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# Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape

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## ABSTRACT

Substantial range declines of the greater bilby (*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*) are thought to have had dramatic effects on ecosystem processes in the Australian arid zone because of their impacts on surface soils. The reintroduction of bilbies and bettongs into a reserve in central Australia provided an opportunity to compare their ecosystem impacts with those of two prevalent fossorial animals; the exotic European rabbit (*Oryctolagus cuniculus*) and the native sand goanna (*Varanus gouldii*). Bilbies and bettongs dug deeper and wider pits, excavating significantly more soil than rabbits or goannas. Pit coverage was four-times greater, and significantly more soil was excavated in the reserve where bilbies, bettongs and goannas were enclosed together compared with a site outside the reserve where rabbits and goannas co-occurred, or within the reserve where goannas occurred alone. Goannas dug fewer holes outside the reserve than in either of the reserve paddocks. Litter and viable seed were restricted almost exclusively to the pits, and soil from pits had higher levels of labile carbon than non-pit surface soils. Compared with surface soils, bilby, bettong and goanna pits contained relatively more labile carbon than rabbit pits. The significantly greater soil excavation by the bilbies and bettongs, and higher concentrations of carbon in their pits, relative to rabbit and goanna pits, demonstrate that these reintroduced fossorial mammals play important roles in the creation of fertile patches in arid landscapes. The results suggest that the extirpation of Australia's mammal fauna has been accompanied by a loss of key ecosystem processes.

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## 1. Introduction

Australia has suffered the highest rate of recently recorded mammal extinctions, with more than 30% of its mammalian fauna now listed as extinct, endangered or vulnerable (Short and Smith, 1994; Department of Environment and Water Resources, 2007). This has largely been attributed to two introduced predators; the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) (Smith and Quin, 1996; Johnson, 2006), as well as habitat fragmentation, overgrazing, altered fire regimes and

the invasion of feral herbivores such as the European rabbit (*Oryctolagus cuniculus*) (Morton, 1990; Short and Smith, 1994). The extinctions have mainly been medium-sized mammals; and throughout most of semi-arid and arid Australia south of the tropics, all ground-dwelling mammals in the critical weight range of 35 g–5.5 kg (Burbidge and McKenzie, 1989) have disappeared (Johnson, 2006). Furthermore, a third of the extant marsupial species have disappeared from more than 50% of their original geographic range (Maxwell et al., 1996). These losses, and the extensive range declines of the

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medium-sized native mammals, have undoubtedly had significant effects on ecosystem structure and function.

Associated with the decline in native mammals has been an eruption in the range of the European rabbit; a medium-sized feral herbivore (Strahan, 1995). The effects of rabbit grazing, combined with extreme drought, can have disastrous consequences for the health and diversity of arid zone vegetation (Wood, 1988; Leigh et al., 1989). For example, grazing by rabbits is implicated in the decline in recruitment of many long-lived woodland trees such as *Acacia* spp. (Lange and Graham, 1983). Rabbits are also a preferred prey species of feral predators, leaving native mammals vulnerable to predation during periodic crashes in rabbit numbers (Jarman, 1986; Smith and Quin, 1996; Johnson, 2006).

Many large-scale conservation efforts within Australia have therefore focussed on reintroducing species to areas where low densities of feral predators and herbivores are maintained by baiting programs or the erection of predator-proof fences (Short et al., 1992; Short and Turner, 2000; Moseby and Read, 2006). Reintroduction of threatened species is an increasingly popular goal of conservation, and is seen as a viable means for restoring population size and preventing extinction, with the ultimate goal being the re-establishment of wild populations of the reintroduced species (Griffiths et al., 1996). Most reintroduction projects have focussed upon the dynamics of reintroduced populations, the practical methods involved and the subsequent success or failure of reintroduction (Fischer and Lindenmayer, 2000; Seddon et al., 2007).

Although the restoration of ecosystems may be a corollary or even a goal of reintroduction, few studies have examined the effects of reintroductions on ecosystem health (however, see Hägglund and Sjöberg, 1999). Since species are being restored to their former range, an examination of the impacts of reintroduction on ecosystem health not only provides a measure of restoration success, but also gives valuable insights into how systems may have functioned prior to the loss of species, and therefore, prior to degradation. The reintroduction of a species will likely alter ecosystems not only through the consumption of resources and other trophic level effects, but also through the modification of habitat. Organisms that modify, maintain, create or destroy structure within the physical environment have been termed 'ecosystem engineers' (Lawton, 1994; Jones et al., 1997; Hastings et al., 2007). Such modifications can affect energy flows and the availability of resources to other organisms, including positive feedback to the engineer itself (Jones et al., 1997; Day et al., 2003). The modification of the abiotic environment by ecosystem engineers can dramatically alter water flows, nutrient levels, micro-organisms, seed capture and habitat quality (Decaens et al., 2002). Ecosystem engineers may also increase species richness, diversity and productivity by creating patches of habitat differing in resource availability, thus enabling organisms of different resource requirements to coexist (Day et al., 2003; Odling-Smee et al., 2003). Numerous examples from terrestrial and aquatic ecosystems have demonstrated that the removal or addition of 'keystone' modifiers from a system can drastically alter the surrounding environment (Gutierrez et al., 2003; Zhang et al., 2003).

