

Foraging animals create fertile patches in an Australian desert shrubland

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Fertile patches are created and maintained by a combination of physical and biologically-mediated processes including soil disturbance by animals. We examined the creation of fertile patches by 4 vertebrates, the greater bilby *Macrotis lagotis*, burrowing bettong *Bettongia lesueur*, European rabbit *Oryctolagus cuniculus*, and Gould's sand goanna *Varanus gouldii* within dunes, ecotones, and swales in a dunefield in arid South Australia. These animals all create pits when foraging for subterranean food resources. We hypothesized that 1) the effect of pits on litter capture would vary among landscapes and animal species, 2) larger pits would trap more litter and seed, 3) pits would contain more viable seed than the surrounding matrix, and 4) the effect of pits on soil chemistry would vary among animal species, and be greater in landscapes with more finely textured soils. We found that litter was restricted almost exclusively to the pits, and was greater in pits with larger openings. Litter capture was greater in ecotones and dunes than in swales. A total of 1307 seedlings from 46 genera germinated from litter samples taken from the pits, but no seedlings emerged from samples taken from soil surrounding the pits. Foraging pits contained significantly higher levels of total C and N than surrounding soil, and total C and N concentrations were greatest in swales and lowest in dunes. Pits contained ca 55% more mineralisable N than surface soils, and pits constructed by bilbies and bettongs contained half the concentration of mineralisable N as those of rabbits and goannas. Concentrations of mineral N and mineralisable N were also greatest in the swales. Our results demonstrate the importance of animal-created pits as nutrient sinks and sites for seedling establishment, and suggest that changes in the composition of arid zone vertebrates may have resulted in profound changes to nutrient and soil dynamics in arid Australia.

Arid and semi-arid landscapes characteristically are resource-limited (Stafford Smith and Morton 1990, Shachak et al. 1999), with essential resources such as water, organic matter, seed, and sediment concentrated within resource-enriched patches (sinks, run-on zone, fertile patches, resource islands) surrounded by a resource-poor soil matrix (source, run-off zone). This patchiness manifests itself as an alternating pattern of vegetated and bare soil (Noy-Meir 1979), and occurs at a range of spatial scales. The discontinuous nature of the vegetation is thought to be controlled and maintained by processes of water erosion and soil deposition, which are driven largely by rainfall amount and intensity (Eldridge et al. 2002), and biological transport mechanisms that sequester water and nutrients from surrounding areas and retain them within the patches (Garner and Steinberger 1989). These fertile patches support most of the diversity and productivity in desert ecosystems (López-Portillo and Montaña 1999, Whitford 2002), and are critically important for the maintenance of landscape stability.

While the effects of abiotic processes on patch formation and maintenance have been the subject of much discussion (Thiery et al. 1995), there is only limited understanding of the biotic processes leading to the creation of fertile patches, although clearly both plants and animals are implicated (Schlesinger and Pilmanis 1998, Garkaklis et al. 2000, 2003). Patches are created through complex biotic interactions between individual plants and soils (Bochet et al. 1999), as well as disturbance by animals in the intervening soil matrix (Boeken et al. 1995, Whitford and Kay 1999, Eldridge and Mensinga 2007). Deposition of litter directly beneath the canopies of plants leads to zones of nutrient enrichment (García-Moya and McKell 1970, Garner and Steinberger 1989), and soil micro-, meso-, and macro-fauna are attracted to these areas of greater soil moisture and nutrient levels, further enhancing the breakdown of litter and subsequent mineralisation of organic matter. Small mammals and reptiles often are attracted to these patches, with their higher concentrations of invertebrate prey (Whitehouse et al. 2002), enhancing the turnover of

resources and therefore reinforcing this patchiness (Boeken et al. 1995).

Animals enhance patchiness directly by “engineering” their physical environment, effectively creating, maintaining, or destroying habitat in the process (Jones et al. 1994). Soil-disturbing animals are typical examples of ecosystem engineers, moving soil while foraging (James and Eldridge 2007) or creating resting sites (Guterman 1997, Eldridge and Rath 2002). In Australia, where >70% of the landmass is arid, many animals create pits while foraging for food, emulating the naturally-occurring pits and depressions on the surface of dryland soils. Any changes in surface topography will affect the flow and distribution of limiting resources. Thus the presence of both abiotically-created and biotically-mediated pits often results in an uneven distribution of organic matter and seeds across the soil surface (Reichman 1984).

Many studies have reported greater capture of water, organic matter, and seed within pits created by animals (Guterman et al. 1990, Guterman 1997, Alkon 1999, Whitford and Kay 1999) compared with the intervening soil matrix. Seeds entrained by wind or overland flow processes are deposited in the pits when they pass through zones of lower wind and water velocity (Reichman 1984). These seeds may be placed within sites of differing favourability for germination, and their distribution within the landscape will determine both the potential areas in which plants can germinate, and the likely composition of plants establishing within a patch (Whitford 2002). Pits may even trap a greater proportion of seeds than the area under shrub canopies (Reichman 1984). Nutrient- and seed-rich patches also attract soil micro-organisms (Santos et al. 1981), reinforcing feedback processes on nutrient levels by increasing the mineralisation of organic matter.

We studied the effects of pits created by 4 vertebrate engineers on seed capture and surface soil nutrients in order to speculate on their potential role in the development of fertile patches. The 4 vertebrates are all fossorial or semi-fossorial. The greater bilby *Macrotis lagotis* and the burrowing bettong *Bettongia lesueur* once were widely distributed across Australia, but were extirpated from our study area in arid South Australia before subsequent reintroduction. The European rabbit *Oryctolagus cuniculus* is a highly successful feral herbivore occurring over large areas of the arid zone (Myers et al. 1994). The indigenous Gould’s sand goanna *Varanus gouldii*, which also has a widespread distribution in the arid zone, is known to create fertile patches in semi-arid woodland environments (Whitford 1998).

