Foraging pits of the short-beaked echidna (*Tachyglossus aculeatus*) as small-scale patches in a semi-arid Australian box woodland

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Abstract

Many animals create disturbances on the soil surface while constructing habitat and resting sites, or foraging for food. This soil disturbance, which is sometimes known as biopedturbation, is a major contributor to landscape patchiness in arid and semi-arid environments. In the semi-arid woodlands of eastern Australia, the Short-Beaked Echidna (*Tachyglossus aculeatus*) creates a mosaic of foraging pits close to the canopies of large trees. The effects of pits on physical, chemical and biological properties of soils were compared at seven sites, each with two levels of disturbance (foraging pit vs. surface) and two canopy locations (under the canopy, in the open) associated with two tree species (*Eucalyptus intertexta*, *Alectryon oleifolius*). Foraging pits trapped twice the mass of litter compared with adjacent non-pit surfaces, and there was more litter under the tree canopies than in the open. Pits contained more bark and leaf material, and larger pits tended to trap more litter. Soil electrical conductivity levels were lower in the pits, and although there were greater concentrations of soil nutrients under the canopy, the concentrations of total carbon, nitrogen and sulphur were lower in the pits compared with the surface. Changes in litter mass did not explain differences in soil carbon, nitrogen or phosphorus. Soil in the pit was moister and more porous, and surface temperatures below the litter in the pits about 2 °C lower than at the surface. Respiration was about 30% greater in the pits, and both the early (sorptivity) and late (steady-state infiltration) stages of infiltration were significantly greater in the pits. Soil micro-arthropods were more abundant in the pits, which supported a different complement of taxa, but a similar diversity, to non-pit surfaces. Our results indicate that echidna foraging pits act as substantial resource traps. Given their extensive distribution in semi-arid woodlands, and their marked influence on soil biogeochemistry, echidnas should be seen as important ecosystem engineers in woodland critical for the maintenance of small-scale patchiness and, therefore, the efficient functioning of arid and semi-arid ecosystems.

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1. Introduction

Theoretical predictions, supported by abundant empirical evidence, indicate that arid and semi-arid landscapes function most efficiently when essential resources such as water, nutrients, organic matter and seed are concentrated into discrete patches (Noy-Meir, 1973, 1979; Tongway, 1995). Many arid landscapes are partitioned into two main patch types; those that accumulate resources, also known

as 'fertile patches' or runon zones, and the intervening zones called infertile patches or runoff zones that act as a source of resources, particularly water (Garner and Steinberger, 1989; Schlesinger et al., 1990). This patchiness manifests itself at a range of scales from that of individual plants to whole landscapes (Mauchamp et al., 2001), and the functionality of the landscape is highly dependent on the extent, distribution and maintenance of this patchiness. The degree to which resources are shed or captured within the different patch types is controlled by the interaction of biota (plants and animals) and geomorphology. Changes in the relative influence of biota and geomorphology have

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a strong influence on how the landscape functions, and, therefore, the resulting diversity and productivity of these systems (Ludwig et al., 1997; Hiernaux and Gérard, 1999; López-Portillo and Montaña, 1999).

A major contributor to spatial heterogeneity in arid and semi-arid landscapes is soil disturbance by animals, sometimes termed biopedturbation (Whitford and Kay, 1999; Whitford, 2002). Soil biota 'engineer' the environment, maintaining, creating or modifying habitat by controlling the availability of resources to themselves and/or other organisms without actually consuming these resources ('ecosystem engineers' *sensu* Jones et al., 1994). Engineering of the soil by animals may occur during foraging, or when animals create bedding sites or other habitat, and may be a one-off or continual process such as when they excavate burrows or warrens (Whitford and Kay, 1999; Eldridge and Rath, 2002; Jackson et al., 2003).

Pits created by animals while foraging function as resource sinks, trapping plant litter, seeds, animal faeces, soil and nutrients. Foraging pits affect the distribution of water, the primary limiting resource in arid ecosystems, by increasing infiltration and the water-holding capacity of the soil (Jones et al., 1994). Foraging pits become sites of enhanced physical, chemical and biological properties compared with the surrounding soil matrix. The combination of altered physical and chemical properties increases the probability of seed germination and plant survival (Steinberger and Whitford, 1983), particularly given that pits and are 'hotspots' for seed capture (Reichman, 1984). Increased plant productivity at the microsite scale has a positive effect on biota, and processes linked to plant establishment and higher microbial abundances contribute to patch scale effects. While pits affect resource distribution at microsite scales, these effects are also apparent at the landscape scale (Whitford, 1998; Eldridge, 2004).

One of the most ubiquitous forms of soil engineering by animals in eastern Australia is the mosaic of pits and scrapings created by the Short-Beaked Echidnas (*Tachyglossus aculeatus*), which they create when foraging for epigeal invertebrates. The echidna is a medium-sized marsupial (monotreme) that is widely distributed throughout much of Australia. Echidnas create a range of disturbances (nose pokes, shallow to deep digs, extensive tracts of bull-dozing) while foraging for macro-invertebrates, particularly termites, ants, beetles and worms (Rismiller, 1999). Although we know of no other published studies to support this, anecdotal evidence suggests that this foraging alters the physical and chemical environment of woodland soils and may influence plant germination and establishment.

A recent study in eastern Australia demonstrated that echidnas excavate in excess of $7 \, t \, soil \, ha^{-1}$ while foraging (Kwok, 2005 unpublished B.Sc. Thesis). Given the large volume of soil excavated, and the extensive area over which echidnas forage in semi-arid ecosystems, we predicted that echidna diggings would have a substantial effect on the creation of small-scale patchiness in semi-arid woodlands.

Our study focused on shallow digs, which are generally concentrated around trees, which are themselves nutrient enriched (Ludwig et al., 2004). Echidna diggings, therefore, have the potential to positively feed back on woodland ecosystems by augmenting existing soil physical and chemical properties moderated by the trees.