The impact of ecosystem engineering is predicted to be greater in harsh environments such as arid and semi-arid areas, where production is limited more by resource flows than by trophic interactions, and where amelioration of habitat is likely to increase the survival of organisms and extend their distributions (Bertness and Callaway, 1994; Crain and Bertness, 2006). Given that reintroductions may often be to degraded areas where species and habitat have been lost, the engineering effects of reintroduced species may be of even greater significance. It has also been suggested that ecosystem engineers can aid restoration efforts by reducing the threshold effort or human input required to restore a landscape to a desired state (Byers et al., 2006).

The greater bilby and burrowing bettong are two marsupials that have been reintroduced to a handful of fenced reserves in Australia. Both species are within the critical weight range (Burbidge and McKenzie, 1989), and were once widely distributed across arid Australia (Morton, 1990; Southgate, 1990a). Greater bilbies now occupy only 20% of their former range and are restricted to a small isolated population in south-western Queensland and low-density populations in the Tanami Desert in the Northern Territory, and the Gibson and Great Sandy Deserts in Western Australia (Southgate, 1990a). Burrowing bettongs were one of the most widely distributed mammals on the continent (Finlayson, 1958) and are now restricted to two predator-free islands off the Western Australian coast (Strahan, 1995). Along with the sand goanna (*Varanus gouldii*), which is widely distributed throughout the arid zone, these two vertebrates create small pits or depressions in the soil surface while foraging (Southgate, 1990b; Whitford, 1998; Robley et al., 2001). Bilbies and bettongs are omnivorous, and dig for seeds, invertebrates, bulbs and fungi (Southgate, 1990b; Gibson, 2001; Robley et al., 2001), while goannas generally forage for invertebrates and small reptiles (King and Green, 1979).

Pits constructed during foraging capture resources that flow across the landscape (Alkon, 1999; Whitford and Kay, 1999; Zhang et al., 2003), intercepting water flows and entrained organic matter and seeds (Guterman and Herr, 1981; Reichman, 1984; Boeken et al., 1995), and creating areas of higher moisture and nutrient-rich hotspots of litter decomposition (Steinberger and Whitford, 1983; Hawkins, 1996; Garkaklis et al., 2003; Eldridge and Mensinga, 2007). The creation of these 'fertile patches' may be an important process that enhances the germination and establishment of plants in resource-depleted landscapes. Pits contribute to microsite-level patchiness, leading to landscape-level increases in spatial heterogeneity of resources. For example, the foraging pits of goannas structure mulga (*Acacia aneura*) landscapes by trapping litter and seeds on the upslope edge of the timbered mulga groves, thus maintaining zonation between the resource-rich groves and the resource-poor inter-groves (Whitford, 1998).

This study was conducted at Arid Recovery, a feral animal-proof enclosure in northern South Australia. The presence of reintroduced bilbies, bettongs and goannas in a large reserve, as well as populations of rabbits and goannas outside the reserve, provided the opportunity to compare the effects of foraging pits created by three native vertebrates with that of pits created by the exotic rabbit. Specifically, the objective

was to examine the engineering effects of the four vertebrate species on soil chemistry, resource capture and plant germination, and therefore, the implications for ecosystem processes in arid shrubland.

The aim of this study was to examine the magnitude of soil excavation and resource capture at both microsite (individual pits) and landscape scales within three landscape elements; dunes, swales and the intervening ecotones, and within three paddocks occupied by different complements of animals that all excavate pits. This study tested a number of predictions about litter and seed capture and soil carbon in relation to foraging pits and landscape elements (dune, ecotone, swale), and about the density of foraging pits in relation to species composition and landscape element. Specifically, these predictions were that: (1) all ecosystem engineers would excavate more soil and dig more pits in the ecotones, because these sites contain elements of both dunes and swales and support the most productive and diverse vegetation community, (2) resource (litter, seed) capture would be greatest in the pits, where litter, soil and seed is retained *in situ* rather than being redistributed by wind and water, (3) the effect of pits and subsequent litter capture on the concentration of labile carbon would be greatest in the swales, where clay contents are greatest, and least on the dunes, and, (4) the ecosystem response would be highly species-dependent, in particular, the effects of bilbies and bettongs would be greater than that of rabbits. The purpose of testing these predictions was to determine whether the loss of reintroduced fossorial animals alters ecosystem processes and if so, in which part of the landscape the effects are likely to be greatest.