These animals construct functionally different pits. Apart from small, shallow scrapings that animals make on the ground, bilby and bettong pits typically are large, cylindrical-shaped holes dug perpendicular to the ground surface. Rabbit pits are wedge-shaped and generally shallower than bilby and bettong pits. Goanna pits range from narrow, ellipsoid pits at an angle of ca 30° to the horizontal, to wedge-shaped excavations similar to rabbit pits but about twice as deep. Most of these pit shapes are readily identifiable in the field, with the exception of bilby and bettong pits which are largely indistinguishable and for this study were not separated. Although the morphology and location of animal-created pits can affect seed capture

(Duval et al. 2005) and therefore subsequent germination, few studies have compared the effects of multiple pit-creating species across different landscapes, and their resulting interactions. Thus, studies to date may have failed to adequately represent the full extent of animal activity on resource capture and patch creation.

We investigated the effect of pits created by these 4 ecosystem engineers in 3 landscapes; dunes, swales, and the intervening ecotones. Our aim was to test 4 hypotheses about animal foraging pits and resource capture in an arid dunefield; specifically, 1) the effect of pits on litter capture varies among animal species and landscapes, 2) pits with a larger opening will trap a greater mass of litter and more seeds, irrespective of animal type, 3) more seedlings will emerge from soil and litter taken from pits than material from the soil matrix, and 4) the effect of pits on soil chemistry varies among animal species, and would be greater in landscapes with more finely (more clay) textured soils (e.g. swales) compared with coarser (sandy) soils (e.g. dunes). We examined these hypotheses by studying the mass of accumulated litter and the concentration of soil nutrients for a large number of pits constructed by all 4 species across 3 landscapes in arid South Australia.

Methods

The study area

Our study was conducted at Arid Recovery, a 86 km² fenced rabbit-, cat-, and fox-free reserve located ca 20 km N of Roxby Downs in arid South Australia (30°29’S, 136°53’E). The landscape is characterised by linear, west-east trending sand dunes ca 80 m wide, and inter-dunal swales ca 500 m wide with a variable cover of stones. Dunes had sandy topsoils (5–10% clay) and supported an open shrubland of sandhill wattle *Acacia ligulata* and narrow-leaved hopbush *Dodonaea viscosa*. The swales had sandy-clay topsoils (35–40% clay) and the vegetation was dominated by chenopod shrubs *Atriplex vesicaria*, *Maireana astrotricha*. The ecotone (transition zone between the swales and dunes) was ca 10–20 m wide and characterised by fine sandy topsoils (25% clay), and vegetated by species found in both the swales and the dunes. The climate is arid, with a long-term mean annual rainfall of ca 160 mm (Arid Recovery 2004). This rainfall is temporally and spatially variable, failing to reach the long-term average of 166 mm in 60% of years (Moseby and O’Donnell 2003). The mean annual maximum temperature exceeds 35°C, and the mean annual minimum is 4°C (Olympic Dam Operations 1994).

Experimental design

We conducted our study in 3 paddocks. The first (“Main enclosure”) was a 14 km² predator-proof paddock from which rabbits have been removed and locally-extinct species reintroduced. The second (“Second expansion”) was an 8 km² paddock within the predator- and rabbit-proof reserve but within which no locally extinct species have been introduced. The third paddock (“Outside”) was outside the reserve within a mining lease operated by Olympic Dam Operations. Main enclosure contained bilbies, bettongs, and

goannas; Second expansion contained goannas only; and Outside contained rabbits and goannas. Historically, Outside paddock has been grazed only intermittently by cattle at low stocking rates and has not been grazed since the reserve was fenced in 1997.

Three “blocks” were selected within each of the 3 paddocks. Blocks were separated by distances of ca 2 km to distribute them evenly across each of the paddocks. Each block was ca 200 by 200 m and included dune, swale, and ecotone landscape elements. Measurement sites ($n = 27$) were randomly selected from within each landscape element, including 3 paddocks each with 3 replicates of the 3 landscapes (dune, ecotone, swale). This design enabled us to make comparisons between 1) the 3 complements of species occurring in the different paddocks, 2) goannas either on their own or with different animals, and 3) bilbies/bettongs and rabbits. In terms of the effects of individual study species, the study was therefore not orthogonal – i.e. not all animals were found in all 3 paddocks. Because there is only one Arid Recovery Reserve, and it was not possible to replicate the treatments elsewhere; the design is therefore pseudoreplicated, and does not allow generalisation about the effects of ecosystem engineers beyond the study site. Nevertheless, a single replicate of a unique ecosystem such as this represents a valuable opportunity to gain information about the effects of locally extinct and feral species.

Paddock characteristics

To determine whether comparisons between species were confounded by their spatial segregation (i.e. whether there were any preexisting differences between paddocks) we compared a number of plant and soil indicators between the 3 paddocks. We measured the cover of plants, litter, and bare ground, and the condition of the soil surface in 10 1-m² quadrats at each of the 27 sites according to the methods of Tongway (1995). This enabled us to derive 3 indices of soil surface health; 1) stability: how the soil withstands erosive forces or reforms after erosion; 2) infiltration: how soil water is partitioned between infiltration and runoff; and 3) nutrients: a measure of how efficiently organic material is recycled into the soil (Tongway 1995). We also measured the density of chenopod shrubs along a 50 by 4 m wide transect at each site.