The aim of our research was to test a number of predictions about the effects of echidna foraging pits (or digs) on litter capture and micro-arthropod habitat, and the chemical and physical properties of soils. Specifically, we predicted that, in comparison with the surrounding soil matrix, pits would: (1) trap and store more litter, (2) have a cooler surface and support soil with more moisture, (3) contain soil with greater concentrations of carbon, nitrogen, phosphorus and sulphur, (4) contain soil with greater infiltration rates, (5) contain soil with higher respiration rates, and, (6) support a more diverse and abundant soil and litter-borne micro-arthropod community. We tested these predictions by examining pits and non-pits and their associated soils in a semi-arid woodland in eastern Australia supporting an active echidna population, as evidenced by their number and density of digs.

2. Methods

2.1. Study area

The study was conducted at Yathong Nature Reserve, which is located approximately 140 km southwest of Cobar in western New South Wales, Australia (32°35′S, 145°35′E). The study site, in semi-arid woodland, was partially cleared in the mid-1900s. Soils within the Reserve are classified as Kandosols (Isbell, 1996) which are characterised by loam to clay-loam surface soils up to 1 m deep overlying light-medium clay B horizons. These soils are gradational, with gradual changes in texture and structure with depth. Detailed profile descriptions are given in Eldridge and Greene (1994). The vegetation is typically open woodland dominated by red box (*Eucalyptus intertexta* R. Ba.), white cypress pine (*Callitris glaucophylla* J. Thompson and L. Johnson) and wilga (*Geigera parviflora* Lindl.). The midstorey component consists of shrubs of the genera *Dodonaea*, *Senna* and *Acacia*, and the understorey was dominated by perennial grasses such as speargrass (*Austrostipa scabra* (Lindl.) S.W.L. Jacobs and J. Everett), white-top grass (*Austrodanthonia caespitosa* (Gaudich.) H.P. Linder) and No. 9 wiregrass (*Aristida jerichoensis* (Domin) Henrard). In most years the herbaceous vegetation occupies approximately 30–40% of the soil surface, with a similar proportion of the surface occupied by biological soil crusts (Eldridge and Greene, 1994). The average annual rainfall is 385.4 mm (BOM, 2005) but is highly temporally variable. Mean daily temperatures in summer (January) ranges from 11.1 to 46.7 °C (range 33.2–18.2 °C; BOM, 2005).

2.2. Experimental design

Samples were collected from seven sites (blocks), each separated by at least 1500 m. Within each site we sampled under two tree species used extensively by foraging echidnas, *E. intertexta* and *Alectryon oleifolium*. These trees have markedly different canopy morphologies and leaf shape and, therefore, might be expected to produce litter with different decomposition characteristics and soil of differing chemical status. However, mean specific leaf area of *Eucalyptus* leaves ($39.4 \pm 1.4\,cm^2\,g^{-1}$; mean $\pm$ SEM) was not significantly different from *Alectryon* leaves ($48.93 \pm 5.2\,cm^2\,g^{-1}$; $t_{9,0.05} = 1.805$, $P = 0.105$). *E. intertexta* has a wide canopy, up to 15 m in diameter, and trunks up to 900 mm diameter at breast height (d.b.h.). *Alectryon oleifolius* was a medium-sized tree with a smaller canopy ($\sim$5 m diameter), d.b.h. of 120–350 mm that densely shaded the soil surface.

All measurements were made from within pits and on the soil surface adjacent to the pits at two microsites associated with each tree species, i.e., under the canopy and out in the open, in order for us to determine possible interactions between pits and canopy locations. Therefore, for each of the seven sites there were two tree species (*Eucalyptus*, *Alectryon*) by two canopy treatments (open and canopy) by two pit treatments (pit and surface) resulting in a total of 56 samples. In the study area, there are typically many more pits under trees (13.4 pits tree^{-1}) compared with an equivalent area in the open (3.0 pits; Kwok 2005). Pits under tree canopies average 400 mm long (range = 120–560 mm), 310 cm wide (90–340 mm) and 90 mm deep (20–280 mm). Pits in the open are slightly smaller (330 mm × 260 mm × 90 mm), and are generally found at the edges of the canopy.

All pit samples were from echidna pits of similar age and size. We used pit characteristics such as the shape of the pit and the angle of the leading edge to select pits of a similar age. We are confident that we could estimate pit age as we have been monitoring pits at Yathong over the past year. For each pit we measured its length and width through the centre, and its depth. The product of these three measures was used to calculate pit volume, using algorithms developed for a large number of pit types in the area (James and Eldridge, unpublished data).

2.3. Soil chemical and physical properties

Approximately 200 g of soil was taken from the bottom of the pits and a similar amount from the adjacent surface to examine whether pits accumulated greater concentrations of nutrients compared to the soil matrix. Soil was collected from the top 2 cm at the surface and in the pits. We determined total nitrogen, carbon and sulphur content of the soils using a high-combustion LECO CNS-2000 Analyser, the available phosphorus test (Rayment and Higginson, 1992), and pH (1:5 soil water and NH$_4$Cl extract) and electrical conductivity using a 1:5 soil–water

suspension shaken for 1 h. Active carbon was also determined using a simplified laboratory method whereby slightly alkaline, dilute KMnO$_4$ reacts with the readily oxidisable (active) carbon, converting Mn(VII) to Mn(II), and lowering the absorbance of 550 nm light (Weil et al., 2003). Apart from the study of litter micro-arthropod diversity and infiltration (described below), all measurements were made on pit or non-pit soil from which the litter had been removed.

To examine whether there was greater water accumulation within the pits, soil samples were collected, below any surface litter, from undisturbed cores 100 mm high × 70 mm wide at each pit and non-pit location ($n = 56$ samples) and the percent moisture content of the soil determined after drying at 105 °C for 24 h. The same sample was used to determine the bulk density of the samples.

2.4. Litter mass, soil respiration and temperature

Litter was collected from pits and the surrounding soil surface to see whether pits trapped more litter than the surface. Samples were collected from an area of $0.04\,m^2$ in both pit and adjacent non-pit microsites, sorted into bark, leaves, twigs and other (seed, insect remains, animal scats, feathers, grasses and other plant parts such as roots), and weighed separately. We used a laser thermometer to measure ambient temperature and the temperature above and below the litter in pits and on non-pit surfaces.