## 2. Methods

### 2.1. The study site

Arid Recovery is located 20 km north of Roxby Downs in arid South Australia (30°29'S, 136°53'E). The landscape is characterised by linear, east-west trending sand dunes and inter-dunal swales, often with a variable surface cover of stones ('gibbers') up to 5 cm in diameter. Dunes were about 200 m wide, had sandy topsoils (5–10% clay) and supported an open shrubland of sandhill wattle (*Acacia ligulata*) and narrow-leaved hopbush (*Dodonaea viscosa*). The intervening gibber swales were about 500 m wide, had sandy-clay topsoils (35–40% clay) and were dominated by shrubs from the family Chenopodiaceae (*Atriplex vesicaria*, *Maireana astrotricha*). The ecotones, intermediate areas between the swales and dunes, were 10–20 m wide, characterised by fine sandy topsoils (25% clay), and vegetated by species found in both the dunes and swales.

The climate is arid, and the rainfall temporally and spatially variable, failing to reach the long-term average of 166 mm in 60% of years (Moseby and O'Donnell, 2003). At the time of the study in December 2003, the mean daily maximum temperature was 34.5 °C and the mean daily minimum was 19.3 °C (Bureau of Meteorology, 2004). The mean annual maximum temperature exceeds 35 °C, and the mean annual minimum is 4 °C (Olympic Dam Operations, 1994).

The Arid Recovery reserve is an 86 km<sup>2</sup> enclosure in which cats, foxes and rabbits have been eradicated and are pre-

vented from reinvading by a 2.5 m electrified vermin-proof fence. Locally extinct mammals were reintroduced into the enclosure in 1999. The enclosure is unique; its large size means that it accommodates the home ranges of the reintroduced animals. Apart from the Perron Peninsula enclosure in Western Australia, Arid Recovery is the largest area of intact arid zone shrubland into which locally extinct animals have been reintroduced.

The study was conducted at two sites within, and one site outside, the reserve. The first reserve site was within 'Main Enclosure', a 14 km<sup>2</sup> paddock where the locally extinct burrowing bettong, greater bilby, greater stick-nest rat (*Leporillus conditor*) and western barred bandicoot (*Perameles bougainville*) have been reintroduced. As the latter two species do not forage in the soil, they were not included in the current study. The second reserve site was within 'Second Expansion', an 8 km<sup>2</sup> paddock within which no locally extinct species have been introduced. However, both Main Enclosure and Second Expansion contain populations of sand goannas. The third site was outside the reserve (termed 'Outside') within a mining lease operated by Olympic Dam Operations. The general area is grazed intermittently by cattle at relatively low stocking rates. However, there has been no cattle grazing in the Outside paddock since the reserve was established, though it is still grazed by rabbits and contains goannas. The three paddocks were therefore relatively similar in their vegetation structure and composition, and would represent typical, though slightly degraded, landscapes within which these animals would have occurred prior to European settlement.

The estimated density of rabbits at the time of the study was 40 per km<sup>2</sup>, an average figure for the four years prior to the study following the release of rabbit hemorrhagic disease (RHD) in 1996, which substantially reduced population densities. However, rabbit densities did fluctuate between 10 per km<sup>2</sup> and 80 per km<sup>2</sup> in the previous four years in response to rainfall, extended dry periods and outbreaks of RHD (Arid Recovery, 2005). Although the bilbies and bettongs were enclosed within Main Enclosure, their estimated densities of 14 per km<sup>2</sup> for each species (Arid Recovery, 2005) were within the range of estimated natural population densities ranging from more than 70 bettongs per km<sup>2</sup> (Noble, 1995) to eight bilbies per km<sup>2</sup> made by Le Soeuf and Burrell on the Nullarbor Plain in 1921 (Southgate, 1990a). Goannas are able to move freely between the three paddocks as juveniles. Estimates of the relative densities of goannas based on measurements of track density were made using 500 m track transects. These indicated 109.6 (± 13.6; mean ± SEM (Main), 41.6 ± 4.6 (Second) and 18.0 ± 1.4 (Outside)) tracks per km (Arid Recovery, unpublished data).

### 2.2. Experimental design

Three 'blocks' were selected within each of the three paddocks, separated by distances of about 750 m. Each block consisted of the three landscape elements; dune, swale and ecotone. Measurement sites were randomly selected from within each landscape element. Main Enclosure contained bilbies, bettongs, and sand goannas, Second Expansion goannas only, and Outside, rabbits and goannas. This design

enabled comparisons to be made between: (1) the three 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 animal species, the study was not orthogonal i.e. not all animals were found in all three 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 to be made about the effects of ecosystem engineers beyond the study site. Nevertheless, a single replicate of a unique ecosystem represents a valuable opportunity to gain information about the effects of both locally extinct and feral species.

### 2.3. Pit density and soil excavation

Two-metre wide belt transects of variable length (50–250 m, depending on the density of pits), and aligned parallel to the direction of the dunes, were used to assess the density of foraging pits of each species at the 27 sites. Only foraging pits were measured, i.e. burrow systems of any animals were not included, and only three burrows were encountered across the 27 sites. The depth, length and width through the centre of each pit encountered on the belt transect were measured, and the type of animal responsible for its creation was determined, based on shape, depth and excavation angle. Pits constructed by bilbies and bettongs were pooled because they could not be distinguished easily from each other due to similar morphologies. While most pits could be assigned to a particular animal, especially those Outside and in Second Expansion, a small proportion of shallow pits in Main Enclosures could have been created by different animals. For the paddock and landscape-scale calculations, we used all pits, irrespective of the engineer creating them. However, for studies of animal effects, only pits of a known origin were used.

