

## Scratching beneath the surface: Bandicoot bioturbation contributes to ecosystem processes

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**Abstract** Animals that forage for food or dig burrows by biopedturbation can alter the biotic and abiotic characteristics of their habitat. The digging activities of such ecosystem engineers, although small at a local scale, may be important for broader scale landscape processes by influencing soil and litter properties, trapping organic matter and seeds, and subsequently altering seedling recruitment. We examined environmental characteristics (soil moisture content, hydrophobicity and litter composition) of foraging pits created by the southern brown bandicoot (*Isodon obesulus*; Peramelidae), a digging Australian marsupial, over a 6-month period. Fresh diggings typically contained a higher moisture content and lower hydrophobicity than undisturbed soil. A month later, foraging pits contained greater amounts of fine litter and lower amounts of coarse litter than adjacent undug surfaces, indicating that foraging pits may provide a conducive microhabitat for litter decomposition, potentially reducing litter loads and enhancing nutrient decomposition. We tested whether diggings might affect seedling recruitment (seed removal by seed harvesters and seed germination rates) by artificially mimicking diggings. Although there were no differences in the removal of seeds, seedling recruitment for three native plant species (*Acacia saligna*, *Kennedia prostrata* and *Eucalyptus gomphocephala*) was higher in plots containing artificial diggings compared with undug sites. The digging actions of bandicoots influenced soil moisture and hydrophobicity, the size distribution of litter and seedling recruitment at a local scale. The majority of Australian digging mammals are threatened, with many suffering substantial population and range contraction. However, their persistence in landscapes plays an important role in maintaining the health and function of ecosystems.

**Key words:** biopedturbation, ecosystem engineering, foraging pits, hydrophobicity, mammal bioturbation, seedling recruitment.

### INTRODUCTION

Animal diggings provide an important source of spatial and temporal heterogeneity of surface soil in many ecosystems (Whitford & Kay 1999; Davidson & Lightfoot 2008). Biopedturbation (animal-caused soil disturbance) occurs when animals forage for food or to construct burrows, nests or rest sites (Eldridge & James 2009). These digging activities have the potential to drive ecosystem processes such as soil formation, water infiltration, nutrient cycling, fungal associations, and seedling recruitment (Garkaklis *et al.* 2004; Davidson *et al.* 2012; Eldridge *et al.* 2012). For example, foraging pits constructed by Australian woylies (*Bettongia penicillata*) create topographical depressions in the soil and reduce soil hydrophobicity, and hence provide a site of preferential water infiltration (Garkaklis *et al.* 1998, 2000; Fleming *et al.* 2014).

By digging for food, many animals alter the resource availability for other organisms, and hence

may be considered as ecosystem engineers (Jones *et al.* 1994). The mechanical turnover of soil by digging animals can increase soil moisture and bury organic matter, bringing it in close contact with soil microorganisms and thereby altering soil microbial activity and litter decomposition (Desmet & Cowling 1999; Eldridge & Mensinga 2007; Eldridge *et al.* 2012, 2015). The microclimate of animal diggings (e.g. moisture and temperature) may favour decomposing biota, and consequently, affect nutrient cycling. Furthermore, conservation reserves that contain reintroduced digging mammals are associated with lower litter mass, potentially reducing fuel loads (Martin 2003; Hayward *et al.* 2016). By altering soil heterogeneity, moisture levels, litter decomposition and nutrient cycling, animal diggings could, therefore, have long-term effects on vegetation growth (Noble *et al.* 2007; Davidson *et al.* 2012). Animal diggings may also influence vegetation composition, altering seedling recruitment *via* a number of potential mechanisms (e.g. altered seed predation rates, seed movement patterns and germination) as well as acting as

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resource sinks and therefore contributing to plant growth (Fleming *et al.* 2014; Valentine 2014).

Heterogeneity and microhabitat of soil surface influences the foraging efficiency of seed predators, such as ants (e.g. Andersen & Ashton 1985; Setterfield 2002), and the soil surface heterogeneity caused by animal diggings may reduce seed removal by predators. Seed predators have the potential to exert strong effects on plant populations by altering patterns of plant establishment (Yates *et al.* 1995; Zhang *et al.* 1997). Heterogeneity of the soil surface resulting from animal diggings influences the distribution and entrapment of seeds (Chambers & MacMahon 1994; Koontz & Simpson 2010). For example, more seeds collect in mounds constructed by kangaroo rats (*Dipodomys spectabilis*) (Koontz & Simpson 2010) and diggings created by the bilby (*Macrotis lagotis*) and boodie (*Bettongia lesueur*) (Newell 2008), compared with undug adjacent soils. In addition, animal diggings offer altered microclimates (e.g. greater water capture; Eldridge & Mensinga 2007) that may be favourable for seed germination (Alkon 1999; James *et al.* 2010; Koontz & Simpson 2010). The burrowing activity of digging animals may therefore alter vegetation structure and composition (Davidson & Lightfoot 2008).

Australia has a large number of digging mammals (29 marsupial and monotreme species), the majority of which have undergone drastic population reductions and range declines over the last 200 years (Fleming *et al.* 2014), likely due to a number of factors, including disease, habitat loss and predation by introduced predators (Johnson & Isaac 2009; Woinarski *et al.* 2015). For example, the once common boodie originally occurred across about 60% of mainland Australia, but this marsupial is now restricted to offshore islands or predator-proof sanctuaries where it has been reintroduced (Short & Turner 1993). Australian mammals that create foraging pits, such as bandicoots and bettongs, have been proposed as ecosystem engineers, due to the altered biotic and abiotic processes that occur as a consequence of the digging, and the flow-on effects in resources for other species (Valentine *et al.* 2013; Fleming *et al.* 2014; Valentine 2014). Much of the research quantifying the role of Australian digging mammals in ecosystem processes has focussed on threatened species (e.g. woylies from semi-arid woodlands; Garkaklis *et al.* 2000), often in predator-proof reserves in arid regions (e.g. bilbies and boodies; Eldridge *et al.* 2010; James & Eldridge 2007). However, a number of digging mammal species still persist (e.g. bandicoots: *Isoodon macrourus*, *Isoodon obesulus* and *Perameles nasuta*), even in highly modified urban environments (Bateman & Fleming 2012; Valentine *et al.* 2013).