Respiration rates of soil from pits and surface soils were measured using the method of Anderson (1982). Soil was sieved to remove organic matter, ensuring that CO_2 production emanated from soil microbes and did not include respiration from plant roots. We rewetted 30 g of soil to field capacity, and placed it in a volumetric flask with 5 ml of water and a 10 ml container of NaOH to absorb any CO_2 produced. Flasks were incubated for 3 days at 26 °C before the NaOH was titrated with hydrochloric acid to determine the amount of CO_2 produced. Respiration was expressed as the amount of CO_2 ($mg\,g^{-1}\,soil\,d^{-1}$) produced from the soil (Anderson, 1982).

2.5. Water flow through the soil

We measured sorptivity ($mm\,h^{-0.5}$), the early phase of infiltration, and steady-state infiltration ($mm\,h^{-1}$), the final stage, at all 56 locations with disc permeameters at a supply potential of $+10$ mm (ponded; Perroux and White, 1988). The permeameter was placed on a steel ring of 220 mm internal diameter, which was gently pressed into the soil to a depth of about 7–10 mm and sealed with moistened soil along the outside edge to prevent leakage of water. In all cases the pit made up more than 80% of the area of the ring so that infiltration was almost entirely through the pit. Litter on the soil surface was left intact to ensure that the surface was as natural as possible and because its removal

may have resulted in the structural breakdown of the surface when water was applied through the permeameter.

Water flow was measured within the pit and adjacent to the pit. The permeameter was run for approximately 30 min, by which time steady state had been achieved. Sorptivity was calculated according to the method of Wooding (1968), and steady-state infiltration according to White (1988).

2.6. Soil and litter micro-arthropods

To determine whether pits supported a more diverse and/or abundant micro-arthropod community, intact samples of soil were collected in cores 100 mm high × 70 mm diameter. Cores were collected soon after sunrise (before 0700 h), as studies have indicated that micro-arthropods migrate back into the soil as ambient temperature increases (Cepeda-Pizarro and Whitford, 1989). Litter was collected from within a circular quadrat 70 mm in diameter (0.004 m^2) in both the pit and the adjacent non-pit surface. Micro-arthropods were extracted from both soil and litter using Tullgren funnels (Wallwork et al., 1985) over a period of 5 days over water using a 60 W heat source over each funnel. The light source was moved closer to the surface of the cores over time in order to produce a heat gradient. Micro-arthropods were examined under a dissecting microscope, identified to order, and enumerated.

2.7. Statistical analyses

Data were checked for homogeneity of variance, independence and normality using Levene's test and other diagnostic tools with the Minitab (1997) statistical package. Data were transformed, where necessary (generally log_{10}, square root) to meet these assumptions. Differences in soil nutrient concentrations, bulk density, infiltration rate (sorptivity, steady state infiltration), litter mass, and soil temperature were tested using a balanced split-plot ANOVA with three error terms. The ANOVA was a nested design with multiple error terms. The whole-plot stratum considered Tree Type effects, the sub-plot stratum examined Canopy effects and its interaction with Tree Type, and the sub-sub-plot stratum partitioned Pit and its two- and three-way interactions with Canopy and Tree Type. Least Significant Difference (LSD) testing was used to examine differences in means.

Patterns of micro-arthropod abundance were examined using non-metric multi-dimensional scaling (MDS) based on a Bray-Curtis similarity matrix using Primer (Version 5). The SIMPER subroutine was used to determine which of the micro-arthropod Orders explained most of the dissimilarity between pits and non-pits, Eucalyptus–Alectryon and canopy-open sites. Differences in the abundance of micro-arthropod Orders between pit and non-pit sites and canopy and open sites were determined using ANOSIM which derives a test statistic (Global R) and a significance

level. We used the DIVERSE function in Primer to calculate abundance and three measures of diversity (number of Orders, richness and evenness) for each of the 56 microsites. Differences in these four measures were tested using ANOVA with the same structure described above.

3. Results

3.1. Litter accumulation

Pits contained more than twice the mass of litter (37.2 ± 6.0 g; mean ± SEM) compared with an equivalent area on the soil surface (18.0 ± 3.6 g; $F_{1,24} = 60.63$, $P < 0.001$). There was a greater mass of litter under the canopy (134.9 ± 17.9 g) compared with sites in the open (86.1 ± 20.9 g; $F_{1,12} = 14.25$, $P = 0.003$), but no significant difference in litter mass under Eucalyptus trees compared with Alectryon trees ($F_{1,6} = 0.69$, $P = 0.44$, Table 1). There was no significant difference in surface litter between Alectryon and Eucalyptus, but in the pits significantly more litter under Eucalyptus than Alectryon ($F_{1,24} = 5.25$, $P = 0.03$, Table 1). We recorded more bark ($F_{1,24} = 44.9$, $P < 0.001$) and leaf material ($F_{1,24} = 107.8$, $P < 0.001$) in the pits compared with the surface, and under the canopy compared with out in the open ($F_{1,6} = 11.4$, $P < 0.05$ for bark, $F_{1,6} = 4.8$, $P < 0.05$ for leaf), but no differences between tree species ($P > 0.37$). Pits of larger volume tended to trap more litter ($F_{1,24} = 6.49$, $P = 0.017$); though pit volume explained only 17% of the variance in litter capture.

3.2. Soil chemical properties

For most nutrients there were clear differences between canopy and open microsites, and pit and non-pit microsites (Figs. 1 and 2, Table 2), and a large number of pit by canopy interactions. Under the canopy, electrical conductivity was greater in surface soils compared with pits. In the open, however, the opposite occurred (interaction: $F_{1,24} = 9.05$, $P = 0.006$). Electrical conductivity was also lower in pit soils under Alectryon but greater in pit soils under Eucalyptus (interaction: $F_{1,24} = 52.9$, $P < 0.001$). There were no differences in soil pH in relation to pits ($P = 0.467$). Surprisingly, the concentrations of total nitrogen and sulphur were significantly lower in the pits (0.15%, 0.012%) compared with the surface soils (0.18%, 0.014% for N, S, respectively) while there was no significant difference in total carbon (Fig. 1, Table 2).