The length, width and depth of an additional 94 pits of a range of sizes and shapes constructed by rabbits, bilby/bettongs and goannas were used to calculate the mass of soil excavated by animals from measurements made of individual pits. Their volume was then calculated by measuring the volume of fine sand required to fill them using a volumetric cylinder. Volume was converted to mass by adjusting for bulk density using soil bulk density data measured in triplicate for each of dune, ecotone and swale soil. A range of linear and non-linear models was fitted to the relationship between soil mass and pit volume, and regression analyses used to evaluate those models with the greatest explanatory power. Irrespective of the type of pit or the animal that created it, the simple product of pit length, width and depth explained 92% of the variance in soil mass ( $F_{1,92} = 935$ ,  $P < 0.0001$ ) and was used to convert pit volume to soil mass for all holes measured at all sites.

### 2.4. Litter capture and soil nutrients in pits

To assess whether pits trapped litter, and if larger pits trapped more litter, the contents of five randomly selected pits were collected, along with a sample for an adjacent non-pit surfaces of the same area, at each of the nine sites in each of the three paddocks ( $n = 270$  samples). Samples were dried at

40 °C for 24 h and weighed. To examine whether nutrient concentrations of pit soils were higher than non-pit soils, samples of the uppermost 2 cm of soil were collected at the same 270 pit and paired non-pit locations, air-dried and passed through a 2 mm sieve. The labile carbon content of these soils was measured using a simplified laboratory technique whereby slightly alkaline, dilute  $\text{KMnO}_4$  reacts with the readily oxidisable (labile) carbon, converting Mn(VII) to Mn(II), and lowering the absorbance of 550 nm light (Weil et al., 2003).

### 2.5. Germination of seeds contained in soil and litter

To determine if there was more viable seed collected in the pits than the surface soil, litter and the underlying 2 cm of soil were collected from an additional 10 pits and 10 adjacent non-pits at each of the nine sites in Main Enclosure only ( $n = 180$  samples). Approximately, 50 g of soil from pits and non-pits was scattered over a layer of approximately 2 kg of propagation sand in shallow trays measuring  $173 \times 142 \times 55$  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 °C 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 nine weeks from March 16th to May 17th and seedlings counted when they emerged from the soil. On July 16th, the litter samples described above were placed in the glasshouse on new propagation sand and the pots watered until October 8th 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.

### 2.6. Statistical analyses

For all tests, the basic unit of measurement was the site. Therefore, individual pit data (e.g. pit dimensions, soil and litter capture) were averaged across transects at each site before statistical analyses. Differences in pit density ( $\log_e$ ) and soil excavation ( $\log_e$ ) were tested using a mixed-models ANOVA after checking for homogeneity of variance using diagnostic tools (e.g. normal and residual plots) within the Genstat statistical package (Payne et al., 1993). The mixed-models ANOVA had two error terms; a whole-plot stratum, which considered paddocks i.e. different combinations of animals; goannas with bilby-bettongs (Main), goannas alone (Second), goannas with rabbits (Outside), and a sub-plot stratum, which considered landscape elements (dune, gibber plain, ecotone) and its interaction with paddocks.

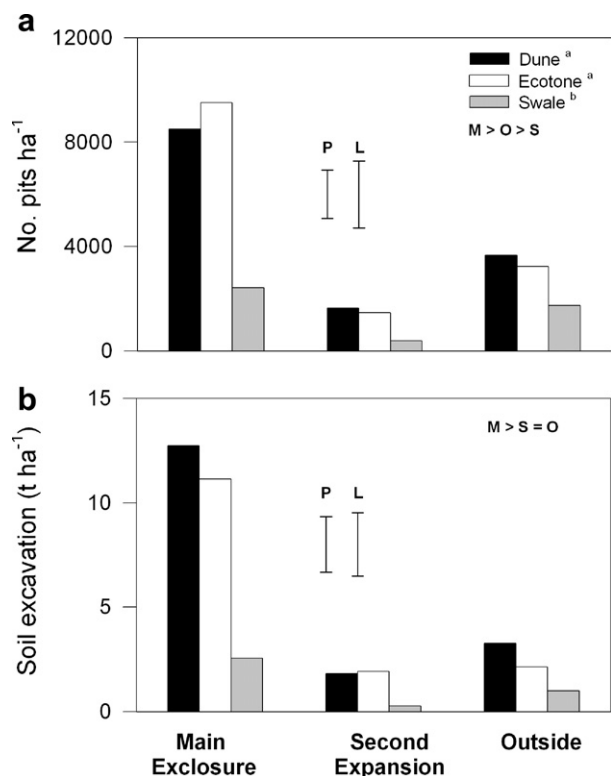
For labile carbon, differences in relation to paddock, landscape element and microsite (i.e. pit vs. non-pit), and their interactions were examined using a mixed-models ANOVA. The whole-plot and sub-plot strata were the same as above. A third stratum examined pit effects and the two- and three-way interactions with paddocks and landscape element, and a fourth stratum accounted for variance among the pits and surface samples for each landscape ele-