In south-western Australia, at least nine digging mammals were present when Europeans settled in

the region (Valentine 2014); however, now the only commonly occurring digging mammals are the echidna (*Tachyglossus aculeatus*; Tachyglossidae) and the southern brown bandicoot (*I. obesulus fusciventor*; Peramelidae). Despite being frequently encountered in urban and wildland areas, the geographic range of the southern brown bandicoot has declined to about 40% of its former distribution (Friend 1990), and the eastern subspecies (*I. obesulus*) is considered nationally endangered under the *Environment Protection and Biodiversity Conservation Act 1999* (Commonwealth of Australia 2015). The potential for southern brown bandicoots to contribute to ecosystem processes is considerable, with an estimated annual turnover of about 3.9 tonnes of soil per individual (Valentine *et al.* 2013). Examining how the foraging activity of southern brown bandicoots alters their environment will assist in further understanding their role in ecosystem engineering.

In this study, we quantified the impact of the digging actions of southern brown bandicoots in terms of: (i) soil moisture and hydrophobicity; (ii) the size distribution of litter; and, (iii) seed removal and seed germination. We predicted that foraging pits created by southern brown bandicoots would reduce soil hydrophobicity, increase soil moisture, alter the size distribution of litter, provide safe sites for seeds and promote seedling recruitment.

## METHODS

### Study site

This study was undertaken in Yalgorup National Park on the Swan Coastal Plain bioregion (Thackway & Cresswell 1995) in south-western Australia (32°50'54.52"S; 115°40'8.72"E). The region has a Mediterranean-type climate with hot, dry summers and mild, wet winters with average annual rainfall of 864 mm (Bureau of Meteorology, station # 009679). The open woodland vegetation is dominated in the overstorey by *Eucalyptus gomphocephala* (tuart), with scattered *E. marginata* and *Corymbia calophylla* and a mid-storey of *Agonis flexuosa*, *Banksia attenuata*, *B. grandis* and *Allocasuarina* spp. The open understorey consists of *Acacia saligna*, *A. pulchella* and various other herbaceous species. Scattered throughout the open woodland are numerous lakes, with *E. rudis* and *Melaleuca raphiophylla* as the dominant tree species with a dense understorey of sedges (e.g. *Gahnia trifida*) (Portlock *et al.* 1993). Our research was conducted over an area of about 6 ha of woodland (bordering Martin's Lake) on the Spearwood Dune system, where soils are yellow-phase Karrakatta sands, and in areas without the dense lake-fringing vegetation. This area supports a naturally occurring population of the southern brown bandicoot and has been the focus of previous research examining the soil turnover of this digging mammal (Valentine *et al.* 2013). The southern brown bandicoot (a medium-sized omnivorous marsupial,

weighing about 1.2 kg) digs foraging pits in search of food items, including invertebrates, subterranean tubers and fungi (Van Dyck & Strahan 2008). The conical-shaped foraging pits are approximately 100 mm across and 70 mm deep, with soil evacuated from the pit forming a spoil heap that covers the undisturbed ground surface and any litter present (Valentine *et al.* 2013).

### Soil and litter properties of bandicoot foraging pits over time

We examined changes in the soil and litter properties of bandicoot foraging pits compared to adjacent undug ground over time. Sixty fresh foraging pits were individually marked (with wooden sticks) in March 2012. We destructively sampled a random selection of 10 of these foraging pits each month for 6 months (March–August) as the foraging pits aged. A 0.5 × 0.5 m quadrat was used to mark the area surrounding each foraging pit ('foraging plot') and a similar area of immediately adjacent undug ground ('undug plot') as its paired control. Each plot-pair was more than 3 m away from other foraging pits to ensure that there was minimal interference between diggings. For each plot, we measured soil moisture (with minimum disturbance of the litter layer), and soil hydrophobicity, and then collected the surface litter.

#### Soil moisture & hydrophobicity

Soil moisture (%) was determined by inserting a three pronged (60-mm) Theta Probe soil moisture sensor (Type ML2x Telta-T Devices Ltd, Cambridge England), which measures soil moisture at 60-mm depth, into the soil (perpendicular to the soil surface) at four 'microsites': (i) on undisturbed ground behind the spoil heap; (ii) on the spoil heap; (iii) mid-way down the foraging pit; and (iv) at the base of the foraging pit. Four measurements were taken at random locations within the paired undug (control) plot.

Soil hydrophobicity (or 'soil water repellency') was determined using the Molarity of Ethanol Droplet (MED) technique (King 1981). Ethanol lowers the liquid surface tension and solid-liquid contact angle, increasing the rate of infiltration into a water-repellent soil (King 1981). The MED technique therefore expresses soil hydrophobicity as the molarity of ethanol solution required to facilitate a drop (of about 40 µm) to penetrate the soil surface within 10 s, where the higher the molarity required reflects greater soil hydrophobicity. Six MED measurements were taken within each plot (at the same microsites where soil moisture was measured with the addition of measurements at the top of the foraging pit and the undisturbed ground in front of the pit; hence an additional two measurements were collected at random locations within the undug plot).

To examine how soil properties varied between the foraging-pit and undug plots, we compared average soil moisture (%) and hydrophobicity (MED) readings from each plot using a three-way Analysis of Variance (ANOVA), with *treatment* (foraging *vs.* undug plot) and *time* (age of foraging pit) as fixed factors (including an interaction term), and plot-pair ID as a blocking factor (to account for paired sites) in Statistix (version 9). *Post hoc* ANOVA was used to examine treatment effects within each sample month, with

*treatment* (foraging *vs.* undug plot) as a fixed factor, blocked by plot-pair ID.

To describe how soil properties varied along the profile of a foraging pit, we compared soil moisture and hydrophobicity (MED) readings from each of the foraging plot microsites (soil moisture: behind, spoil, mid-slope, pit-base; MED: behind, spoil, top-slope, mid-slope, pit-base, front) and the first reading from its paired undug plot (undug) using a three-way ANOVA with *microsite* and *time* (age of foraging pit) as fixed factors (including an interaction term), and plot-pair ID as a blocking factor. *Post hoc* ANOVA was used to examine effects within each sample month, with *microsite* as a fixed factor, blocked by plot-pair ID. Tukey's Honestly Significant Difference (HSD) tests were used to examine significant differences among microsite locations.

#### Size distribution of litter

We collected all exposed surface litter within each plot (down to mineral earth, excluding litter that was covered by the spoil heaps) into paper bags. Samples were oven dried (70–80°C) until a constant weight was obtained (usually 3 days), and then passed through a series of sieves to obtain three litter size categories: coarse (litter >10 mm), medium (5–10 mm) and fine (<5 mm); material <0.05 mm was considered as soil or organic matter and therefore not included. Each litter category sample was weighed and the relative proportions of litter within each size-class were calculated. When the foraging pits were 3- and 4-month old (June and July), litter samples were analysed from only nine plots (as opposed to 10 plots in other months) due to the loss of sample bags.