Averaged across tree species and pit types, concentrations of active carbon, total carbon, nitrogen and sulphur, phosphorus and EC were significantly higher under the canopies compared with the open sites (Figs. 1 and 2, Table 2). Surface pH did not differ significantly between canopy and open microsites ($P = 0.062$), and while there was no change from the surface to pit under the canopy, values in the pits were markedly greater than the surface out in the

Table 1
ANOVA results for soil chemical and physical analyses

Attribute	Effect	F-statistic	P-value	Effect
Total carbon (%)[a]	Canopy	106.9	<0.001	C>O
	Can*Pit	11.12	0.003	C: P<S; O: P = S
Total nitrogen (%)[a]	Canopy	107.02	<0.001	C>O
	Pit	8.37	0.008	P<S
	Can*Pit	10.42	0.004	C: P<S; O: P = S
Available phosphorus (mg kg^{-1})[a]	Tree	19.84	0.004	E<A
	Canopy	25.38	<0.001	C>O
	Pit	131.03	<0.001	P<S
	Pit*Tree	8.23	0.008	A: P<S; E: P≪S
	Can*Tree	5.88	0.023	A: C>O; E: C≫O
Total sulphur (%)[a]	Canopy	69.82	<0.001	C>O
	Pit	11.24	0.001	P<S
	Can*Pit	10.57	0.003	C: P<S; O: P = S
Active carbon (mg kg^{-1})	Canopy	7.70	0.018	C>O
EC (dS m^{-1})[a]	Canopy	125.62	<0.001	C>O
	Pit	16.57	<0.001	P>S
	Pit*Tree	9.05	0.006	A: P<S; E: P>S
	Can*Pit	52.94	<0.001	C: P<S; O: P>S
pH (1:5 water)	Tree	28.40	0.002	E>A
	Can*Pit	14.90	0.001	C: P = S; O: P>S
Soil moisture (%)[a]	Canopy	24.00	<0.001	C>O
	Pit	58.74	<0.001	P>S
	Can*Pit	6.26	0.020	C: P = S; O: P>S
Bulk density (Mg m^{-3})	Canopy	7.96	0.017	C<O
	Pit	14.72	0.001	P<S
Sorptivity (mm h$^{-0.5}$)	Canopy	19.36	0.001	C>O
	Pit	22.34	<0.001	P>S
Steady-state infiltration (mm h^{-1})[a]	Canopy	32.56	<0.001	C>O
	Pit	32.97	<0.001	P>S
Respiration (mg CO$_2$ g^{-1} soil d^{-1})	Pit	4.47	0.045	P>S

Degrees of freedom = 1,6 (Tree species), 1,24 (Canopy), 1,24 (Pits). E = *Eucalyptus*, A = *Alectryon*; C = canopy, O = open; P = pit, S = surface. Superscripts [a] = $\log_{10}$ transformed; ≪ much less than, ≫ much greater than. Non-significant effects are not shown.

open (interaction: $F_{1,24} = 14.9$, $P = 0.001$). For both total carbon and total nitrogen, nutrient concentration was lower in the pits under the canopy, but not significantly different between pit and surface out in the open (interaction: $F_{1,24} = 11.12$, $P = 0.003$ for carbon, $F_{1,24} = 10.42$, $P = 0.004$ for nitrogen). Similarly for total sulphur, there were no significant differences between pit and surface out in the open, but pit soils had lower concentrations under the canopy (interaction: $F_{1,24} = 10.57$, $P = 0.003$, Table 2).

We detected significant tree species effects only for phosphorus and pH (Table 1). Phosphorus under *Alectryon* trees ($17.3 \pm 2.8\%$) was significantly greater than that under *Eucalyptus* trees ($11.1 \pm 1.4\%$), while pH levels under *Eucalyptus* trees (6.67 ± 0.1) were significantly greater than those under *Alectryon* trees (6.28 ± 0.18; Table 2). There was no significant difference in electrical conductivity

between tree species ($P = 0.84$). There were also some significant pit by tree interactions for phosphorus, with much lower concentrations in the pits than the surface under *Eucalyptus* compared with *Alectryon* (interaction: $F_{1,24} = 8.23$, $P = 0.008$), and was much greater under the canopy compared with the open under *Eucalyptus* compared with *Alectryon* (interaction: $F_{1,6} = 5.88$, $P = 0.023$).