ment  $\times$  paddock combination. The same approach was used to test for differences in litter capture (in pit samples only) in relation to paddock and landscape element. The analysis was restricted to pit samples because litter was found at only four of the 135 surface locations, and the paucity of data precluded any formalized statistical testing for litter mass. The whole- and sub-plot strata were the same as above, while a third stratum accounted for the variance among the 10 pits for each landscape element  $\times$  paddock (animal treatment) combination. For all analyses, significant differences between means were examined using least significant difference testing.

### 3. Results

#### 3.1. Soil excavation and density of foraging pits

Averaged across all paddocks, pits occupied 0.9% of the surface of the dunes and ecotones, but only 0.2% of the surface of the swales. Pit density also varied between landscape elements, with fewer pits in the swales ( $1515 \pm 342$  pits  $\text{ha}^{-1}$ , mean  $\pm$  SEM) compared with the dunes or ecotones ( $4667 \pm 968$  pits  $\text{ha}^{-1}$ ;  $F_{2,12} = 8.87$ ,  $P = 0.004$ , Fig. 1a), but there was no significant landscape element by paddock interaction ( $F_{4,12} = 0.51$ ,  $P = 0.727$ ). Trends in soil excavation were similar



**Fig. 1** – Mean (a) density of pits (pits  $\text{ha}^{-1}$ ) and (b) soil excavation ( $\text{t ha}^{-1}$ ) for all animals in relation to landscape element. Bars indicate the 5% least significant difference for different paddocks (P) and landscape elements (L). Significant differences between the three paddocks (M = Main Enclosure, S = Second Expansion, O = Outside), summed over landscape elements, are indicated.

to pit density, with significant differences between landscape elements ( $F_{2,12} = 26.0$ ,  $P < 0.0001$ ). The mass of excavated soil averaged  $5.99 \pm 1.55$   $\text{t ha}^{-1}$  in the dunes,  $5.06 \pm 1.55$   $\text{t ha}^{-1}$  in the ecotones and  $1.27 \pm 0.33$  in the swales (Fig. 1b). Ninety per cent of soil excavation was on the dunes and ecotones.

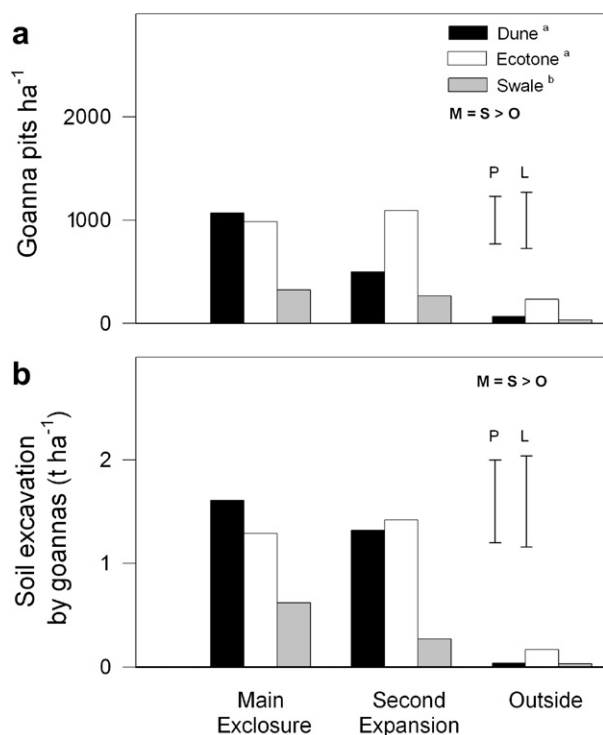
In general, pits excavated by bilby–bettongs and goannas were deeper (median depth = 80 mm) than rabbit pits (50 mm), and the openings of bilby–bettong foraging pits were wider (140 mm diameter) than either goanna (110 mm) or rabbit (90 mm) pits. There were substantial differences between the three different groups of engineers. On average, pit coverage was four-times greater where bilbies, bettongs and goannas occurred together (Main, 4.3%) compared with sites where rabbits and goannas occurred together (Outside, 1.2%), and very low where goannas occurred alone (Second, 0.6%). Pit density also differed significantly between the three groups of animals ( $F_{2,6} = 31.47$ ,  $P = 0.001$ ), ranging from  $6813 \pm 1500$  pits  $\text{ha}^{-1}$  for bilbies–bettongs plus goannas (Main), to  $2878 \pm 585$  pits  $\text{ha}^{-1}$  (rabbits and goannas, Outside) and  $1157 \pm 260$  pits  $\text{ha}^{-1}$  for goannas only (Second; Fig. 1a). More soil was excavated in Main (bilby–bettongs with goannas) compared with Second (goannas alone) or Outside (goannas with rabbits;  $F_{2,6} = 13.30$ ,  $P = 0.012$ , Fig. 1b). There was no significant interaction, however, between species and landscape element ( $F_{4,12} = 3.18$ ,  $P = 0.699$ ).