Litter mass and soil nutrients

To assess whether pits trapped litter, and if pits with larger openings trapped more litter, we collected the contents of 10 randomly-selected pits at each of 9 sites (3 blocks containing each of the 3 landscape elements) in Main enclosure, and 5 pits at each of 9 sites in both Second expansion and Outside ($n = 180$). For each pit we also recorded its diameter through the centre, percent cover of bare ground, litter and plant cover surrounding the pit, and the animal responsible for digging the pit (but not differentiating pits constructed by bilbies and bettongs). Litter was dried at 40°C for 24 h and weighed. To determine whether concentrations of total carbon (C), nitrogen (N), and sulphur (S) from pit soils were higher

than non-pit soils, we collected soil samples from the same 90 pits in Main enclosure at 3 microsites: 1) beneath the litter at the bottom of the pit, 2) in undisturbed soil adjacent to the pit but at the same depth as the pit, and 3) from the surface soil 10 cm from the pit entrance ($n = 270$ samples). We chose to measure total C, N, and S as they provide an indication of the total potential nutrient availability in soils, and we were interested in whether animal foraging activity might lead to an increase in carbon, nitrogen, and sulphur pools, as all 3 elements are cycled through biological processes. Total C, N, and S were determined using a high combustion LECO CNS-2000 CNS analyser.

We also collected litter and surface soil (<2 cm depth) from an additional 5 randomly selected pits (and 5 adjacent surfaces of the same size) at each of the 9 sites in each of the 3 paddocks ($n = 270$ samples), noting also the diameter of the pits. Litter was treated as above. Soil was air-dried, passed through a 2 mm sieve, and analysed for mineral nitrogen ($\text{NH}_4^+ + \text{NO}_3^-$) and mineralisable N, according to method 4 of Gianello and Bremner (1986). This method measures the amount of N mineralised over 16 h of anaerobic digestion at 100°C, providing an index which represents the potential pool of N available to plants, and present at the time of sampling. Although this index cannot be compared numerically with NH_4^+ and NO_3^- , the values should be highly correlated with exhaustive aerobic soil incubation for N mineralisation (Gianello and Bremner 1986).

Plant germination

To determine if more viable seed accumulated in the pits than surface soil, we collected separately, soil and litter samples from the bottom of the same 90 pits in Main enclosure, and soil and litter samples from the soil surface adjacent to the same 90 pits at a distance of 10 cm from the pit entrance. Approximately 50 g samples of the soil only from either pit or adjacent surface were scattered over a layer of ca 2 kg of propagation sand in shallow trays measuring 173 × 142 × 55 mm. Control trays were also set up containing propagation sand only to control for the presence of any glasshouse weeds. Trays were placed in the glasshouse at average temperatures ranging from 14° to 19°C, and allowed to germinate under natural light conditions. An automatic sprinkler system delivered water to the trays for 1 min twice daily (09:00 and 15:00 h). The trial was run for 9 weeks (16 March–17 May 2004) and seedlings counted when they emerged from the soil. Only 4 individuals (*Digitaria ciliaris*) emerged from the soil seedbank. On 16 July, litter samples described above were placed in the glasshouse on new propagation sand and the pots watered until 8 October 2004. Seedlings were counted and removed from the trays once they could be identified. Unidentified seedlings were transplanted to larger pots and grown until they could be positively identified.

Statistical analyses

Differences in litter capture and soil nutrient concentrations were examined using a mixed-model analysis of variance (ANOVA). For analyses of litter, mineralisable N, and

mineral N ($\text{NH}_4^+ - \text{NO}_3^-$), the main plots were paddocks (Main enclosure, Second expansion, Outside), and the sub-plots landscapes (dune, ecotone, swale) and their interaction with paddocks. A third stratum considered treatment (pit vs surface) effects and its 2- and 3-way interactions with paddock and landscape. The paddock, landscape, and treatment factors were fixed, and the replicate factor was random. Species-specific animal effects were tested using the same 2-stratum analysis described above by using only data for bilbies-bettongs from Main enclosure, goanna data from Second expansion, and rabbit data from the Outside paddock. For species-specific effects we examined separately both average litter mass per pit, and litter mass m^{-2} of pit opening (to account for potentially different-sized pits dug by different animals). Differences in total carbon, nitrogen, and sulphur ($\log_e(10x + 0.0001)$ transformed) were tested with a mixed-model ANOVA with 2 error terms using data from Main enclosure only. The whole-plot stratum considered landscapes, and the sub-plot stratum microsites (i.e. surface, pit, or adjacent) and its interaction with landscapes. For all analyses, data were checked for homogeneity of variance, independence, and normality using Levene's test and other diagnostic tools within the Genstat statistical package (Payne et al. 1993) and transformed where appropriate to stabilise the variances. In all cases, significant differences between means were compared using Tukey's least significant difference (LSD) testing.

Total litter mass (g pit^{-1}) was analysed using exploratory non-parametric classification and regression trees (CART), as implemented in Crawley (2003). The CART technique forms a decision tree which, similar to multiple regression analysis, seeks to predict total litter mass from the set of independent explanatory variables, which were: paddock, replicate, landscape, animal creating the pit, pit size, and percent cover of bare ground, litter or plant cover surrounding the pit. The construction process splits the response variable into subsets, according to whether or not they are less than a particular value of one of the continuous explanatory variates (a regression split) or discrete explanatory variates (a classification split). At any split-point, the decision rule that is finally adopted yields the greatest reduction in the residual deviance (maximum separation of resulting sub-groups). The advantage of CART is that no assumptions are made regarding the underlying distribution of the values of the predictor variables, and the analysis can

handle data which are highly skewed or multi-modal, and categorical predictors with either an ordinal or non-ordinal structure (Breiman et al. 1984). To avoid over-fitting the model, a parsimonious sub-grouping was declared at the formation of 6 subgroups after examining a scree plot. Regression analyses were used to examine possible relationships between 1) pit opening (diameter) and mass of litter trapped, 2) litter mass and soil nutrients (total C, N and S, mineralisable N, and $\text{NH}_4^+ - \text{NO}_3^-$) in the pits, and 3) pit opening and the abundance and diversity of seedlings.