Given the strong links between soil nutrient concentration and the accumulation of litter in the soil (e.g., Burke et al., 1998), we expected reasonable correlations between the mass of litter accumulating under the canopy and the concentrations of total carbon and active carbon in the soil. However, we found no meaningful relationships between either total carbon, active carbon, total nitrogen or phosphorus, and the mass of litter across pits and adjacent soil surfaces, considered either together or separately ($P > 0.07$).
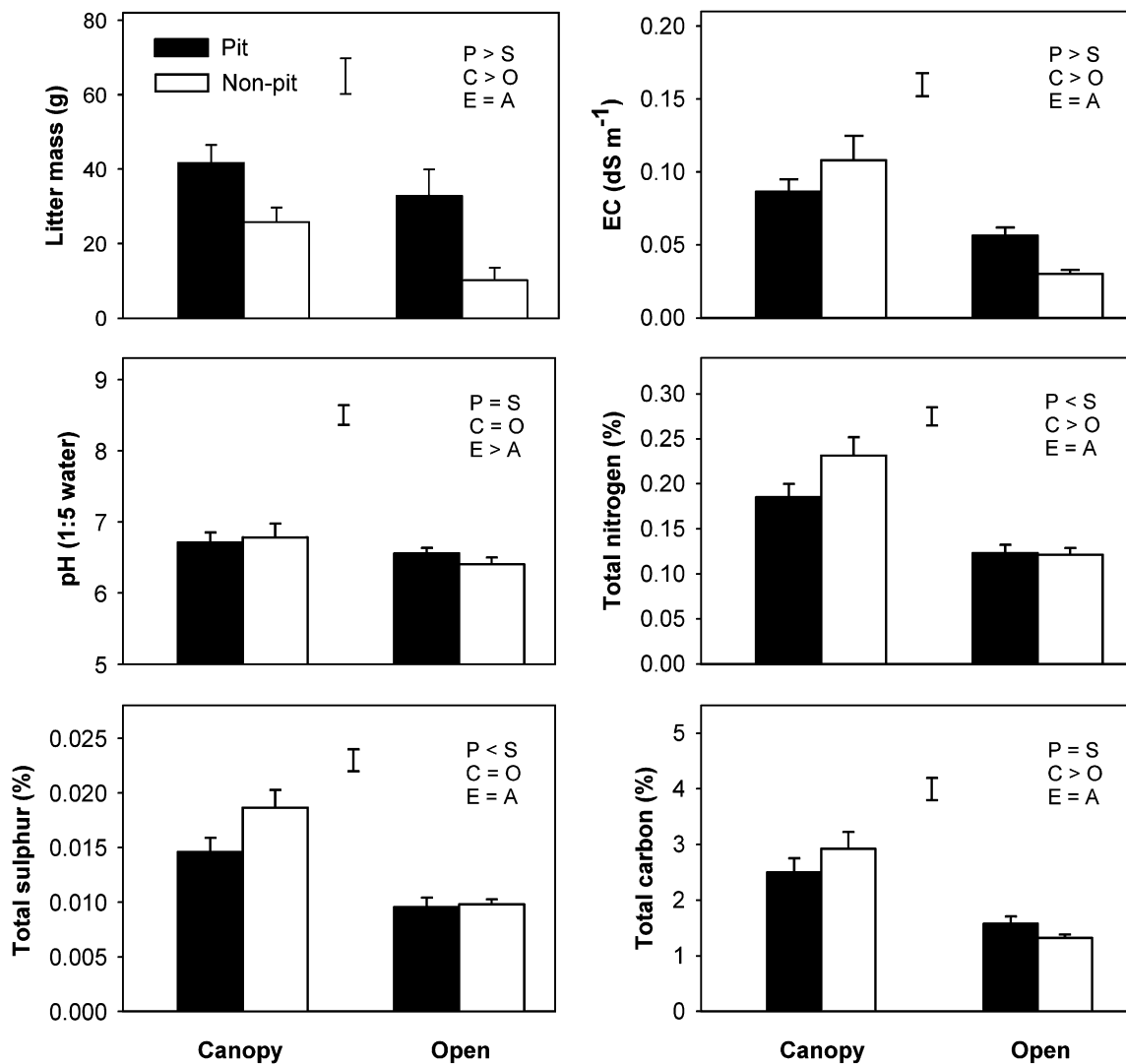
Fig. 1. Mean ($\pm$SEM) litter mass, electrical conductivity, pH, total nitrogen, total sulphur and total carbon in relation to canopy type and pit treatment. P = pit, S = surface, E = *Eucalyptus* A = *Alectryon*, C = canopy, O = open. Bar indicates 5% LSD for interactions.

3.3. Soil physical properties

Soil bulk density was significantly lower in the pits ($1.22\pm0.06\,Mg\,m^{-3}$) compared with the surface ($1.36\pm0.07\,Mg\,m^{-3}$), and under the canopy ($1.22\pm0.06\,Mg\,m^{-3}$) compared with the open microsites ($1.36\pm0.07\,Mg\,m^{-3}$), but there was no significant difference between tree species ($P>0.61$, Table 2). Increases in the mass of litter accumulating in the pits were associated with declining soil bulk density ($F_{1,24}=7.21$, $P=0.012$) but the predictive power was low ($R^2=0.19$).

There were clearly defined differences in soil physical properties between pit and non-pit microsites. Pit soils were significantly moister ($1.7\pm0.2\%$) than non-pit soils ($1.1\pm0.2\%$), and canopy soils ($1.7\pm0.3\%$) were moister than soils in the open ($1.1\pm0.01\%$; Fig. 2, Table 2). However, there was no significant difference in soil moisture between different tree species ($P=0.26$, Table 2). Increases in soil moisture in the pits were much greater

for sites in the open compared with those under the canopy ($F_{1,24}=6.26$, $P=0.02$).

Ambient temperatures were generally high when the survey was conducted ($\sim41\,°C$). Temperatures below litter was significantly cooler in the pits (by $2.2\,°C$) and under the canopy (by $5.1\,°C$) compared with the non-pit and open microsites ($P<0.008$, Table 1), but temperature did not differ significantly between tree species (Table 1). Temperature above the litter was independent of pit, canopy or tree species type ($P>0.05$).