Goannas dug fewer holes when they occurred with rabbits than when they occurred either on their own or with bilbies and bettongs ( $F_{2,6} = 5.66$ ,  $P = 0.042$ ; Fig. 2a), and this was consistent across all three landscape elements. Goannas excavated significantly more pits in the dunes and ecotones compared with the swales ( $F_{2,12} = 7.79$ ,  $P < 0.009$ ), but there was no significant paddock by landscape element interaction ( $F_{4,12} = 0.46$ ,  $P = 0.76$ ). The mass of soil excavated by goannas in the presence of rabbits was only about a third that in the presence of bilbies and bettongs, or when they occurred alone ( $F_{2,6} = 5.6$ ,  $P = 0.043$ , on  $\log_{10}x + 0.01$  transformed data; Fig. 2b). Trends among landscape elements were the same as for soil excavation. Goannas dug similar-sized pits (mass soil pit $^{-1}$ ) when they occurred alone, with rabbits, or with bilbies and bettongs ( $F_{2,6} = 0.66$ ,  $P = 0.55$ ).

While bilbies and bettongs dug about four-times as many pits in Main as rabbits dug outside the reserve (Fig. 2a), the results were not significant because of the variability in density between sites ( $P = 0.21$ ). However, bilbies and bettongs excavated significantly more soil (five to eight-times) than rabbits ( $F_{1,4} = 15.7$ ,  $P = 0.017$ ; Fig. 2b), and soil excavation was significantly greater in the dunes and ecotones compared with the swales ( $F_{1,4} = 15.7$ ,  $P = 0.017$ ).

#### 3.2. Foraging pits, litter and soil carbon

Litter was found almost exclusively in the pits ( $16.1 \pm 1.3$  g) compared with the surface immediately adjacent to the pit ( $0.07 \pm 0.04$  g), and this was consistent across all paddocks and landscape elements. Litter was found in only four surface samples. Pits in the ecotones and swales captured a greater mass of litter (18.0–20.4 g) compared with pits in the dunes (9.9 g;  $F_{2,12} = 4.33$ ,  $P = 0.038$ ). Concentrations of labile carbon ( $\text{sqrt}_{x+0.5}$  transformed) were greatest in the pits compared with the surface ( $F_{1,18} = 142.0$ ,  $P < 0.0001$ ) and greatest in the



**Fig. 2** – Mean (a) density of goanna pits (pits ha<sup>-1</sup>) and (b) soil excavated by goannas (t ha<sup>-1</sup>) in relation to landscape element. Bars indicate the 5% least significant difference for different paddocks (P) and landscape elements (L). Significant differences between the three paddocks (M = Main Enclosure, S = Second Expansion, O = Outside), summed over landscape elements, are indicated. Note that only data from pits that could be positively ascribed to goannas are presented here.

swales (213 mg C kg<sup>-1</sup> soil), intermediate in the ecotones (135 mg C kg<sup>-1</sup> soil), and least in the dunes (93.3 mg C kg<sup>-1</sup> soil;  $F_{2,12} = 19.68$ ,  $P < 0.001$ ; Table 1). Concentrations of labile carbon in pits constructed by bilby-bettongs and goannas were 50% greater than surface concentrations, while concentrations in pits constructed by rabbits were only 19% greater (interaction:  $F_{2,18} = 12.1$ ,  $P < 0.001$ ). In general, there were poor relationships between labile carbon concentration in the soil and the mass of litter in the pits ( $R^2 < 0.10$ ), though relationships were stronger when we limited our analyses to one

**Table 1** – Mean density of pits (pits ha<sup>-1</sup>) and soil excavation (t ha<sup>-1</sup>) for bilbies-bettongs (Main Enclosure) and rabbits (Outside)

Attribute	Dune		Ecotone		Swale	
	Bilby	Rabbit	Bilby	Rabbit	Bilby	Rabbit
No. of pits ha <sup>-1</sup>	1100 <sup>a</sup>	250 <sup>b</sup>	1017 <sup>a</sup>	150 <sup>b</sup>	186 <sup>a</sup>	83 <sup>a</sup>
Soil excavation (t ha <sup>-1</sup> )	4.29 <sup>a</sup>	0.43 <sup>b</sup>	2.51 <sup>a</sup>	0.26 <sup>b</sup>	0.44 <sup>a</sup>	0.10 <sup>a</sup>

For a given attribute, different superscripts indicate a significant difference between bilbies-bettongs and rabbits for a particular landscape element at  $P < 0.05$ .

engineer in one landscape. Overall, the increase in labile carbon with increasing litter mass was greatest for bilbies and bettongs and least for rabbits.