Two matrixes, one comprising the type of litter found in the pits (frass, leaves, twigs, etc.) and the other the abundance of each plant species germinating in the pits, both by landscape type, were converted to similarity matrixes using the Bray Curtis similarity coefficients contained within the PRIMER (ver. 5) statistical package (Clarke and Gorley 2001). These were then subjected to non-metric multi-dimensional scaling (NMDS) and scree plots used to determine the appropriate number of dimensions in which to examine the results. Hypothesis tests, defined a priori, were performed using ANOSIM which derives a test statistic (Global R) and a significance level to determine differences in the suite of litter or plant species in relation to landscape and paddock. The DIVERSE function of Primer was used to calculate 4 community measures (number of species, number of individuals, Margalef's richness, and evenness) for each of the 90 germination trays. Differences in composition of seedlings between the 3 landscapes were examined with a Kruskal-Wallis test and multiple-comparison tests described in Siegel and Castellan (1988). Samples from the 10 pits in each site by landscape combination were pooled resulting in 3 independent values for each landscape.

Results

Paddock characteristics

There were no significant differences in plant cover, litter cover, bare soil, or the 3 indices of soil surface health between the 3 paddocks (Table 1). Although there were about a third fewer *Atriplex vesicaria* shrubs in Second expansion than the other paddocks, the differences were not significant (Table 1).

Table 1. Mean (\pm SEM) cover of plants, bare soil, and litter, indices of soil health, and density of *Atriplex vesicaria* in the three paddocks. Data were analyzed with a mixed-model ANOVA.

Attribute	Paddocks and animals present						p-value
	Main enclosure bilby, bettong, goanna		Second expansion goanna		Outside rabbit, goanna		
	Mean	SEM	Mean	SEM	Mean	SEM	
Plant cover (%)	15.4	3.15	16.5	2.00	13.9	2.38	0.59
Bare soil %	63.7	4.55	63.4	2.74	62.6	3.83	0.33
Litter cover %	15.4	2.91	15.4	1.96	17.6	2.45	0.06
Stability (%)	47.0	0.82	49.0	1.16	48.9	1.87	0.26
Infiltration (%)	46.7	3.14	47.6	2.89	48.1	1.93	0.70
Nutrient (%)	22.4	1.33	21.7	0.71	23.5	0.98	0.45
<i>A. vesicaria</i> density ha^{-1}	7633	2028	4933	1828	7033	3434	0.54

Litter capture in the pits

Litter was restricted almost exclusively to the pits ($F_{1,18} = 85.7$, $p < 0.0001$; Fig. 1), and a significant treatment \times landscape interaction indicated that litter capture was substantially greater in pits in the dunes and ecotones than in swales ($F_{2,18} = 84.2$, $p = 0.023$, Fig. 1). This landscape effect was non-significant, however, when pit opening was taken into account ($p = 0.075$, Fig. 2b). There were no significant differences in litter capture between the 3 paddocks (6.81 ± 0.84 g pit⁻¹ Main; 5.55 ± 1.04 Second; 5.84 ± 0.99 Outside; $p = 0.94$). Trends were the same whether we analysed data for all pits found within a paddock, or restricted our analyses to species-specific pits (i.e. analysis only of bilby-bettong pits from Main enclosure, goanna pits from Second expansion, and rabbits pits from outside the enclosure).

Litter capture tended to increase with the size of pit openings, which explained 27% of the variance in litter mass in the ecotones ($F_{1,58} = 34.4$, $p > 0.001$) and 23% in the swales ($F_{1,58} = 18.2$, $p > 0.001$), but only 12% in the dunes ($F_{1,58} = 8.9$, $p = 0.004$). There was a strong relationship between pit opening size and the mass of litter trapped in bilby-bettong pits ($F_{1,71} = 44.2$, $p < 0.0001$, $R^2 = 0.38$). For rabbit ($F_{1,40} = 7.59$, $p = 0.009$) and goanna ($F_{1,63} = 13.1$, $p = 0.001$) pits, however, the predictive power of pit opening size was relatively poor ($R^2 = 14\%$). CART analysis indicated that the size of pit openings was the best predictor of the mass of litter trapped, followed by the percentage cover of litter surrounding the pit, then percentage plant cover surrounding the pit.

Composition of trapped litter

Litter composition varied among landscapes (Global $R = 0.31$, $p = 0.001$, Fig. 3), with a lower mass of leaf, and a greater mass of the “other” component (mainly frass, invertebrates, and dung) in pits in the swales than pits in dunes or ecotones. When analyses were restricted to the relatively large seeds of *Atriplex*, *Maireana*, and grass inflorescences only, dunes differed significantly from both ecotones and swales ($p = 0.044$). As expected, most of the differences were due to a greater mass of *Atriplex* seed

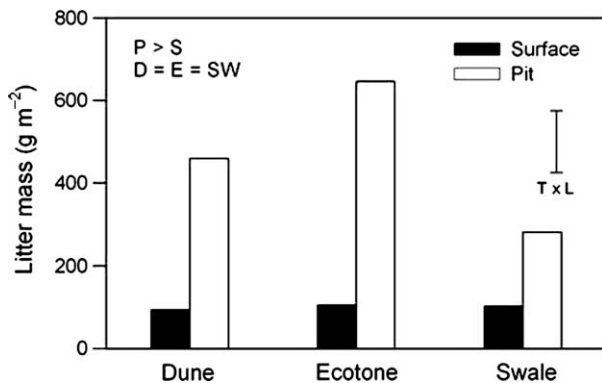


Figure 1. Mean litter mass (g m⁻²) in pits and surface soils in the dunes, ecotones, and swales. The 5% LSD bar for the treatment (pit vs surface) by landscape (dune, ecotone, swale) interaction is shown. P = pit, S = surface, D = dune, E = ecotone, SW = swale.