To compare the breakdown of litter (distribution of litter size-classes) between the foraging-pit and undug plots, we analysed the proportion of litter in each size-class from each plot using a three-way ANOVA, with *treatment* (foraging *vs.* undug plot) and *time* (age of foraging pit;  $n = 10$  for each month, except for 3- and 4-month-old plots,  $n = 9$ ) as fixed factors (including an interaction term), and plot-pair ID as a blocking factor. *Post hoc* ANOVA was used to examine treatment effects within each sample month, with *treatment* (foraging *vs.* undug plot) as a fixed factor, blocked by plot-pair ID.

#### Seed removal and germination in artificial pits

To examine the influence of diggings on seed removal and seedling germination, we located 12 naturally occurring canopy gaps (ideal seedling recruitment sites for the species we investigated; Ruthrof *et al.* 2015), each more than 30 m apart. The dominant tree species (mostly *E. gomphocephala*) surrounding each gap were visually assessed for canopy seed storage, to prevent natural seed fall confounding the experiment. None of the nearby tree species had canopy seed storage that was visually detected. Within each canopy gap, we established two 1 × 1 m plots (within 3 m of each other) on undisturbed ground. One plot remained undisturbed ('undug plot'). For the paired artificial-pit plot, we dug (using a trowel) eight diggings, matched for shape and size to natural bandicoot foraging pits by placing a plaster cast of a natural foraging pit (Valentine *et al.* 2013) within each artificial pit.

To check that the artificial pits contained similar levels of soil moisture and hydrophobicity to natural pits, we

measured these variables (methods described above) for four natural pits and four artificial pits within the study area, but outside of the established plots. There was no difference in either soil moisture (one-way ANOVA:  $F_{1,6} = 1.42$ ,  $P > 0.05$ ) or soil hydrophobicity (one-way ANOVA:  $F_{1,6} < 0.01$ ,  $P > 0.05$ ) between the artificial pits and natural foraging pits, indicating our artificial pits were good representatives of natural foraging pits.

#### Seed removal

The seed removal experiments were two-fold (i) to examine if the increased surface heterogeneity altered ant foraging efficiency, and (ii) to incorporate any differences in seed removal rates in the seedling recruitment trials. We examined the seed removal rates between artificial-pit plots and undug plots in April 2012, using cafeterias placed in the middle of each plot. Cafeterias were constructed by gluing the bases of plastic 50-mm diameter Petri dishes to 100 × 100 mm recycled hardwood boards for stability, with the boards partially submerged into the ground (after Yates *et al.* 1995). Three 10 × 10 mm openings, equidistant from each other, were melted into the sides of the Petri dishes to allow entry by ants but not vertebrates, and to minimize disturbance by rain or wind (Yates *et al.* 1995; Ruthrof *et al.* 2002). The lids of the Petri dishes were fastened in place with electrical tape. A paired control cafeteria consisted of the identical design, but had an adhesive barrier (Tacgel, Manufacturer) painted on the wooden board to exclude ants. Ten seeds each of three locally occurring native plant species (*E. gomphocephala*, *A. saligna* and *Kennedia prostrata*) were placed inside each cafeteria. Four days later, the cafeterias were collected and the remaining seeds for each species were counted. There was no evidence of seed removal from the control cafeterias.

To compare seed removal from cafeterias between the artificial-pit and undug plots, we analysed the proportion of seeds remaining for each plant species using a two-way ANOVA, with *treatment* (artificial-pit *vs.* undug plot) as a fixed factor and plot-pair ID as a blocking factor.

#### Seed germination

Following the seed removal trial (above), we seeded each plot with seeds from five locally occurring species, including the three species used in the seed removal trial: *E. gomphocephala* (23.8 g m<sup>-2</sup> plots with chaff), *A. saligna* (0.8 g m<sup>-2</sup> plots) and *K. prostrata* (2.5 g m<sup>-2</sup> plots), as well as *Melaleuca systena* (0.5 g m<sup>-2</sup>) and *B. grandis* (0.25 g m<sup>-2</sup> plots). Seeds were mixed with vermiculite (to bulk-up the mixture) and scattered by hand. The number of seedlings of each species was counted on a weekly basis for 18 weeks following seeding. In the final week of observations (week 18), we visually recorded the location of where seedlings were growing in the artificial-pit plots, either in an artificial pit, spoil heap or on the undug surface. Seedlings of *B. grandis* were only observed in about one quarter of the plots, and were excluded from analysis due to their low germination rate. Despite none of the nearby trees containing canopy seed storage, the seedling recruitment for *E. gomphocephala* in one plot (an artificial-pit plot) was an order of magnitude greater than other

plots. Subsequently, we excluded this paired-plot from seedling recruitment analyses.

Generalized additive mixed models (GAMM; Zuur *et al.* 2009) were used to examine the effect of artificial diggings and time since seeding on the number of seedlings. We used GAMMs, rather than assuming linear fits, as there were nonlinear relationships over time. GAMM models were fitted using the *gam* function of the MGCV package in R (Wood 2006; version 2.15.2, R Development Core Team 2012). The importance of the fixed predictor *treatment* (artificial-pit *vs.* undug plots) and *time since seeding* (fitted as a penalized regression spline) were explored by comparing all possible models of the one and two predictors (five models; including an intercept-only model). The most complex model represented the interaction between *time since seeding* and *treatment* (with a separate smoother for each treatment over time). All models were fitted using maximum likelihood (ML) estimation (Zuur *et al.* 2009). The random effect of paired-plot was included using the *bs = 're'* argument within the *gam* call (Wood 2008). The alternative models were compared using the Akaike's Information Criterion for small sample sizes (AICc; Burnham & Anderson 2002). AICc values ( $\Delta\text{AICc} < 2$ ), their associated weights and adjusted  $R^2$  values were used to select the optimal model.

#### General statistical analyses

Data are presented as means with ±95% confidence interval (CI) throughout. As readings of soil moisture were obtained directly as readings of percentages, a binomial/Bernoulli distribution (which might ordinarily be applicable to percentage and proportional data) could not be used, as these require frequencies. Similarly, the proportion of litter was calculated from two continuous weights rather than frequencies, thus a binomial/Bernoulli distribution was also inappropriate. Soil moisture and litter proportions were thus transformed using an arcsine square-root (as recommended for percentage data, Zar 1999) and treated as Gaussian in analyses. Hydrophobicity data are collected on a scale of 0–5, which also does not fit well to the statistical distributions typically available in *gim*, and instead were transformed using an arcsine square-root and treated as Gaussian in analysis. Seedling counts were modelled directly using a negative binomial distribution.