### 3.3. Foraging pits and germination

No plants germinated from surface soil, and only four *Digitaria ciliaris* (Poaceae) plants emerged from soil taken from the pits. However, 1307 individuals from 46 genera emerged from litter samples taken from the pits. Three species, two forbs from the family Chenopodiaceae (*Atriplex holocarpa*, *A. vesicaria*) and the grass *Eragrostis dielsii*, contributed 53% of all germinants (A. James, unpublished data).

## 4. Discussion

This study demonstrated that foraging pits constructed by four ecosystem engineers contained more litter and seeds, and were sites of enhanced labile carbon compared with the intervening soil matrix. The two locally extinct, reintroduced fossorial mammals (bilbies and bettongs) dug substantially more pits than either goannas or rabbits, the remaining arid zone engineers, suggesting that neither goannas nor rabbits have assumed the engineering role of bilbies and bettongs. Indeed, the amount of soil excavated by rabbits was only 13–20% that of bilbies and bettongs when the latter occurred at population densities comparable to pre-European levels. There is therefore strong evidence that the reintroduction of locally extinct engineers is a critical issue to consider, not only for species conservation, but for the creation of patches of enhanced resources, and for the potential impacts on ecosystem function.

Foraging and subsequent pit formation created a mosaic of two contrasting patch types; resource-rich pits, and the adjacent resource-poor soil matrix. In this study, the soil surface had only a sparse litter cover, and foraging pits were effective litter traps, typical of many desert environments (Reichman, 1984). Unlike surface soil, the soil in the pits was nutrient- and seed-rich, and the germination experiment clearly supported the second prediction that resource capture is greatest in the pits compared with the intervening soil matrix. Foraging pits and depressions are substantial repositories of seed (Reichman, 1984), contrasting with the matrix where seed densities are typically very low (Whitford, 2002). Indeed, field-based observations after rainfall support the finding that pits are foci for plant germination (Sparkes, 2001). The low-density of seed and litter in the matrix is attributed to surface runoff (Shachak et al., 1991; Boeken et al., 1995), comminution and photo-oxidation of litter by sandblasting (Moorhead and Reynolds, 1989; Whitford, 2002), and the winnowing effect of wind on litter and seed (Reichman, 1984). More litter was trapped in the dunes and ecotones than in the swales, probably due to both the greater pool of available litter and the movement of mobile sand into the pits, effectively trapping litter *in situ* within successive layers of sand. The ability to retain nutrients will depend on the clay content of the soil, and the substantially greater levels of clay in the swales (35–40%) compared with the ecotones (25%) or dunes (5–10%) are driving the potential for different landscapes to retain mineral-

ized nutrients, and thus significant differences in levels of carbon found in each landscape.

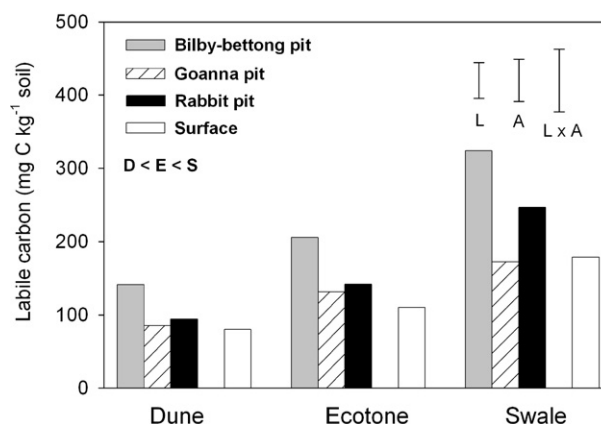
This study demonstrated substantial differences in pit density, soil excavation and litter capture between landscape elements, with levels in the swales substantially lower than in the dunes or ecotones, which were comparable. This partially confirms the first prediction that activity is greatest in the ecotones, and suggests that pit-derived fertile patches will not be created uniformly across all landscape elements, given that formation depends on both the characteristics of the pits (density, size, integrity, longevity) and the extant vegetation. Variation in pit density at a site could be due to differences in (1) digging rates, (2) pit longevity, or (3) a combination of both (Alkon and Olsvig-Whittaker, 1989). In this study, the variation lies with differences in digging rates, as those sites with more pits corresponded with the landscape element in which pits would have had a higher turnover (i.e. shorter half-life), due to the mobility of the sandy soil that accumulates within them. While there was also significantly more soil excavation in both the dunes and ecotones compared with the swales (Fig. 2), the effect of foraging pits is predicted to be greatest in the ecotones, where the soils have higher nutrient levels than the dunes.

The ecotones receive litter and seed from both the dunes and swales, while mobile sand from the dunes anchors litter in the pits. Although the ecotone is a relatively narrow zone, small differences in nutrients, seed retention and moisture levels within the pits would be expected to increase the diversity of patch types, promoting the germination and persistence of both dune- and swale-dependent species. Irrespective of landscape type, foraging pits, with their tendency to trap more litter, and hence, more seeds would contribute to the development of enhanced sites of germination, consistent with studies in arid areas worldwide (Guterman and Herr, 1981; Reichman, 1984; Alkon and Olsvig-Whittaker, 1989; Shachak et al., 1991; Boeken et al., 1995). The direct effect of animal digging and pit creation would therefore be to increase landscape-level productivity (Bianchi et al., 1989).