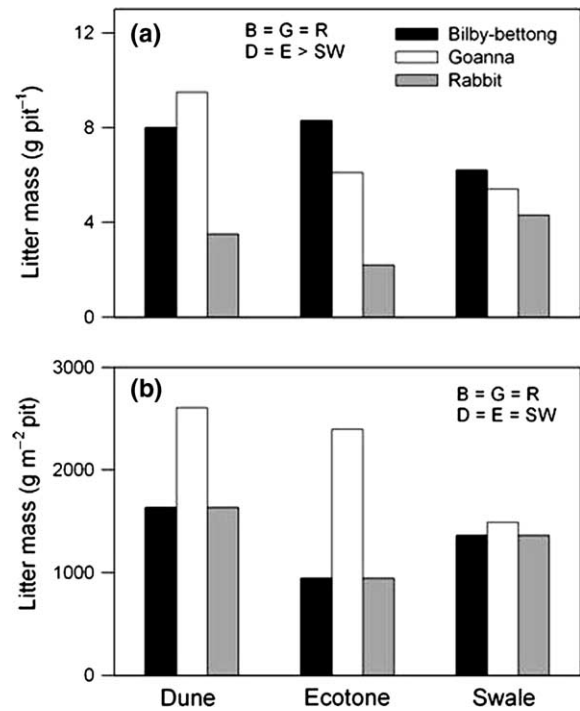


Figure 2. Litter capture (a) g pit⁻¹ and (b) g m⁻² of pit opening, in relation to landscape and type of animal. B = bilby/bettong, G = goanna, R = rabbit, D = dune, E = ecotone, SW = swale.

trapped in pits in the ecotones and swales than in the dunes. The composition of trapped litter differed between Main enclosure and Outside (Global $R = 0.29$, $p = 0.002$), but there were no differences between Second expansion and either of the other 2 paddocks ($p > 0.05$).

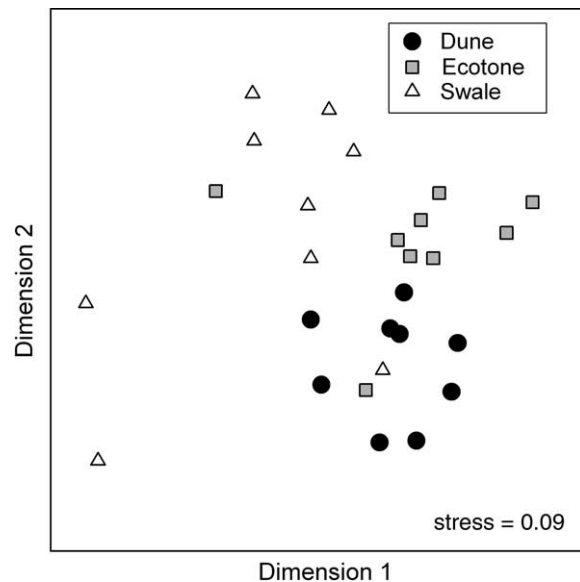


Figure 3. The first two dimensions of the MDS biplot based on the composition of litter captured within the pits. The axes are scaled by standard deviates of the normalized scores, and the low stress of 0.09 indicates that the data can be effectively represented in two dimensions.

Germination of seed from the pits

No plants germinated from the surface soil, and only 4 *Digitaria ciliaris* (Poaceae) plants emerged from pit soil (3 from dunes and 1 from the swales). However, 1307 seedlings from 46 genera emerged from litter samples taken from the pits. Three species – the forbs *Atriplex holocarpa* and *A. vesicaria* (Chenopodiaceae) and the grass *Eragrostis dielsii* – comprised 53% of all germinating seedlings (Table 2). There were large differences in the species composition among the 3 landscapes (e.g. 85% of *Atriplex holocarpa* germinated from litter in pits in the swales compared with 4% from the dunes), but differences were significant for only 4 species (Table 2). There were twice the number of *Atriplex vesicaria* plants in the ecotones and swales compared with the dunes (Kruskal-Wallis $H=7.28$, $p=0.026$, $DF=2$), 6 times more *Dactyloctenium radulans* ($H=7.0$, $p=0.030$, $DF=2$) in the ecotones and swales, 6 times more *Eragrostis dielsii* ($H=6.33$, $p=0.042$, $DF=2$) in the dunes and swales, and 6 times more *Atriplex spongiosa* ($H=14.0$, $p=0.001$, $DF=2$) in the swales.

There was no significant difference in plant composition in the 3 landscapes (Global $R=0.292$, $p=0.68$). Fewer species germinated from litter captured in pits in the dunes than litter from the ecotones, while pits in the swales differed only slightly from the other landscapes ($F_{2,82}=7.28$, $p=0.046$). There were no significant differences in the number of individuals, richness (Margalef's index), or evenness ($p>0.49$) among landscapes. Contrary to our expectation, larger pits supported neither more individual seedlings ($p=0.80$) nor more species ($p=0.54$). Similarly, there were no differences in abundance nor species diversity in relation to the mass of litter trapped in the pits ($p>0.14$).

Total carbon, nitrogen and sulphur

The pits in Main enclosure contained 3 times the concentration of total C (0.62%) and twice the concentration of total N (0.03%) than either surface soils or soils at depth

Table 2. Total abundance of common plant species germinating from litter collected from 90 pits in Main enclosure in 3 landscape positions (summed over replicates). Only species with >10 seedlings across all landscapes are shown. Different superscripts indicate a significant difference in seedling numbers between landscapes at (Tukey LSD, $p<0.05$).

Species	Landscape		
	Dune	Ecotone	Swale
<i>Atriplex holocarpa</i>	9	30	216
<i>Atriplex vesicaria</i>	33 ^a	128 ^b	62 ^b
<i>Eragrostis dielsii</i>	82 ^a	106 ^b	32 ^a
<i>Atriplex spongiosa</i>	2 ^a	13 ^a	77 ^b
<i>Digitaria ciliaris</i>	36	24	29
<i>Dactyloctenium radulans</i>	6 ^a	40 ^b	41 ^b
<i>Crassula sieberiana</i>	7	19	44
<i>Calotis hispidula</i>	2	2	42
<i>Rhodanthe stricta</i>	0	0	29
<i>Gnephosis</i> sp.	5	3	20
<i>Tetragonia eremaea</i>	0	5	15
<i>Wahlenbergia</i> sp.	1	8	9
<i>Plagiosetum refractum</i>	16	2	0