## RESULTS

### Soil and litter properties of bandicoot foraging pits over time

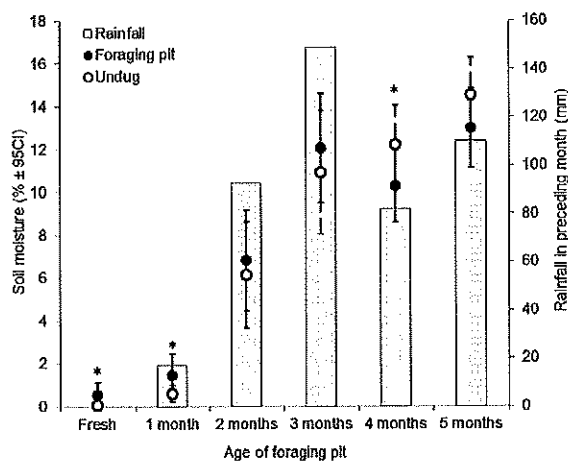
#### Soil moisture & hydrophobicity

Soil moisture increased over time and varied between bandicoot foraging-pit and undug plots (Table 1; Fig. 1). Prior to the winter rainfall, foraging-pit plots had higher soil moisture content than undug plots, but after the winter rains had commenced (May

**Table 1.** ANOVA *F*-values for soil moisture (%), Hydrophobicity (Molarity of Ethanol, MED), and the proportion of different-sized litter in foraging-pit vs. undug plots (*treatment* effect) over time

Variable	Treatment	Time	Treatment × Time	Post hoc ANOVA: Treatment					
				Fresh d.f. = 1,9	1 month d.f. = 1,9	2 months d.f. = 1,9	3 months d.f. = 1,9	4 months d.f. = 1,9	5 months d.f. = 1,9
Soil moisture (%)	1.26 d.f. = 1,99	290.65*** d.f. = 5,99	2.74* d.f. = 5,99	25.96***	40.03***	0.43	0.86	18.67**	4.68 <sup>^</sup>
Hydrophobicity (MED)	98.43*** d.f. = 1,27	11.74** d.f. = 1,27	5.97* d.f. = 1,27	183.66***	15.37**	–	–	–	–
Fine litter	9.52** d.f. = 1,95	16.03*** d.f. = 5,95	1.91 d.f. = 5,95	<0.00	8.38**	8.02**	12.89** <sup>†</sup>	0.28 <sup>†</sup>	0.19
Medium litter	1.44 d.f. = 1,95	2.24 <sup>^</sup> d.f. = 5,95	0.14 d.f. = 5,9	0.01	3.28	1.98	0.56 <sup>†</sup>	0.15 <sup>†</sup>	0.76
Coarse litter	6.73* d.f. = 1,95	12.75*** d.f. = 5,95	1.75 d.f. = 5,95	0.02	7.61**	4.79 <sup>^</sup>	7.44* <sup>†</sup>	0.07 <sup>†</sup>	0.46

Asterisks indicate significant (\**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001) results; values approaching significance (<sup>^</sup>*P* < 0.06) are also identified. <sup>†</sup>Due to sample loss, the error term for the degrees of freedom (d.f.) for these *F*-values was 8 instead of 9. Post hoc ANOVAs for each variable report *treatment F*-values within each sample period.



**Fig. 1.** Soil moisture (mean %  $\pm$  95% CI) for bandicoot (*Isododon obesulus*) foraging-pit plots and undug plots sampled over a 6-month period (March–August 2012) as the foraging pits aged. Rainfall data for the month preceding sampling are superimposed (Australia's Bureau of Meteorology station #009624). Asterisks (\*) indicate significant (*P* < 0.05) differences between treatment types (foraging-pit vs. undug plots) within each sampling period.

2012, when foraging pits were 2 months of age), the foraging-pit plots did not differ (or had less overall soil moisture) from the undug plots (Table 1; Fig. 1).

Soil hydrophobicity (MED) also changed over time and between treatments (Table 1), but was always lower in the foraging-pit plots compared with the undug plots. Analyses were only conducted on data collected in March and April when foraging pits were fresh and 1-month old,

respectively, as there was no hydrophobicity from May onwards due to the start of winter rainfall. The freshly dug foraging pits had the lowest hydrophobicity ( $3.06 \pm 0.31 \text{ mol L}^{-1}$  ethanol solutions required for soil penetration), which increased as the foraging pit aged ( $4.10 \pm 0.62 \text{ mol L}^{-1}$ ), although this remained lower than the hydrophobicity of the undug plots (fresh:  $5.07 \pm 0.14 \text{ mol L}^{-1}$ ; 1 month:  $5.2 \pm 0.01 \text{ mol L}^{-1}$ ).

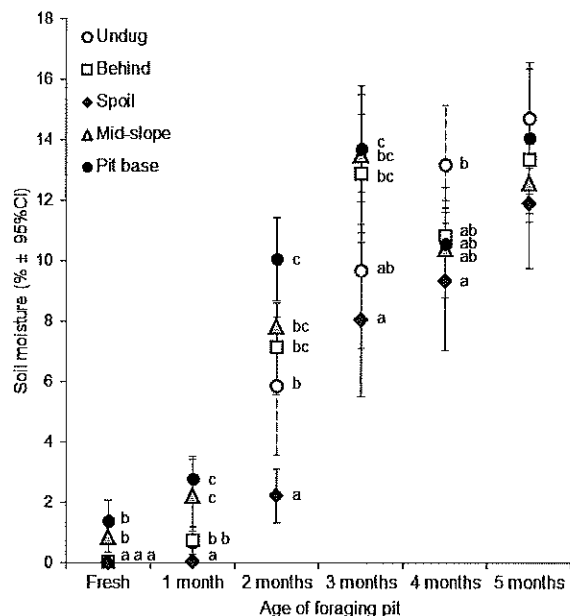
Both soil moisture and hydrophobicity varied among the microsite locations along the profile of a foraging pit (Table 2). Soil moisture also varied with age of the foraging pit and the significant *treatment* × *time* interaction term indicated different changes over time among microsite locations (Table 2; Fig. 2). The pit-base and mid-slope of the foraging pit consistently recorded the highest soil moisture readings as the foraging pit aged, with the exception of the last 2 months sampling when most microsite locations contained similar moisture levels (Fig. 2). When freshly dug, soil moisture was higher for the pit-base and mid-slope, while the spoil heap and adjacent undug locations were dry prior to winter rainfall (Fig. 2). The lowest soil moisture was recorded for the spoil heap over subsequent months (Fig. 2). By the time the foraging pits were 5-month old (August 2012), there was no difference in soil moisture among microsite locations (Table 2; Fig. 2).