Respiration was about 30% greater in pit soils ($0.18\pm0.04\,mg\ CO_2\,g^{-1}\,soil\,d^{-1}$) compared with surface soils ($0.14\pm0.03\,mg\ CO_2\,g^{-1}\,soil\,d^{-1}$; Fig. 2, but there were no significant difference between canopy and open microsites or between the two tree species ($P>0.62$, Table 2). Although we expected an increase in respiration in response to increasing soil moisture, no significant relationships were detected ($P=0.06$).
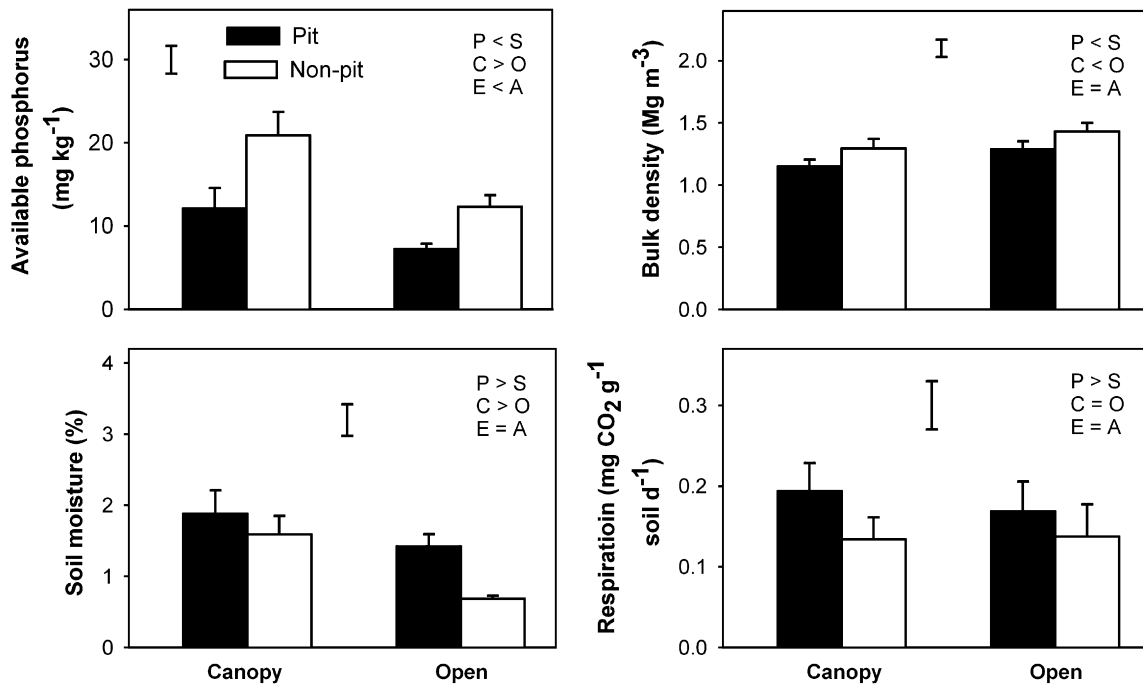
Fig. 2. Mean ($\pm$SEM) available phosphorus, bulk density, soil moisture and soil respiration in relation to canopy type and pit treatment. P = pit, S = surface, E = *Eucalyptus* A = *Alectryon*, C = canopy, O = open. Bar indicates 5% LSD for interactions.

Table 2
ANOVA results for litter, plant and micro-arthropod analyses

Attribute	Effect	F-statistic	P-value	Effect
Temp below litter (°C)	Canopy	30.31	<0.001	C<O
	Pit	8.47	0.008	P<S
Bark mass (g)[a]	Canopy	11.36	0.010	C>O
	Pit	44.97	<0.001	P>S
	Pit*Tree	9.10	0.006	S: E = A; P: E>A
Leaf mass (g)[b]	Canopy	4.81	0.051	C>O
	Pit	107.77	<0.001	P>S
Twig mass (g)[b]	Canopy	31.51	<0.001	C>O
Other mass (g)[b]	Canopy	8.88	0.011	C>O
Total litter mass (g)[b]	Canopy	14.25	0.003	C>O
	Pit	60.63	<0.001	P>S
	Pit*Tree	5.25	0.031	S: E = A; P: E>A
Number of orders	Canopy	12.87	0.004	C>O
	Pit	5.51	0.028	P>S
Number of individuals (0.04 m^{-2})	Pit	21.37	<0.001	P>S
	Can*Pit	4.94	0.036	C: P = S; P>S
Richness	Canopy	8.23	0.014	C>O
Evenness	Pit	10.56	0.003	P>S

Degrees of freedom = 1,6 (Tree species), 1,24 (Canopy), 1,24 (Pits). E = *Eucalyptus*, A = *Alectryon*; C = canopy, O = open; P = pit, S = surface. Superscripts ^{a} = log$_{10}$ transformed, ^{b} = sqrt transformed prior to ANOVA. Non-significant effects are not shown.

3.4. Water flow through the soil

There were clear differences in infiltration between canopy and open sites, and between pit and non-pit microsites (Table 2, Fig. 3). Sorptivity and steady-state infiltration were about twice as much in the pits ($352.6 \pm 60 \, \text{mm h}^{-0.5}$, $75.9 \pm 17 \, \text{mm h}^{-1}$) compared with the surface ($192.1 \pm 34 \, \text{mm h}^{-0.5}$, $38.0 \pm 6.3 \, \text{mm h}^{-1}$, for sorptivity and infiltration, respectively) and under the canopies ($358.8 \pm 52 \, \text{mm h}^{-0.5}$, $80.1 \pm 15 \, \text{mm h}^{-1}$) compared with out in the open ($185.9 \pm 42 \, \text{mm h}^{-0.5}$, $33.8 \pm 8 \, \text{mm h}^{-1}$, for sorptivity and infiltration, respectively), but there was no significant difference in either sorptivity or steady-state infiltration between the two tree species ($P > 0.05$, Table 2). Increases in soil bulk density were associated with significant exponential declines in steady-state infiltration and sorptivity ($F_{2,53} = 5.8$ and 5.2, $P < 0.01$). Trends were similar when we considered pits and non-pit surfaces separately.