(C: $F_{2,174}=79.7$, $p<0.001$; N: $F_{2,174}=22.7$, $p<0.001$). All three landscapes differed significantly in total C and N, with concentrations greatest in the swales (0.56%, 0.04% for C and N respectively), intermediate in the ecotones (0.31%, 0.02%), and least in the dunes (0.23%, 0.01%; C: $F_{2,81}=30.64$, $p=0.004$; N: $F_{2,81}=10.37$, $p=0.026$). There also was twice the amount of total S in the dunes (0.002%) than the ecotones ($F_{2,81}=13.51$, $p=0.017$; Fig. 4). However, total S did not differ between the 3 microsities (range: 0.02–0.05%; $p=0.08$), and there were no significant microsite \times landscape interactions ($p>0.05$). Increases in litter trapped in the pits corresponded with increases in total C for both ecotones ($F_{1,28}=7.65$, $p=0.01$, $R^2=0.19$) and swales ($F_{1,28}=8.47$, $p=0.007$, $R^2=0.2$), but not for dunes ($p=0.40$).

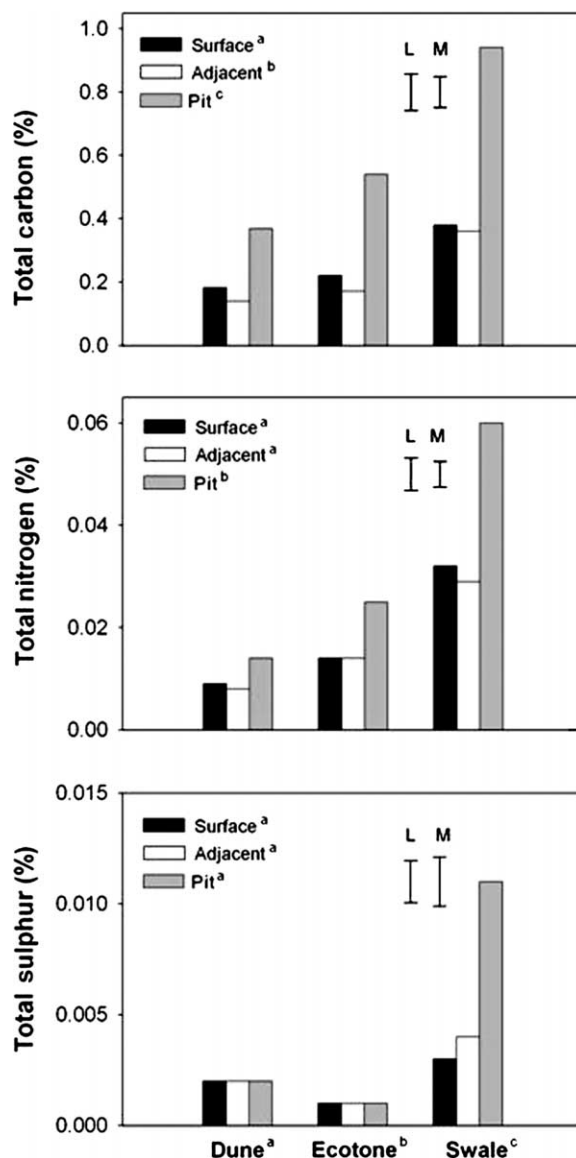


Figure 4. Mean concentration of total carbon (%), total nitrogen (%), and total sulphur (%) in relation to landscape and microsite. The 5% LSD bars for landscape (L) and microsite (M) are shown. Different superscripts between landscapes or microsities indicate a significant difference at $p<0.05$.

Ammonium-nitrate and mineralisable nitrogen

Mineral N ($\text{NH}_4^+ + \text{NO}_3^-$) concentrations in the swales ($6.29 \pm 0.85 \text{ mg kg}^{-1}$) were more than twice those in the dunes or ecotones ($F_{2,12} = 14.6$, $p < 0.001$ on $\log_{10}(x+1)$ transformed data) and 36% greater in the pits than the surface ($F_{2,12} = 14.6$, $p < 0.001$ on $\log_{10}(x+1)$ transformed data; Fig. 5A). A significant pit \times landscape interaction ($F_{2,18} = 4.8$, $p = 0.021$ on $\log_{10}(x+1)$ transformed data) indicated that the increase in $\text{NH}_4^+ + \text{NO}_3^-$ concentrations in the pits over and above that at the surface was much greater for swale soils than for dune soils. It also indicated that the relative importance of pits, in terms of $\text{NH}_4^+ + \text{NO}_3^-$ concentrations, increased with increasing soil clay content of the soil (i.e. from dune to swale).

Soils in the swales contained more than twice the concentration of mineralisable N compared with those in dunes and ecotones ($F_{2,12} = 38.2$, $p < 0.001$ on $\log_{10}(x+1)$ transformed data), and pits contained ca 55% more mineralisable N than surface soils ($F_{1,18} = 37.1$, $p < 0.001$ on $\log_{10}(x+1)$ transformed data; Fig. 5B). There were no significant pit \times landscape interactions ($p = 0.53$). Interestingly, pits constructed by bilbies and bettongs (Main enclosure) contained only half the concentration of mineralisable nitrogen as those constructed by goannas (Second expansion) or rabbits (Outside; $F_{2,6} = 15.4$, $p = 0.004$ on $\log_{10}(x+1)$ transformed data).