Hydrophobicity (MED) was most severe for undug soils, while the soil actively modified by bandicoots (spoil heap, top-slope, mid-slope and pit-base of the foraging pit) had the lowest hydrophobicity (Fig. 3). Hydrophobicity was also higher in the 1-month-old sample ( $4.25 \pm 0.36 \text{ mol L}^{-1}$ ) compared with the fresh sampling period ( $3.36 \pm 0.38 \text{ mol L}^{-1}$ ).

**Table 2.** ANOVA *F*-values for soil moisture (%) and hydrophobicity (Molarity of Ethanol, MED) collected from different *microsites* along the profile of the foraging pit as the foraging pit aged (*time*)

Variable	<i>Microsite</i>	<i>Time</i>	<i>Microsite</i> × <i>Time</i>	<i>Post hoc</i> ANOVA: <i>Treatment</i>					
				Fresh d.f. = 4,36	1 month d.f. = 4,36	2 months d.f. = 4,36	3 months d.f. = 4,36	4 months d.f. = 4,36	5 months d.f. = 4,36
Soil moisture (%)	33.56*** d.f. = 4,261	401.02*** d.f. = 5,261	4.21*** d.f. = 20,261	21.30***	24.65***	12.57***	7.16***	3.22*	1.53
Hydrophobicity (MED)	14.97*** d.f. = 6,117	11.44** d.f. = 1,117	1.04 d.f. = 6,117	14.26***†	5.23***†	–	–	–	–

Asterisks indicate significant (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ) results. †There were seven *microsite* locations where MED was collected and the treatment degrees of freedom for these *F*-values was 6, and for the error term, 54 (d.f. = 6,54). *Post hoc* ANOVAs for each variable report *microsite* *F*-values within each sample period.

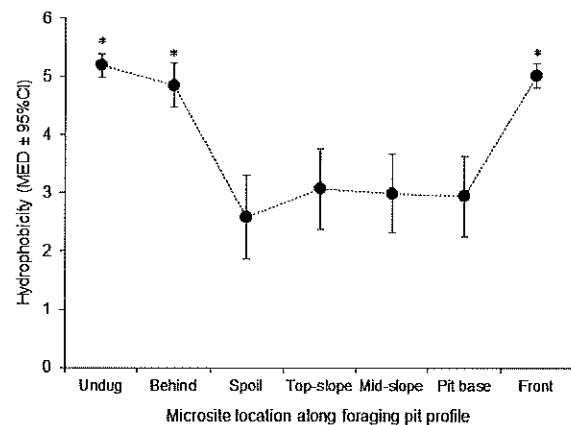


**Fig. 2.** Soil moisture (mean %  $\pm$  95% CI) at five *microsite* locations along the profile of bandicoot foraging pits measured over a 6-month period (March–August 2012) as the foraging pits aged. The ‘*spoil*’, ‘*mid-slope*’ (of the pit) and the ‘*pit-base*’ are *microsite* locations that have been disturbed by a bandicoot, the ‘*behind*’ *microsite* is located directly behind the *spoil* heap, and the ‘*undug*’ *microsite* is adjacent undisturbed ground. Letters indicate significant (Tukey’s HSD,  $P < 0.05$ ) differences among locations within each sampling period.

#### Size distribution of litter

The proportion of fine (<5 mm) and coarse (>10 mm) surface litter varied with time and between foraging pit and undug plots (Table 1; Fig. 4). Initially, when the foraging pits were fresh, there was no difference in the size distribution of litter between foraging and undug plots (Table 1; Fig. 4). By 1–3 months, a greater proportion of the fine-sized litter (but a lower proportion of coarse-sized litter) was

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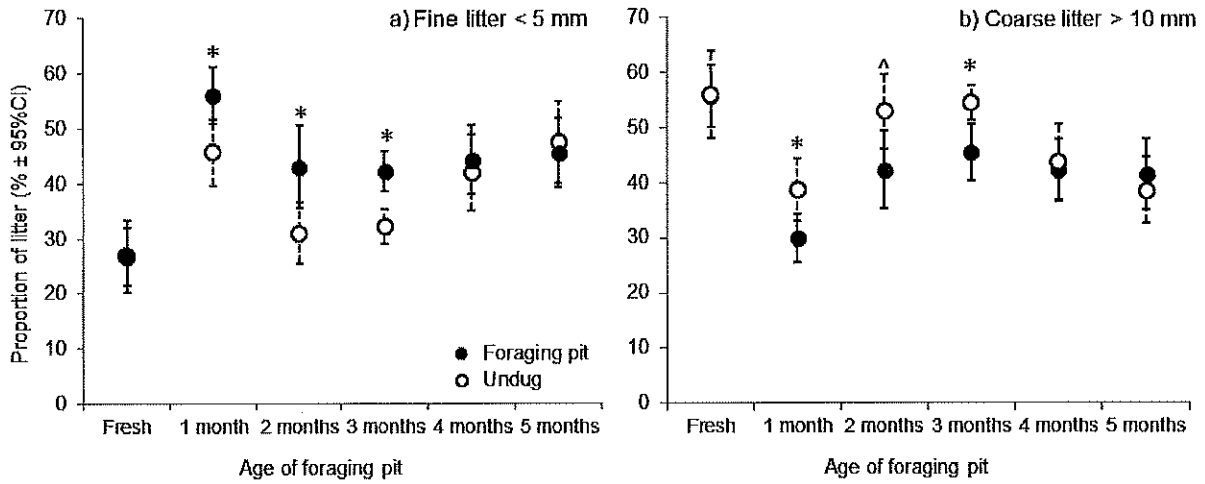
**Fig. 3.** Soil hydrophobicity (mean Molarity of Ethanol, MED  $\pm$  95% CI) from seven *microsite* locations along the profile of bandicoot foraging pits. The ‘*spoil*’, ‘*top-slope*’ (of the pit), ‘*mid-slope*’ (of the pit) and the ‘*pit-base*’ are *microsite* locations that have been disturbed by a bandicoot, the ‘*undug*’ (adjacent undisturbed ground), ‘*behind*’ (the *spoil* heap) and ‘*front*’ (in front of the pit hole) are *microsite* locations that have not been disturbed by a bandicoot. Asterisks (\*) indicate significant (Tukey’s HSD,  $P < 0.05$ ) differences between *microsite* locations.

present in the foraging-pit plots compared with the undug plots (Table 1; Fig. 4). There was no difference in the proportion of medium-sized litter between dug and undug plots.

