiltration had been achieved at all locations. Steady-state infiltration was calculated according to the method of White (1988). At the cessation of infiltration runs, a section across each plot was carefully excavated and the depth to the wetting front at five points was measured. Wetting front is expressed as a depth per litre of applied water in order to standardize depths between runs receiving different amounts of infiltration. In the absence of data on the relationship between wetting front depth and amount of water in these soils, a linear relationship was assumed between applied water and depth to the wetting front.

Particle size analyses

At four locations within the area of the colony, approximately 50 g of soil was collected from each of six depths in areas between nests (0–50, 50–100, 100–150, 150–200, 200–250 and 250–300 mm) and all soil comprising the tori of 20 nest entrances. Particle size analyses of a 50 g subsample of the torus soil and material from the six depths were undertaken according to Loveday (1974) using the hydrometer method.

Analyses

Simple linear regressions were used to determine the relationship between the dependent variables and the independent variables after testing for normality (Minitab 1989). No data were transformed. Differences in mean infiltration rates were tested using Student t-tests with pooled variance (Minitab 1989). In this paper, all results are expressed as mean±s.e.

Table 1. Diameters (mm) of nest entrance and torus for active and inactive holes

	Entrance		Torus	
	Active	Inactive	Active	Inactive
Mean	15·4	22·0	52·3	80·3
s.e.	0·37	0·78	1·04	2·60
Range	2–50	6–62	12–135	76–85
n	442	176	382	3

Results

Density of Nest Entrances

On a total transect area of 70 m^2, 618 nest entrances were recorded and measured (Table 1). Although this is equivalent to a density of 88 000 entrances ha^{-1}, these densities have not been found over extensive areas (Eldridge and Pickard, unpubl. observations). Seventy-two per cent of the entrances (442) were active, i.e. there was evidence of current usage by ants (Table 1). On any 1 m^2 quadrat, the density of nest entrances ranged from 0 to 37 m^{-2}. On the dense quadrats, entrances occupied up to 0·9% of the surface area of the soil.

Nest Entrance Shape and Size

Nest entrances were circular and averaged 17±0·4 mm in diameter. The main vertical section of the nests extended into the soil to a depth of 110±5 mm (Fig. 2). Radiating out from the main vertical section were a number of horizontal anastomosing channels. These channels, which were variable in size, had a cylindrical cross section and accounted for approximately 32% of the total nest volume.

There was a significant linear relationship between nest volume and diameter of the nest entrance ($R^2 = 0{\cdot}60$, $P = 0{\cdot}0001$, $n = 14$). Inclusion of the depth of the hole as a descriptor variable did not improve the accuracy of estimating nest volume ($R^2 = 0{\cdot}60$, $P = 0{\cdot}0001$, $n = 14$).

Surrounding the nest entrances were torus-like mounds of bioturbate removed from the nest chamber, possibly during nest construction but possibly as a mechanism for capturing prey (Anderson 1990). Observations of the heights of the tori, particularly prior to infiltration runs when the tori were removed, confirmed that they were slightly less than Mitchell's (1988) reported value of 24 mm. The mean diameters of the active and inactive tori were 52±1 mm and 80±3 mm respectively (Table 1). Nest entrances and tori diameters of inactive nests were consistently larger than those of active nests ($P = 0{\cdot}001$; Table 1).

Ponded Water Infiltration

Water infiltration on soils with nest entrances (23±1·8 mm min^{-1}) was significantly faster ($P \ll 0{\cdot}001$) than that on soils without nest entrances

Table 2. Mean, standard error of the mean and median infiltration rates (mm min^{-1}) for soils with and without nest entrances

	Ant nest with entrances	Control soil without entrances
Mean	23·3	5·6
s.e.	1·8	1·4
Median	4·7	24·0
n	29	10