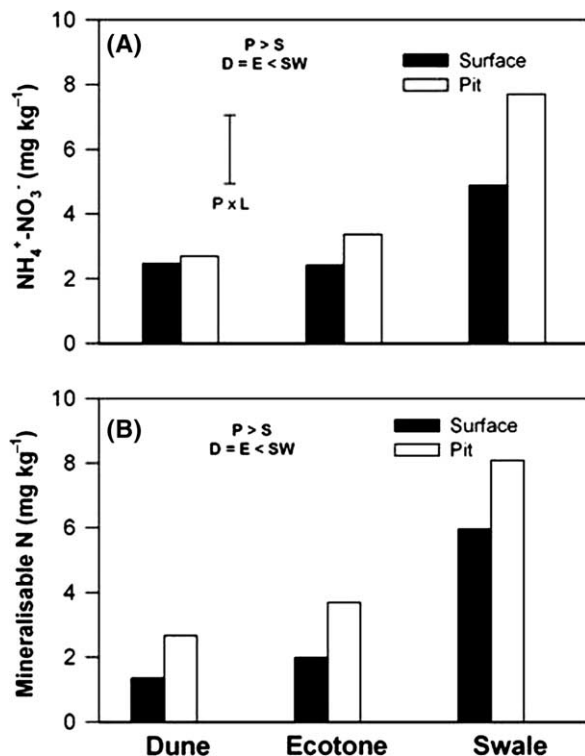


Figure 5. Mean concentration of (A) $\text{NH}_4^+ - \text{NO}_3^-$ and (B) mineralisable nitrogen in relation to landscape and microsite. The 5% LSD bar for the landscape by microsite interaction is shown for $\text{NH}_4^+ - \text{NO}_3^-$. There was no significant landscape by microsite interaction for mineralisable N. P = pit, S = surface, D = dunes, E = ecotones, SW = swales.

Apart from moderate correlations between litter capture in pits and the concentration of mineralisable N in pits constructed by goannas in the ecotones ($r = 0.62$, $p = 0.014$), and by rabbits in the swales ($r = 0.59$, $p = 0.021$), there were no significant relationships between the mass of litter in the pits, nor the mass of litter in the pits (adjusted for differences in the size of the pit opening), and either mineralisable nitrogen or $\text{NH}_4^+ + \text{NO}_3^-$.

Discussion

Our study demonstrated that foraging pits are effective traps for both litter and seed. While most pits contained litter, the surface soil was only sparsely litter-covered, consistent with the first hypothesis and studies from other desert systems (Reichman 1984). The consistently greater mass of litter captured in the pits, up to 20-times that from an equivalent area of adjacent non-pit soil surface (Fig. 1), suggests that pits are confining litter and entrained seed within areas that would otherwise be resource-poor. Sparse litter and low seed densities in the inter-pit areas have been attributed to runoff from the surface (Shachak et al. 1991, Boeken et al. 1995) and the winnowing effect of the wind (Reichman 1984). Pits play an important role in litter capture, complementing other patch types such as fallen logs and shrub hummocks (Tongway et al. 1989, del Valle et al. 1999, Whitford 2002) that function as focal points for litter accumulation and for invertebrate and vertebrate herbivores (Steinberger and Whitford 1983), further reinforcing organic matter additions to the soil. Thus, pits not only represent an additional litter sink, but may also act as hotspots for seed capture and plant germination away from established shrub patches.

The extensive germination of seed from pit-resident litter (Table 2) confirms our fourth hypothesis that pits are substantial seed traps. Pits are known to be safe sites for plant germination (Alkon 1999), and studies from the South African Karoo have shown that >96% of all seedlings in an inter-dunal swale were restricted to animal pits (Dean and Milton 1991). Similarly in the Negev Desert, bedding sites of ibex *Capra ibex nubiana* supported most of the surviving plant seedlings (Gutterman 1997), and in the Great Basin Desert, almost all Indian rice-grass *Oryzopsis hymenoides* seedlings originated from seeds captured in rodent pits (Longland 1995). Seed capture in animal pits can also have flow-on effects at larger spatial scales. For example, in western NSW, capture of seeds within goanna pits is thought to contribute to the capture and retention of water and sediments in banded mulga landscapes and therefore to the maintenance of vegetation patterning (Whitford 1998).

In our study we cannot say how much of the original seed cache might have been removed by ants, rodents, or reintroduced mammals. Nevertheless, at this single point in time, pits contained substantial seed from a large number of genera, some known to be important food items of the bilby (e.g. *Dactyloctenium radulans* and *Crotolaria* spp., Southgate 1990, Gibson 2001). It is unclear therefore whether there is a treasure effect whereby animals might be attracted to the caches of seeds in the pits (Gutterman 1997) or whether seed-rich microsites may increase crowding of seedlings in

situ (Huntley and Inouye 1988). Other studies have shown that surface-borne seeds are accessible to predation by invertebrates and rodents, and conditions generally are unfavourable for germination (Steinberger and Whitford 1983, Whitford 2002). We found no apparent relationship between pit opening size and the number of seedlings, and contrary to our expectation, larger pits supported neither more individual seedlings nor more species. This is an important finding, as it suggests that an assortment of small pits may be as effective as a few large pits. This suggests that pits of a range of sizes, created by a suite of different-sized soil-digging animals, may be equally important for trapping litter and seeds. We suspect that pit age would also have an important effect on litter capture, with older pits trapping more litter and seeds that become incorporated with wind-blown soil as the pits slowly degrade and fill in.

While pit opening was the best predictor of mass of litter trapped in all landscapes, particularly the swales and ecotones, the relationship was not consistent between animal species, supporting our second hypothesis. The lack of stronger predictive power is not surprising, given that we could not accurately age the pits, potentially confounding the results with pit age. While pit opening explained 38% of the variance in litter mass in bilby-bettong pits, the predictive power for rabbit and goanna pits was low. Rabbit pits are relatively shallow and may be unable to retain litter for long periods. Conversely, goanna pits, unlike those of the other engineers, are deeper (11.0 cm) than bilby-bettong pits (9.1 cm), inclined at an angle of ca 30° to the horizontal, and the entrance has generally smaller (albeit not significantly so) openings (0.039 m²) than bilby-bettong pits (0.047 m²), giving them a smaller surface area to volume ratio. Research from the northern Chihuahuan Desert indicated that the trapping efficiency of small heteromyid rodent pits with narrow entrances was greater than that of similar-sized pits with larger entrances (Steinberger and Whitford 1983). This suggests that the effectiveness of pits as resource sinks may be related more to their capacity to retain material rather than any innate capacity to capture it, reinforcing our view that a mixture of pit sizes is advantageous.