#### Seed removal and germination in artificial foraging pits

##### Seed removal

There was no difference in the seed removal between artificial-pit and undug plots for any of the three plant species examined (*A. saligna*:  $F_{1,11} = 0.27$ ,  $P > 0.05$ ; *E. gomphocephala*:  $F_{1,11} = 0.08$ ,  $P > 0.05$ ; *K. prostrata*:  $F_{1,11} = 0.75$ ,  $P > 0.05$ ). *Eucalyptus gomphocephala* seeds showed the greatest rate of seed removal



**Fig. 4.** The proportion (mean  $\pm$  95% CI) of (a) fine litter (<5 mm) and (b) coarse litter (>10 mm) collected from the surface of bandicoot foraging-pit plots and adjacent undug plots measured over a 6-month period (March–August 2012) as the foraging pit aged. Asterisks (\*) indicate significant ( $P < 0.05$ ) differences between treatment types (foraging-pit vs. undug plots) within each sampling period, the caret (^) indicates approaching significance ( $P < 0.06$ ).

( $45.8 \pm 13.0\%$  of seeds removed after 4 days) and *A. saligna* seeds the least ( $20.8 \pm 8.3\%$ ); *K. prostrata* showed intermediate values ( $30.3 \pm 14.3\%$ ).

*Seed germination*

Seedlings of *A. saligna*, *E. gomphocephala* and *K. prostrata* initially appeared in plots 4 weeks after seeding, and *M. systema* seedlings 6 weeks after seeding. Between weeks 6–18, when most seedlings emerged, the average number of seedlings observed in artificially dug plots was at least three times that of undug plots for *A. saligna* ( $5.3 \pm 0.5$  vs.  $1.3 \pm 0.2$  seedlings), *K. prostrata* ( $2.5 \pm 0.3$  vs.  $0.9 \pm 0.2$  seedlings) and *E. gomphocephala* ( $10.1 \pm 1.2$  vs.  $4.5 \pm 0.6$  seedlings), but not for *M. systema* ( $2.6 \pm 0.5$  vs.  $2.0 \pm 0.4$  seedlings). For all four plant species, only one model was selected as the optimal model. For all plants except *M. systema*, these models included both *treatment* and *time since seeding* factors (Table 3; Fig. 5). The top model for both *A. saligna* and *K. prostrata* included *time since seeding* with a different intercept for *treatment*: higher seedling numbers were observed in the artificial-pit plots (Table 3; Fig. 5). This

relationship was particularly strong for *A. saligna* (adjusted  $R^2 = 0.75$ ). The number of seedlings for *E. gomphocephala* was best described by the interaction term (*treatment*  $\times$  *time since seeding*) (Table 3; Fig. 5), where the number of seedlings in artificial-pit plots was substantially higher, and followed a different trajectory through time compared with undug plots. The top model for *M. systema* included *time since seeding* (Table 3; Fig. 5), although this model only had marginal support (adjusted  $R^2 = 0.14$ ).

During week 18, the majority of seedlings (79% of *A. saligna*, 61% of *E. gomphocephala*, 65% of *K. prostrata* and 65% of *M. systema*) within the artificial-pit plots were observed growing in what was originally an artificial bandicoot dig. By this time, most of the original spoil heaps had eroded into the artificial pits, and the spoil-pit structure was becoming challenging to differentiate.

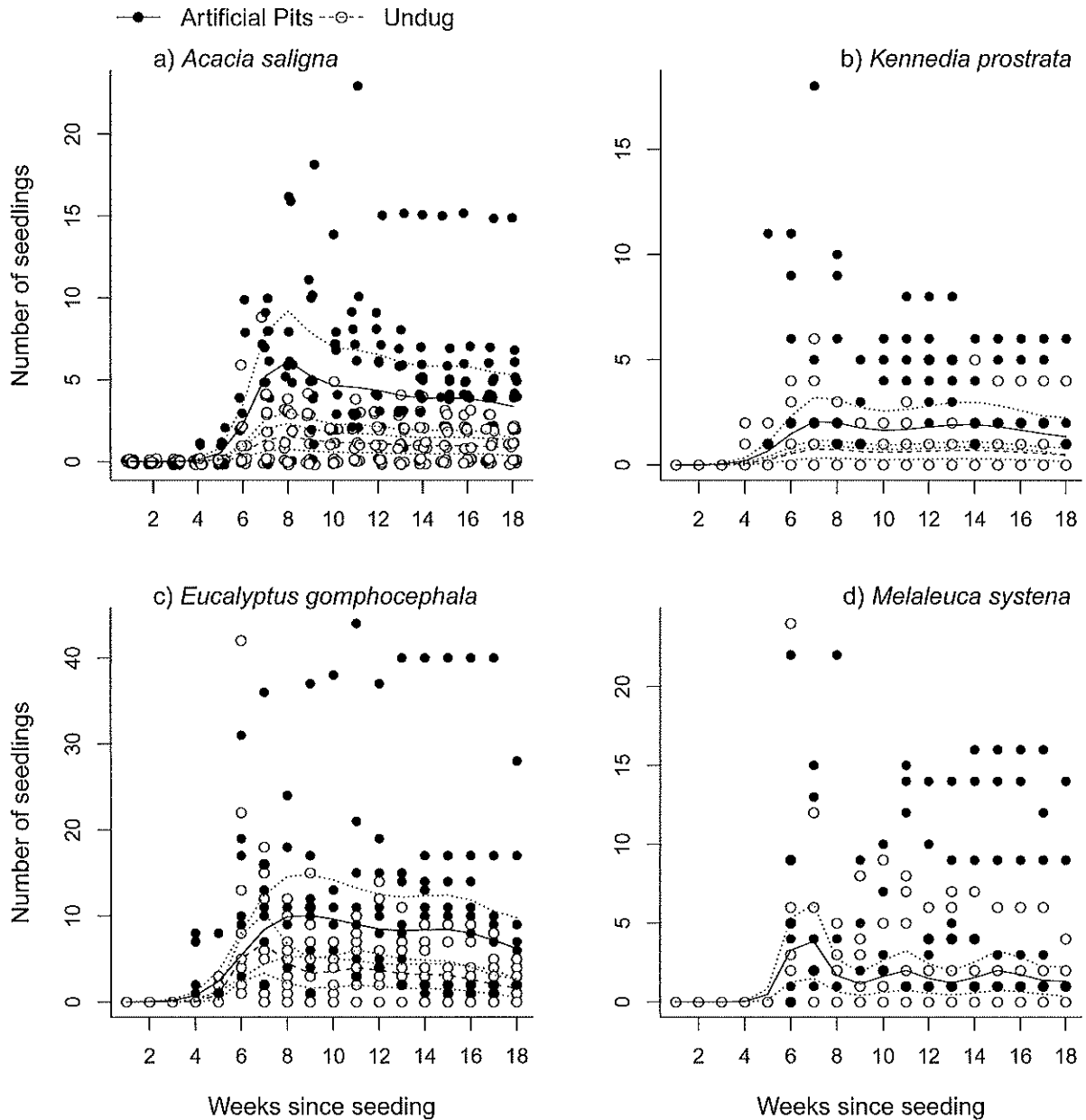
**DISCUSSION**

Our research indicates that southern brown bandicoots alter the availability of resources for other