3.5. Soil and litter micro-arthropods

Less than 20 micro-arthropods were extracted from litter, so we present data on micro-arthropods from soil only. We detected clear differences in the complement of micro-arthropods in the pit and non-pit microsites (Global $R = 0.11$, $P = 0.011$), but no significant difference between canopy and open microsites ($P = 0.15$). Mites (Acari) were the most abundant group, accounting for 74% of the dissimilarity between pit and non-pit microsites. Mites, collembola, termites and one ant morphospecies
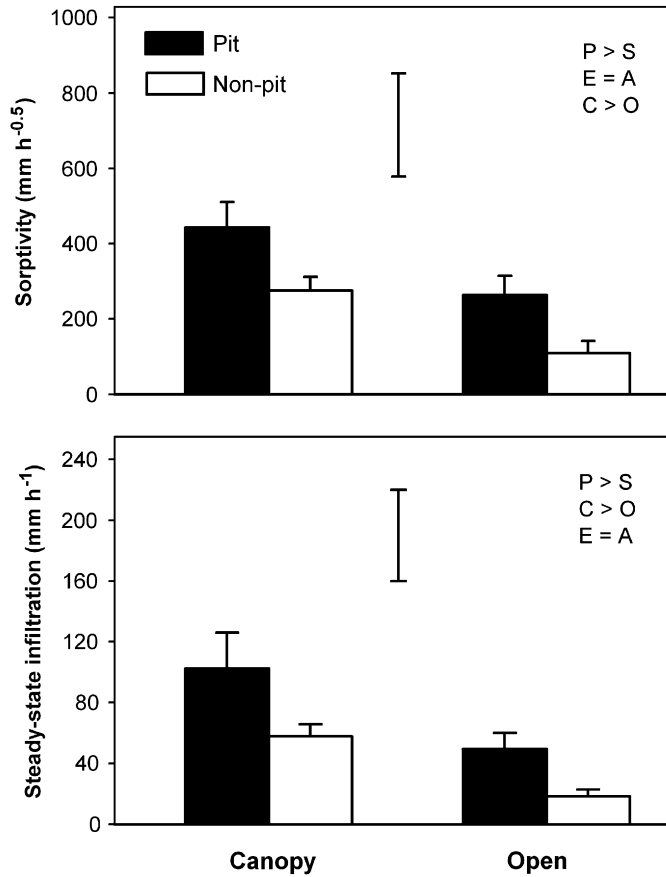
Fig. 3. Mean ($\pm$SEM) sorptivity (mm h$^{-0.5}$) and steady-state infiltration (mm h^{-1}) in relation to canopy type and pit treatment. P = pit, S = surface, E = *Eucalyptus* A = *Alectryon*, C = canopy, O = open. Bar indicates 5% LSD for interactions.

Table 3
Diversity and abundance of morphological groups of micro-arthropods found in pits and non-pit soils

Order	Morphological groups			
	Diversity (no. of morphological groups)		Abundance (individuals 0.004 m^{-2})	
	Pit	Surface	Pit	Surface
Acari	2	2	2621[a]	498[b]
Collembola	2	2	237	146
Isoptera	1	1	51	95
Hymenoptera	8	4	48	84
Pseudoscorpionida	1	1	16	8
Coleoptera	2	0	4	0
Araneae	1	1	2	1
Diptera	1	1	1	1
Hemiptera	0	1	0	1

Different superscripts within a row indicate a significant difference at $P < 0.001$.

(*Iridomyrmex* sp.) accounted for 91% of the dissimilarity between pit and non-pit micro-arthropods.

Significantly, more micro-invertebrate Orders were found in the pits (4.39 ± 0.38) compared with the surface (3.25 ± 0.31; Table 3), and under the canopy (4.46 ± 0.38) compared with the open (3.18 ± 0.30) microsites. The number of individuals was also significantly greater in the pit microsites (106.9 ± 16.2 individuals per 0.004 m^2 of pit) compared with non-pit microsites (30.2 ± 4.9 individuals per 0.004 m^2 of pit), and there was a greater increase in the number of individuals from surface to pit in the open microsites compared with under the canopy ($F_{1,24} = 4.9$, $P = 0.036$). There was no significant difference in the number of Orders of micro-arthropods or the number of individuals between the two tree species. Micro-arthropod richness was significantly greater under the canopy compared with out in the open, but there was no significant difference in richness between *Alectryon* and *Eucalyptus* microsites or pit and non-pit microsites. The evenness of micro-arthropod distribution was significantly different between pit and non-pit microsites (Table 3), but it was not significantly different between tree or canopy microsites. A significantly greater number of mites was found in the pits compared with the surface (Kruskal–Wallis $H = 14.35$, df = 1, $P < 0.001$).

We expected increases in micro-arthropod richness with increasing soil moisture and litter mass given the strong relationships found in other studies (e.g., Cepeda and Whitford, 1989). However, in our study, the richness of micro-arthropods across pits and surface soils together or separately, was independent of changes in moisture and litter mass ($P > 0.314$).

4. Discussion

In this semi-arid woodland, echidna foraging pits captured substantial quantities of organic matter, providing habitat for micro-arthropods and altering some soil biogeochemical properties. Pits trapped twice the mass of litter compared with that remaining on the soil surface (Fig. 1), supporting our first prediction. Eucalypts are known to shed large amounts of woody material (Briggs and Maher, 1983; Eldridge and Rath, 2002), and pits under the canopy captured more litter than those in the open (Table 1). In our study, larger pits (with wider openings) tended to trap more litter. Given that larger pits tended to be deeper and thus have a greater volume, we suggest that litter accumulation is more efficient in deeper pits as it is more difficult for material to be removed once it has been deposited. This may seem at odds with studies of heteromyid rodent foraging pits in the Chihuahuan Desert, where pits with smaller entrances were more effective at trapping and holding litter than pits with larger entrances (Steinberger and Whitford, 1983). Differences between echidna pits and those of other animals probably relate to variation in pit shape, given that echidna pits are larger and shallower, basin-shaped structures compared with the smaller cone-shaped pits dug by rodents. Nonetheless, pits of variable shape and size will hold litter in situ more

effectively than if it remains on the soil surface (Santos and Whitford, 1981; Whitford, 2002). Also, pits are more effective at retaining litter when that litter is covered by soil. Our observations indicate that this occurs when soil is deposited by wind or when kangaroos (or other animals) disturb soil under tree canopies while creating bedding sites (Eldridge and Rath, 2002).

Litter also had the effect of significantly reducing soil surface temperature, though only by a few degrees, but nonetheless supporting our second proposition. Litter is known to moderate fluctuations in soil temperature and reduces losses in soil moisture (e.g., Vossbrinck et al., 1979; Wallwork et al., 1985; Montana et al., 1988; Zaady et al., 1996; Mohr et al., 2005). Lower temperatures would also increase the period over which litter-active micro-arthropods remain above-ground before retreating into the soil as temperature increases (Cepeda-Pizarro and Whitford, 1989). Reduced evaporation resulting from lower temperatures would increase the period over which soil moisture is optimum for microbial decomposition of organic matter (Steinberger and Whitford, 1983; Jacobson and Jacobson, 1998; Whitford, 2002). Further, the observed higher rates of respiration in the pits (Fig. 2) suggests to us greater microbial and micro-arthropod abundance in the pits (e.g., Ayarbe and Kieft, 2000).