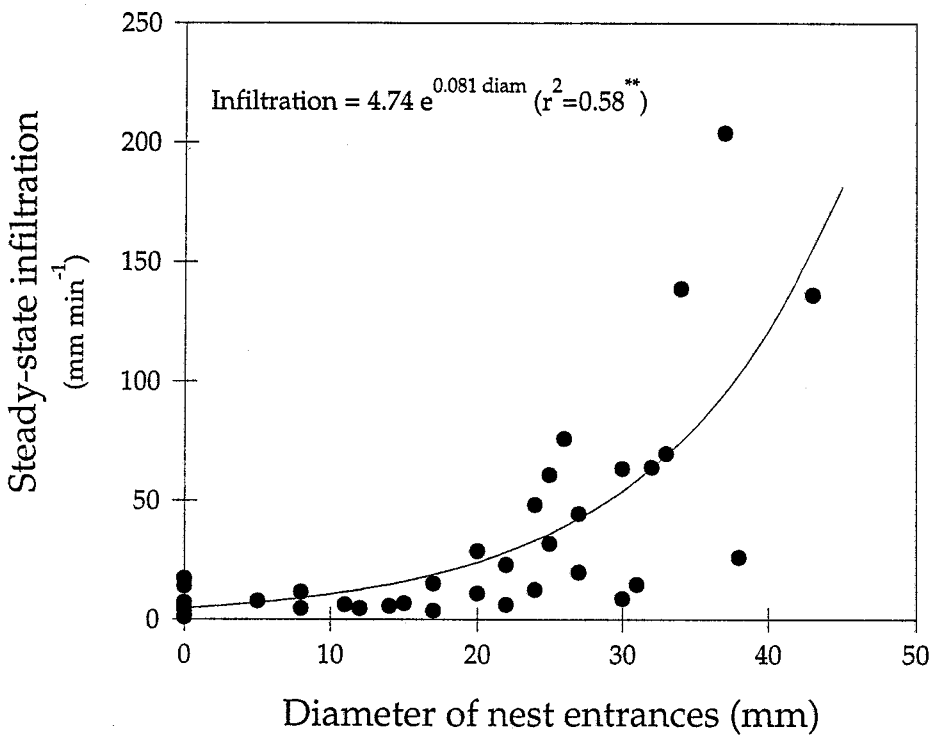

Fig. 3. Relationship between infiltration rate (mm min^{-1}) and entrance diameter of *Aphaenogaster barbigula* nests.

(6±1·4 mm min^{-1}) (Table 2). There was a significant positive relationship between nest entrance diameter and steady-state infiltration measured with the disc permeameter (Fig. 3), thus

$$I = 4{\cdot}743\, e^{0{\cdot}081D} \qquad (R^2 = 0{\cdot}58,\ P < 0{\cdot}001,\ n = 39)\,, \tag{1}$$

where I is the infiltration rate at steady state (mm min^{-1}) and D is the nest entrance diameter (mm).

On pooling all nest entrances, there were no significant relationships between depth to wetting front and either nest entrance diameter or nest volume ($P > 0{\cdot}05$). For nests with volumes <10 cm^3, wetting front depth was independent of nest volume. For nests with volumes 10 cm^3 or greater, however, wetting front increased significantly with nest volume:

$$\mathrm{WF} = 58 \cdot 5 + 0 \cdot 62\,\mathrm{NV} \qquad (R^2 = 25 \cdot 5,\ P = 0 \cdot 004,\ n = 27)\,, \qquad (2)$$

where WF is depth to the wetting front L^{-1} infiltrated water and NV is total nest volume.

Particle Size Analyses

Material in the tori comprised 16·5, 5·0, 54·0 and 24·5% clay, silt, fine sand and coarse sand respectively. There were no apparent differences in particle size distribution between this material and that at any of the six depths sampled (mean = 17·8, 4·1, 54·4 and 23·7 for clay, silt, fine sand and coarse sand respectively).

Discussion

Nest entrances of the funnel ant *Aphaenogaster barbigula* are a common ground feature over extensive areas of semi-arid eastern Australia, particularly where the soils are aeolian in origin. The large number of nest entrances at the site at Yathong Nature Reserve indicated that these soils support huge colonies of these ants.

Density and Distribution of Nest Entrances

At the study site, the average density of *Aphaenogaster barbigula* nest entrances was 8·8 m^{-2}, and on dense quadrats entrances occupied up to 0·9% of the surface area of the soil. As discussed in the Introduction, this represents one end of the spectrum where these ants are concentrated over hundreds of square metres at exceptionally high densities. On similar soils in many other parts of Yathong Nature Reserve, nests occurred at smaller densities or as scattered individuals. At this study site, the density of nest entrances was considerably greater than 1500 m^{-1} reported by Mitchell (1988) for *A. longiceps* in a temperate environment near Sydney. Much lower densities, however, have been reported for other ants. For example, Briese (1982) reported a total density of 3900 holes ha^{-1} for 22 different species of ants on a heavy clay on the Riverine Plain in southern Australia. There the total ant community occupied <1% of the total surface area of the soil. Nests of *Iridomyrmex purpureus* in South Australia occupied 0·4% of the landscape (Greenslade 1974).

Observations of nest entrances suggested that the density of entrances is greater adjacent to trees and fallen timber. Mitchell (1988) recorded that mounds, often crowded together and overlapping, were more common adjacent to logs on the soil surface and around the bases of trees. Concentration of nests near fallen timber may enhance ant survival by reducing the chances of predation, increasing the availability of food supplies or by providing safe sites for the entrance structures. The torus-like structures are easily destroyed by rain splash (Mitchell 1988 and personal observations) so that locating the nest entrances adjacent to or under logs may increase the longevity of these structures. Similarly, the ants may be responding to higher levels of nutrients (e.g. organic carbon and nitrogen) in the vicinity of decomposing logs where they develop into ‘fertile patches’. A similar situation occurs where xylophagous termites occupy mounds formed when branches lying across the slope accumulate wind- and water-borne sediments and nutrients on the uphill side (Tongway *et al.* 1989).