**Table 3.** Top-ranking generalized additive mixed models (GAMM) for the number of seedlings recorded for *Acacia saligna*, *Kennedia prostrata*, *Eucalyptus gomphocephala* and *Melaleuca systema* with different model combinations of *treatment* (artificial-pit vs. undug plots) and *time* (time since seeding)

Species	Model	d.f.	Adjusted- $R^2$	$\Delta$ AICc	AICc weight
<i>Acacia saligna</i>	<i>Treatment</i> + <i>Time</i>	19.45	0.75	0	0.99
<i>Kennedia prostrata</i>	<i>Treatment</i> + <i>Time</i>	18.65	0.62	0	0.99
<i>Eucalyptus gomphocephala</i>	<i>Treatment</i> $\times$ <i>Time</i>	23.94	0.462	0	0.98
<i>Melaleuca systema</i>	<i>Time</i>	18.42	0.13	0	0.75

Models included are the top-ranking model for each response variable ( $<2 \Delta$ AICc).



**Fig. 5.** Relationships (including the GAMM-fit  $\pm 95\%$  CI) for weeks since seeding and the number of seedlings of (a) *Acacia saligna* (adjusted  $R^2 = 0.75$ ), (b) *Kennedia prostrata* (adjusted  $R^2 = 0.60$ ) and (c) *Eucalyptus gomphocephala* (adjusted  $R^2 = 0.62$ ) in plots with artificial pits (solid circles; solid GAMM-fit line) and undug soil (open circles; dashed GAMM-fit line) and (d) the GAMM-fit ( $\pm 95\%$  CI) for weeks since seeding for *Melaleuca systema* (adjusted  $R^2 = 0.14$ ); observed over an 18-week period.

species by altering soil hydrophobicity, changing soil moisture levels and potentially enhancing nutrient decomposition. Using the conceptual framework proposed by Jones *et al.* (1994), southern brown bandicoots are an example of a 'case 4 allogenic ecosystem engineer', whereby their digging actions alter a resource from one state (e.g. undug soil) to another (e.g. dug/manipulated soil), with the altered state

modulating resources (e.g. soil moisture) for other species (e.g. plants, as evidenced by higher seedling recruitment). The disturbance of soil by bandicoots while foraging for food, contributes to ecosystem processes at localized scales through altered soil moisture levels, hydrophobicity and the distribution of litter sizes (Fig. 6). When fresh, the soil that had been actively manipulated by bandicoots was typically



characterized by greater moisture, and less hydrophobicity than undisturbed soil. Within a month, foraging pits contained greater amounts of fine litter and lower amounts of coarse litter than adjacent undug surfaces, indicating that foraging pits may provide a conducive microhabitat for litter decomposition, potentially reducing litter loads and enhancing nutrient decomposition (Fig. 6). Although there was no difference in the predation of seeds between artificially dug and undug plots, seedling recruitment for three native plant species was higher in the plots containing artificial diggings.

### Soil and litter properties of foraging pits over time

As found for many Australian soils (Roberts & Carbon 1972), the undisturbed soils of Yalgorup National Park exhibited severe hydrophobicity prior to the onset of the winter rains. This hydrophobicity was significantly lower in fresh bandicoot foraging pits. The short-term changes in hydrophobicity along the bandicoot foraging-pit profile were comparable to those recorded for woylies by Garkaklis *et al.* (1998), with the area manipulated by the bandicoots and woylies being the least water-repellent. This temporary reduction in soil hydrophobicity (and associated increase in water infiltration into the soil profile) may

be very important in severely water-repellent soils. Following an initial decrease in hydrophobicity (Garkaklis *et al.* 1998), woylie foraging pits become more water-repellent as they age (after 2–3 years), likely due to an accumulation of litter in pits over time and fungal hyphae which colonize the litter, eventually developing similar hydrophobicity as evident in adjacent undug soil (Garkaklis *et al.* 2000). Therefore, hydrophobicity characteristics associated with foraging pits vary over time, according to the amount of organic matter captured (Garkaklis *et al.* 2000; Eldridge & Mensinga 2007).

The lower hydrophobicity of fresh foraging pits probably contributed to greater water infiltration, resulting in the observed greater soil moisture compared with the surrounding undisturbed ground (Fig. 6). The difference in soil moisture among microsite locations lasted for several months; but was absent when the pit was 5 months of age, possibly due to soil saturation by winter rainfall. The ability of foraging pits to provide sites of greater water infiltration and lower evaporation rates has been recorded for a range of digging mammals (Garkaklis *et al.* 1998; Whitford & Kay 1999; Eldridge & Mensinga 2007). While the mid-slope and base of the pits had higher levels of soil moisture, the spoil heap had the lowest soil moisture levels of all microsite locations along the bandicoot foraging-pit profile. Spoil heaps of other digging mammals, such as

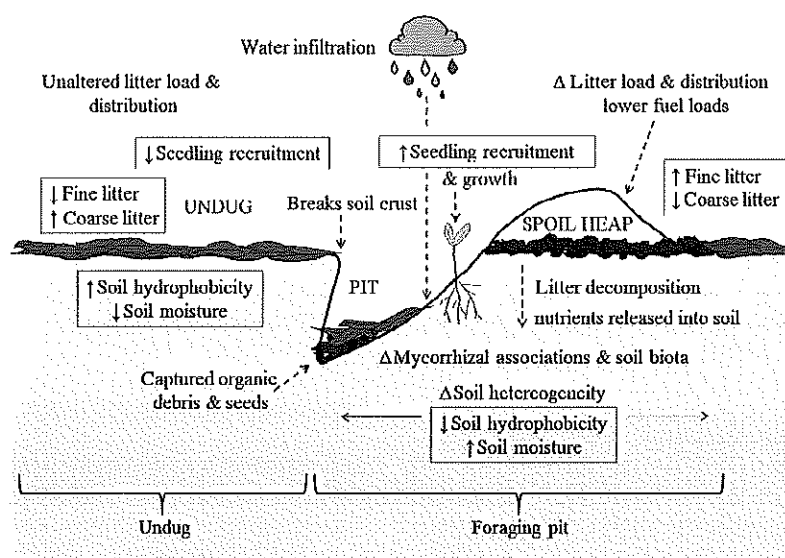


Fig. 6. Schematic representation of how a foraging pit may alter biotic and abiotic processes (modified from Fig. 1 of Valentine 2014). The enclosed boxes represent results detected during our study comparing attributes between a bandicoot foraging pit and adjacent undug ground. The area surrounding the foraging pit contains lower soil hydrophobicity, higher soil moisture, a higher proportion of fine litter and lower proportion of coarse litter (within the first 3 months of creation) and more seedling recruitment than adjacent undisturbed ground. Foraging pits may also capture organic debris and seeds, while the spoil heaps may enhance litter decomposition, potentially releasing nutrients into the soil and alter fuel loads (Valentine 2014). As the foraging pit ages, the spoil heap erodes into the pit, potentially covering captured seeds and providing sites for recruitment.