For a given pit opening, significantly more litter was captured in pits in the dunes and ecotones than in the swales, consistent with our hypothesis of variable capture between landscapes. We suggest that the effect of pit opening on litter capture is moderated by interactions between physical and morphological characteristics of the pits (e.g. shape, depth, angle of excavation), and abiotic features such as soil texture and landscape position. For example, the soils on the dunes and ecotones have predominantly sandy surface textures (sands to loamy sands) and are weakly aggregated, and therefore highly erodible by wind. We have observed that surface sand and entrained litter are deposited in the pits during wind storms, and the build up of successive layers of sand in the pit prevents litter from being remobilised. Apart from wind and water, animals also cover litter with soil while foraging or reworking old bedding sites (Dean et al. 1999, Eldridge and Rath 2002, Garkaklis et al. 2004, Bancroft et al. 2005). Further, when animals dig into sandy soils, the pit edges often collapse. We suggest that the ability of pits to retain litter increases with declining stability of the

surrounding soil, although pits excavated in more stable clay soils are likely to persist for longer than those in sandy soils (James unpubl.). The fact that litter cover close to the pit was a good predictor of capture in the pits could indicate that pits trap locally-derived plant material. The dunes and swales are populated by different vegetation types; whereas dunes are sparsely covered by larger shrubs that shed more litter, swales are covered by shorter chenopods. The extent to which litter is trapped within a community in which it is derived would depend on the density of pits and natural obstacles close to the point of litter fall. It could also indicate that the general area (i.e. mosaic of pit and non-pit) is an area of low wind velocity and therefore a site of high litter coverage (e.g. a run-on zone). Wind velocities on the elevated dunes are presumably different to the flat swales, which may also have an effect on the movement of both litter and soil.

Trapping of litter beneath layers of soil has important implications for breakdown of organic matter and mineralisation of carbon and nitrogen in desert systems. Litter moderates fluctuations in soil temperature, with lower temperatures increasing the period over which litter-active micro-arthropods remain above-ground (Cepeda-Pizarro and Whitford 1989). The mixing of sand and litter will bring soil-borne fungi and micro-arthropods into direct contact with organic matter, and the mulching effect is likely to reduce evaporation, and retain soil moisture for longer periods (Wallwork et al. 1985, Jacobson and Jacobson 1998, Mohr et al. 2005). Thus the trapping of litter in animal-created pits is an effective means of holding litter in situ and allowing it to be broken down by microbes, thereby contributing to soil nutrients (Jones et al. 2006). In contrast, material remaining on the surface is subject to abiotic breakdown by ultraviolet light and comminution by wind, making it unavailable to microbes and micro-arthropods and contributing little to soil nutrient pools.

As nitrogen is a limiting resource in deserts, its distribution has important implications for plant community composition (Schlesinger et al. 1990). Most nitrogen occurs in the top few cm of the soil (Murphy et al. 1998), and digging is therefore likely to truncate this N profile and lead to lower N concentrations through erosion of topsoil. The addition of litter to desert soils results in the immobilisation of much of this mineralised N by microbes, reducing its availability for plants in the short-term (Zaady et al. 1996). Over longer periods, however, decomposing litter provides a slow release of N. Thus, unlike the rapid, short-duration flush of N following rainfall in desert systems, the slow release of N from pit-resident litter may sustain the soil microbial biomass for longer periods, allowing plant growth to persist later into the season (Zaady et al. 1996). In our study, pits contained greater concentrations of total C and total N than adjacent non-pit soils, and this effect was greatest in the swales and least in the dunes (Fig. 4). Similarly, mineralisable N was 50% more abundant in pits than in the non-pit surface. Our results suggest that the pits that we sampled had sufficient time to develop a nutrient profile through decomposing organic material. This was particularly the case for goanna and rabbit pits, but less so for bilby-bettong pits, which turn over more rapidly due to the greater chance that the bilby-bettong pits we selected would be younger, given the high density of animals. Given

the inherently low nutrient status of Australian desert soils (Stafford Smith and Morton 1990), even small inputs of soil nutrients through litter decomposition in animal pits are likely to have important consequences for soil fertility and therefore plant establishment.

The relationships between landscape position, litter capture, and soil C and N concentrations suggest that the development of fertile patches will not be uniform across this arid shrubland. While dunes and ecotones trapped more litter, ecotones and swales retained more C and N from litter decomposition, probably because the soils have a greater percentage of fine material. We suggest that pits will have their greatest effect on resource capture in the ecotones where tradeoffs between litter capture and decomposition and nutrient adsorption to fine particles is greatest. Similarly the propensity for pits to trap litter differed among animal species, probably due to differences in pit morphology. This could result in differences in seed capture and plant germination in pits of different animal species. When these effects are combined with differences in per-capita rates of excavation between species (James and Eldridge 2007), the likely effects of the decline in medium-sized fossorial mammals is a dramatic alteration to resource movement and patterns of fertile patch creation in the Australian arid zone. Reintroduction of bettongs and bilbies to parts of their former range provides the opportunity to further investigate the links between these species and resource dynamics and whether they play a unique role in ecosystem function and restoration.

Acknowledgements – We thank Celeste Ellice, Jeff Turpin, Nicki Munro, Katherine Moseby, and John Read for assistance with field work, and Jess Mason, Sarah Howcroft, and Jessica Bryant for assisting with laboratory work. Frank Hemmings identified many of the glasshouse plants, and Geoff McDonnell helped with the germination trials. Wendy and Steve Williams analysed soil nitrogen. We thank Ian Oliver for comments on an earlier draft, and Terry Koen for undertaking the detailed statistical analyses. This study was supported by Arid Recovery, a joint conservation initiative between BHP Billiton, Univ. of Adelaide, SA Dept for Environment and Heritage, and the Friends of Arid Recovery.

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