We attribute greater infiltration in the pits (Fig. 3) to the greater number of macropores; biopores > 0.84 mm in diameter that are created by invertebrates and plant roots (Devitt and Smith, 2002) and predominate close to the canopies of large trees (Eldridge and Freudenberger, 2005). Echidna digging would also have destroyed the largely hydrophobic biological soil crust (Eldridge and Greene, 1994), reducing runoff from the crust, exposing surface macropores, and resulting in greater levels of infiltration. Pit soils were also more porous, i.e., they had lower bulk densities (Fig. 2), most likely due to greater litter incorporation and greater abundance of soil organisms which increase soil porosity levels (Lee and Foster, 1991). Lower soil bulk density results directly from digging, which aerates the soil (Huntly and Inouye, 1988; Alkon, 1999; Whitford and Kay, 1999; Kerley et al., 2004; Mohr et al., 2005).

The expectation that greater litter capture in the pits would result in elevated concentrations of biologically derived nutrients (e.g., Burke et al., 1998; Whitford, 2002) was not realized. Rather, we found no differences in total or active carbon between pit and non-pits, nor any meaningful relationships between litter accumulation and the total carbon concentrations in the soil. In arid and semi-arid soils, carbon is strongly concentrated in the near surface layers (Tongway et al., 2003), and digging would, therefore, truncate this distribution of nutrients. However, as pits age, and litter decomposes and carbon mineralisation increases, we would expect increases in the concentration of carbon.

Similarly, contrary to our expectation, lower concentrations of nitrogen were detected in the pits compared with the surrounding soil matrix (Fig. 1), contrary to studies that report increased nitrogen in animal-created pits (Steinberger and Whitford, 1983; Whitford and Kay 1999; Eldridge and Rath, 2002). Litter is a substantial sink for mineralised nitrogen in many ecosystems (e.g., Parker et al., 1983; Blaire et al., 1992; Zaady et al., 1996), and while nitrogen accumulates in litter during the early phase of decomposition, it is not released until the latter stages. In our study, much of the litter in the pits was coarse Eucalypt leaves, with some bark and twigs falling directly from the canopy. High levels of N immobilised during decomposition of coarse litter, a consequence of its high C:N ratio (Zaady et al., 1996), likely explain the lower concentrations of nitrogen in the pits. In studies in the Chihuahuan Desert, applications of fungicides indicated that fungi are responsible for the immobilisation of nitrogen caused by decaying litter (Santos et al., 1984), and pits are known to be sites of enhanced fungal populations (Hawkins, 1996). Further depletion of nitrogen and other nutrients from pit soils could result from leaching brought about by the higher infiltration rates and greater moisture storage in the pits (e.g., Garkaklis et al., 2003). Concentrations of sulphur and phosphorus were also lower in the pits compared with the soil matrix (Table 2). Phosphorus and sulphur are likely to have been recycled from deeper soil layers by trees and shrubs, being deposited in the surface layers through litter fall (Ludwig et al., 2004). Subsequent digging by echidnas would have dispersed these nutrients across the soil surface, reducing any patches of high concentration.

Nutrient loads in litter fall will ultimately affect the concentration of nutrients in the soil below the canopy (Wardle, 1993). Concentrations of total nitrogen, available phosphorus, total sulphur, organic carbon and active carbon were higher in soil under the canopies compared with the open areas (Figs. 1 and 2). Greater concentrations of nitrogen under the tree canopies could result from a combination of increased throughflow and stemflow (Belsky et al., 1989), as well as depositions of aeolian dust, which contain high amounts of nitrogen. Together these will likely enhance populations of micro-organisms responsible for the breakdown and cycling of nutrients.

Most micro-arthropods in our study were extracted from soil, and very few were found in litter despite the fact that samples were collected at dawn before increases in diurnal temperature force micro-arthropods to retreat into the soil (Cepeda-Pizzaro and Whitford, 1989). Abundance and richness of soil micro-arthropods were greater in the pits compared with the surface, but only abundance was significant ($P = 0.001$), partially confirming our fifth prediction. While micro-arthropod richness varied little between pits and surface soils, it was greater under the tree canopies (Table 3) and increased with increasing litter mass. This suggests to us that the pits in our study, which were all of a similar age and size, may not be providing the necessary range of habitats required for a diverse community of litter-dwelling micro-arthropods. Our observations

on litter decomposition in artificial pits of the same age indicate that pits close to eucalypt canopies are dominated almost exclusively by eucalypt litter, while those further from the canopy contain a mixture of grass, tree, shrub and herb litter. Given the links between litter type and soil biota (e.g., Santos et al., 1984), we would expect some differences in the soil biota population with increasing distance from the canopy.

At the landscape scale, foraging by echidnas results in a mosaic of pits in different stages of development and recovery, similar to that observed for other soil foraging animals such as porcupines (Shachak et al., 1991) and bettongs (Garkaklis et al., 2003). Parallel studies of animal disturbances at patch and landscape scales at Yathong Nature Reserve indicate a substantially greater density of echidna digs close to the canopies of large eucalypts (Kwok, 2005 unpublished B.Sc. thesis). The increased concentration of nutrients in pits close to tree canopies augments existing higher concentrations of biologically-derived nutrients under trees resulting from nutrient accumulation and recycling (Ludwig et al. 2004). We expect that strong positive feedback processes would operate under tree canopies as pits increase soil nutrients, in turn increasing plant growth and water accumulation and, therefore, habitat for soil organisms. Ultimately, these processes would be expected to result in greater food resources for echidnas, stimulating further foraging (*sensu* Huntly and Inouye, 1988).

Our study showed that echidna foraging pits have multiple effects on ecosystem processes. Although the pits were not nutrient-rich compared with the surrounding soil matrix, they did trap more organic matter, created a cooler and moister habitat compared, and provided habitat for a range of soil micro-arthropods.

Acknowledgements

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