Nest Entrance and Torus Shape

Plaster casts of the ant nests revealed a relatively simple nest structure, with a main shaft supporting associated chambers and galleries. Surrounding the nest entrance was a large volcano-like accumulation of bioturbate. The reason for this torus is unknown. The structure may be designed to capture prey (Anderson 1990), prevent overland flow from entering the nest chamber, or maintain the integrity of the nest entrance. Similar structures around spider burrows are hypothesized to avoid flooding from surface runoff (P. Fairweather, personal communication). It is more likely, however, that the torus is merely a consequence of nest building activities. In the Yathong study, only 3 of the 176 inactive nest entrances had intact tori. The small number of tori on inactive entrances, compared with the large number on active entrances (Table 1), suggests that once the nest entrance is inactive the torus quickly deteriorates. Field observations confirm that once the ants cease clearing material from the entrance, litter (particularly leaves) falls into the holes and rapidly captures sediment, eventually infilling the holes. Inactive holes are usually completely filled within 2–4 months, by which time it is almost impossible to determine where the hole was situated. Rain falling on recently abandoned entrances accelerates the decomposition process.

Although nest entrances reported in this study were sampled once only (May 1991), nest entrance activity is currently being monitored on permanent quadrats in the same area. Preliminary observations suggest that nest entrances are moderately long-lived, remaining active for between 9 and 12 months. Nest entrances have a turnover rate of 2·3, i.e. change their location approximately twice yearly, and at any time period <20% of nests are inactive (Eldridge and Pickard, unpubl. data). This means that although some nest entrances become inactive, ceasing to enhance infiltration over and above that on the control soils, new entrances are continually recruiting. The net result of this death and recruitment of nest entrances is a relatively constant total density of active entrances throughout the year.

Water Infiltration

In contrast with termites and earthworms, there is little direct quantitative evidence of the effects of ant galleries on water infiltration rates. At Yathong Nature Reserve, the presence of nest entrances on loamy sands significantly increased infiltration of water compared with entrance-free soils (Table 2). As nest entrance diameter increased, there was a significant increase in infiltration (Fig. 3) and, for the majority of nest entrances, an increase in the depth of water penetration. On mulga soils in a semi-arid environment in Western Australia, Majer *et al.* (1987) also recorded considerably greater mean infiltration rates on ant nest soils (8·3 min L^{-1}) compared with surrounding soils (27·2 min L^{-1}). These infiltration values are approximately half as fast as those recorded in the present study, but were recorded from nests of four ant species with nest entrances much smaller (2–8 mm diameter) than *Aphaenogaster* spp.

There is no evidence that the presence of cryptogamic soil crusts on the control soils contributed to lower infiltration rates. Nor is there evidence that soil surface conditions were markedly different between control and ant nest soils, except that control areas, being devoid of nest entrances, had a slightly greater area available for vegetative cover. Other work at Yathong Nature Reserve has shown that infiltration is independent of cryptogam cover, but strongly influenced by soil physical properties on soils with a high macroporosity status (Eldridge 1993). A more obvious explanation for increased infiltration on the ant soils therefore is the marked increases in macroporosity resulting from the subterranean galleries and channels associated with the ant colony.

Ants influence infiltration rates through changes in soil physical properties, particularly the mixing of soil particles and their deposition at the surface. Clay enrichment on mound soils compared with nearby non-mound soils has been proposed as being responsible for increases in infiltration and soil moisture status in the surface of nest-occupied soils (e.g. Lyford 1963; Baxter and Hole 1967; Salem and Hole 1968). This was not borne out by this study, however, as the particle size distribution of the nest-free soils at depths to 300 mm was not significantly different from bioturbate on the surface.

Despite the high saturated infiltration rates on the soils at this site, even in the absence of nest entrances, ponding occurs readily on most surfaces. A substantial number of litter trains were observed up to 5 m long, 0·1 m wide and 0·05 m deep at the site after only 24 mm rainfall. Litter trains result from the deposition of sticks, dung and debris carried down the slope by overland flow of water. Deposition occurs when the water flow is impeded. In November 1992, steady rainfall of 59 mm over a five-day period generated sufficient runoff to destroy the tori and inundate the nest chambers in the study area.

Conclusions

Nest entrances of *Aphaenogaster barbigula* are a common feature of some aeolian soils in semi-arid eastern Australia, where they sometimes occur in massive subterranean colonies. In these colonies, nest entrances occupy up to 0·9% of the landscape where they have a marked effect on ponded water infiltration. By influencing patterns of infiltration in these semi-arid areas, *Aphaenogaster barbigula*, like other macroinvertebrates, probably contribute to the development of landscape heterogeneity, albeit on a small scale.

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