echidnas, have lower bulk density than undisturbed soils due to aeration of the soil, which may accelerate evaporation (Eldridge & Mensinga 2007) and hence reduce soil moisture. The spoil heaps may also have an umbrella affect, preventing water from infiltrating the underlying litter and soil layers.

The foraging-pit plots had higher amounts of fine-sized litter and lower amounts of coarse litter for the first 3 months following disturbance. The greater proportion of fine litter particles in foraging-pit plots reflects the potential role of digging mammals in litter decomposition and altering fuel loads (Fig. 6). The excavation of soil by bandicoot foraging may speed up litter decomposition by mixing organic matter with soil, and enhancing microbial activity (Desmet & Cowling 1999; Eldridge & Mensinga 2007; Valentine 2014; Eldridge *et al.* 2015). The process of altering organic matter distribution and composition and consequently creating a mosaic of fertile patches will likely have flow-on effects for plant community composition (Alkon 1999; Desmet & Cowling 1999; Davidson & Lightfoot 2008; Eldridge *et al.* 2012). Altering the size distribution of litter has been suggested as a mechanism by which digging mammals may alter fuel loads, potentially changing fire intensity and behaviour (Martin 2003; Fleming *et al.* 2014; Hayward *et al.* 2016), although this has yet to be experimentally established. Recent research (Hayward *et al.* 2016) shows that where digging mammals have been reintroduced inside conservation sanctuaries, litter mass and cover were much lower than outside the reserves. Our study provides further evidence that digging mammals may alter fuel loads, with foraging-pit plots containing smaller litter particles (compared with undug surfaces) within a month of being dug. Given that the southern brown bandicoot can create up to 45 foraging pits per night (Valentine *et al.* 2013), the capacity of these digging mammals to alter fuel loads may be substantial where they occur in abundance. Another avenue to explore would be how the physical structure of the foraging pit encourages or prevents certain litter sizes from being distributed by wind.

#### Seed removal and germination in artificial foraging pits

In our study, the undulating surface heterogeneity created by artificial diggings did not alter foraging efficiency (in terms of seed removal) by seed predators. However, the experiment showed that seed predators removed seeds from the different plant species at different rates. The physical characteristics of seeds, such as size and elaiosome/seed ratios, are important in specific seed preferences of the main seed predators, ants (Andersen & Ashton 1985; Hughes & Westoby 1992). In our experiment,

*E. gomphocephala* seeds had the highest removal rates and were the smallest (and lightest) of the three species examined. Although artificial diggings did not reduce seed removal, animal diggings can create a safe site by trapping seeds in the foraging pit (e.g. James *et al.* 2009, 2010; Koontz & Simpson 2010; Travers *et al.* 2012; see Fig. 6), burying the seeds as the pit decays (Newell 2008), and overall contributing to increased seedling germination, plant recruitment and growth (Alkon 1999; Dickman 2006; Noble *et al.* 2007; James *et al.* 2010).

The presence of artificial pits contributed to greater seedling recruitment for three of the plant species tested (especially for *A. saligna* and *E. gomphocephala*). The higher number of seedlings observed in artificial-pit plots may have been facilitated by (i) the undulating surface heterogeneity (caused by diggings) reducing seed removal by wind or seed predators, (ii) the diggings collapsing and slightly burying seeds, and hence protecting them, or (iii) the diggings being more favourable sites for germination than in undisturbed soil (Fig. 6). In addition, within the artificial pit plots themselves, we observed the majority of seedlings growing in an area that we artificially manipulated, indicating that the disturbance caused by bandicoots may directly influence germination. Small-scale variations in physical and biotic factors provide a range of microsites, some of which will provide the optimal requirements for seed germination (Chambers & MacMahon 1994). The disturbance created by a digging mammal creates small-scale fertile patches (Alkon 1999; Desmet & Cowling 1999; James *et al.* 2009), and may therefore benefit some plant species over others. Both *E. gomphocephala* and *A. saligna* respond well to disturbances, such as ripping and fire (Milton & Hall 1981; Ruthrof *et al.* 2003, 2013), and the diggings created by bandicoots may similarly favour seedling recruitment for these species. Further research is required to specifically examine the mechanisms facilitating seedling recruitment in animal diggings.

#### Implications for conservation and management

The extensive loss of digging mammals, both in Australia and globally, has been linked with a deterioration in ecosystem function and health (Davidson *et al.* 2012; Fleming *et al.* 2014) and in some woodlands, foraging activities by digging mammals is greatest surrounding healthy trees (Moore *et al.* 2014). The majority of Australian digging mammals have suffered widespread range contraction and population loss, with six species now considered extinct (Fleming *et al.* 2014). In predator-proof sanctuaries, where such species have been reintroduced, their foraging or burrowing activities are linked to the

restoration of ecosystem processes (James & Eldridge 2007) and the potential to alter fuel loads (Hayward *et al.* 2016). In this study, we have shown that southern brown bandicoots are ecosystem engineers, as their digging actions initially increase soil moisture, reduce hydrophobicity, change the size distribution of litter (potentially reducing fuel loads and enhancing nutrient decomposition) and increase seed germination of key local plant species (Fig. 6). In their search for food, bandicoots create numerous foraging pits on a daily basis, continually turning over soil and making localized disturbances (Valentine *et al.* 2013). Bandicoots may, therefore, be functionally similar to other previously abundant Australian digging marsupials (e.g. woylies; Garkaklis *et al.* 2004; bilby and boodie; James *et al.* 2009), and their continued persistence may be critical for maintaining ecosystem processes. The potential resilience of bandicoots to human-mediated disturbances may also provide the opportunity to reintroduce these digging mammals where soil turnover is required for ecosystem health and function (Valentine *et al.* 2013).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Schematic representation, and photograph of a bandicoot foraging pit.

**Figure S2.** Photograph of the cafeteria trial in the middle of an artificial-pit plot.