While mechanisms driving the formation of fertile patches are similar for all animal species, differences in pit morphology and the magnitude of soil excavation will govern the degree to which different complements of engineers will impact upon landscape processes. Few studies have considered multi-species engineering effects and the resulting landscape impacts (Brown and Heske, 1990; Milton et al., 1997; Machicote et al., 2004), and this study indicates that, at least for arid shrubland at Arid Recovery, all engineers are not equal. Pits of bilbies and bettongs were deeper and wider than those of rabbits, and the effectiveness of pits at enhancing soil carbon over and above levels in the soil matrix was much greater for bilby-bettong and goanna pits (50% increase) than rabbit pits (19% increase). As predicted, there were significant differences in soil excavation and pit density between species, confirming the fourth prediction. The cover of pits within the Main Enclosure was more than four-times greater than outside the reserve. Together bilbies, bettongs and goannas dug significantly more pits (Main; Fig. 1) than goannas and rabbits together (Outside; Table 1), and both dug more pits and excavated a greater mass of soil than goannas alone (Second; Fig. 2).

Some differences in pit density could be attributed to goannas, which had slightly higher densities in Main Enclosure compared with Second Expansion or Outside (Arid Recovery, unpublished data). Goannas excavated significantly more soil in Main Enclosure in the presence of the reintroduced species than they did in the Second Expansion where they occurred alone. This is an interesting result, given that goannas are free to move between enclosures as juveniles and would not be adversely affected by the predator-proof fencing. Indeed, outside the reserve, in the presence of rabbits, goannas excavated only one-third the amount of soil as inside the reserve, although this difference can in part be attributed to the presence of predators outside the fenced reserve.

The critical issue arising from this study is whether the European rabbit, the dominant fossorial mammal over much of arid Australia, has assumed the ecosystem engineering role of displaced bilbies and bettongs. The data demonstrate that rabbits have not matched the mass of soil excavated by locally extinct animals, and there is a suggestion that they produce markedly fewer pits. Bilbies and bettongs dug about four-times as many pits, accounting for five- to eight-times more soil excavation than rabbits (Fig. 3) again confirming the prediction of a species-specific engineering effect. This effect is amplified when one considers per capita pit construction, given that there were approximately 40% fewer bilbies and bettongs than rabbits. Densities of bilbies and bettongs inside the Main Enclosure were well within the range of reported natural pre-European densities (Southgate, 1990a; Noble, 1995). Furthermore, pit densities of bilbies and bettongs in this study (200–1100 pits ha<sup>-1</sup>) were slightly below rates reported for other closely-related bettong species such as *Bettongia penicillata* (5000–16,000 ha<sup>-1</sup> yr<sup>-1</sup>, Garkaklis et al., 2004), *Bettongia gaimardi* (500–3000 ha<sup>-1</sup>, Johnson, 1994), and the potoriod *Potorous tridactylus* (2250 pits ha<sup>-1</sup>



**Fig. 3** – Labile carbon concentrations (mg C kg<sup>-1</sup> soil) of soil from pits of three groups of animals and an adjacent soil surface, across three landscapes. Bars indicate the 5% least significant difference for different animal (A), landscape element (L) and the landscape element by animal interaction (L × A). Significant differences between the three landscapes (D = dune, E = ecotone, S = swale), summed over animal groups, are indicated.

year<sup>-1</sup>, Claridge et al., 1993). Although the relationship between population size and pit density is likely to be complex, an understanding of per capita impacts is important, given historic fluctuation in rabbit densities and the fact that rabbits are probably being suppressed by predators across most of arid Australia.

Thus this study compared two scenarios, the current situation across arid Australia where rabbits and introduced predators exist in the absence of native fossorial mammals, and the pre-European situation, where bilbies and bettongs were widespread in the absence of rabbits and introduced predators. Regardless of their effect on fertile patch creation, it is likely that any small contribution by rabbits would be greatly outweighed by their devastating impacts on plant recruitment and survival in arid Australia (Lange and Graham, 1983; Denham and Auld, 2004). We argue therefore that the local extinction of native fossorial mammals is likely to have had significant impacts on landscape processes, given that their role has not been assumed by either existing native animals (goanna) or exotic herbivores (rabbits).

Reintroduction of bilbies and bettongs therefore likely has positive and unique impacts on the restoration of fertile microsites in arid Australia. The reintroduction of species not only alters the number and distribution of fertile patches, but also sheds light on some of the ecosystem engineering processes that have been lost with the extirpation of Australia's mammal fauna. The linkages between the main soil-foraging animals in arid Australia and their relative roles in structuring and maintaining landscape heterogeneity in desert ecosystems is deserving of more attention.

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