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CAN REINTRODUCTIONS OF THE BILBY AND BETTONG AID ECOSYSTEM RESTORATION IN ARID AUSTRALIA?

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ABSTRACT
The 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 rangelands because of their impacts on surface soils. We studied the effects of their reintroduction on litter and seed capture and soil nutrient levels compared with two prevalent fossorial animals; the European rabbit (*Oryctolagus cuniculus*) and the sand goanna (*Varanus gouldii*). Bilbies and bettongs dug deeper and wider pits and excavated significantly more soil than rabbits or goannas. Litter and viable seed was restricted almost exclusively to the pits and soil in the pits had significantly higher levels of labile carbon and mineralisable nitrogen than 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 bilbies and bettongs and the higher concentration of carbon in their pits, demonstrate that these reintroduced fossorial mammals play important roles in the creation of fertile patches. This study demonstrates that through habitat modification, reintroduced species can affect ecosystem function by enhancing resource retention at a local scale.

INTRODUCTION
In the arid and semi-arid rangelands of Australia where almost all medium-sized ground dwelling-mammals have been lost (Burbidge and McKenzie 1989, Johnson 2006), increasing focus is being placed on reintroducing species to parts of their former range (Short *et al*. 1992, Short and Turner 2000, Moseby and Read 2006). Whilst the primary goal of these species reintroductions has been the establishment of wild populations, there is increasing recognition of their potential to aid the restoration of ecosystem function. The reintroduction of species will likely alter ecosystems not only through the consumption of resources but also through the modification of habitat. Species that modify, maintain or create habitat have been termed 'ecosystem engineers' (Jones *et al*. 1997) and have been found to dramatically alter water flows, nutrient availability, seed capture and plant germination though soil disturbances created whilst foraging (Garkaklis *et al*. 2000, Decaens *et al*. 2002). This may have a considerable impact in arid and semi-arid landscapes where resources are limited and concentrated within fertile patches surround by a resource-poor soil matrix (Stafford Smith and Morton 1990, Shachak *et al*. 1999). These fertile patches support most of the diversity and productivity in desert ecosystems (López-Portillo and Montaña 1999, Whitford 2002) and any changes in surface topography will likely alter the flow and distribution of resources, and may enhance resource retention at a local scale. Ecosystem engineers may have a large impact on restoration, by creating patches of differing resource availability that allow species with different resource requirements to coexist (Day *et al*., 2003; Odling-Smee *et al*., 2003) and by reinstating biotic and abiotic resource flows that have been altered through degradation (King and Hobbs 2006).

Two species to suffer major range declines, the greater bilby (*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*), are both prolific diggers, creating small pits or depressions in the soil surface while foraging for seeds, invertebrates, bulbs and fungi (Southgate 1990, Robley *et al*. 2001).

We studied the effects of reintroduction of the greater bilby and the burrowing bettong on ecosystem function, soil nutrient levels and the capture of litter and viable seed in an arid South Australian dunefield. We compared the ecosystem engineering effect of the reintroduced species with two widespread animals, the exotic European rabbit (*Oryctolagus cuniculus*) and the native Gould's sand goanna (*Varanus gouldii*) which also create foraging pits in the soil. The study was conducted within Arid Recovery, a reserve where bilbies, bettongs and goannas were enclosed together compared with a site outside the reserve where rabbits and goannas co-occurred, and a site within the reserve where goannas occurred alone. We measured the density of foraging pits and the amount of soil excavated in three landscapes (dune, ecotone and swale) at three plots within each paddock. We also sampled a subset of 10 pits and 10 surface areas at each plot; collecting litter, and sampling labile carbon, mineralisable nitrogen and mineral nitrogen ($NH_4^+ + NO_3^-$). Litter and soil samples were taken from 90 pits and 90 surface areas in the main exclosure of the reserve (containing bilby, bettong and goanna pits only) and germinated in a glasshouse.

RESULTS

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, with litter restricted almost exclusively to the pits ($F_{1,\ 18}$ = 85.7, P<0.0001, Figure 1). Unlike surface soil, the soil in the pits was nutrient-rich, with significantly higher levels of labile carbon ($F_{1,18}$=142.0, P<0.0001; Figure 2), 55% more mineralisable nitrogen ($F_{1,18}$= 37.1, P<0.001) and 36% more mineral nitrogen ($F_{2,12}$=14.6, *P*<0.001) than surface soil. Pits were also seed-rich, a total of 1307 seedling from 46 genera germinated from litter samples taken from the pits whilst no seedlings emerged from samples surrounding the pits.

As predicted, there were significant differences in soil excavation and pit density between species. Bilbies and bettongs dug about four-times as many pits, accounting for five- to eight-times more soil excavation than rabbits ($F_{1,4}$ = 15.7, P = 0.017). Together bilbies, bettongs and goannas dug significantly more pits than goannas and rabbits together, and both complements of species dug more pits and excavated a greater mass of soil than goannas alone ($F_{2,\ 6}$= 13.30, P= 0.012). Pits of bilbies and bettongs were deeper and wider than those of rabbits (Bilby: median depth = 80mm, median width of pit opening = 140mm, Rabbit: median depth = 50mm, median width of pit opening = 90mm), 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) ($F_{2,18}$= 12.1, P<0.001; Figure 2).

DISCUSSION

The significantly greater soil excavation by bilbies and bettongs and greater concentrations of carbon in their foraging 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 shed light on some of the ecosystem engineering processes that have been lost with the extirpation of Australia's mammal fauna and demonstrate that in arid areas reintroduced fossorial mammals can enhance resource retention at a local scale.

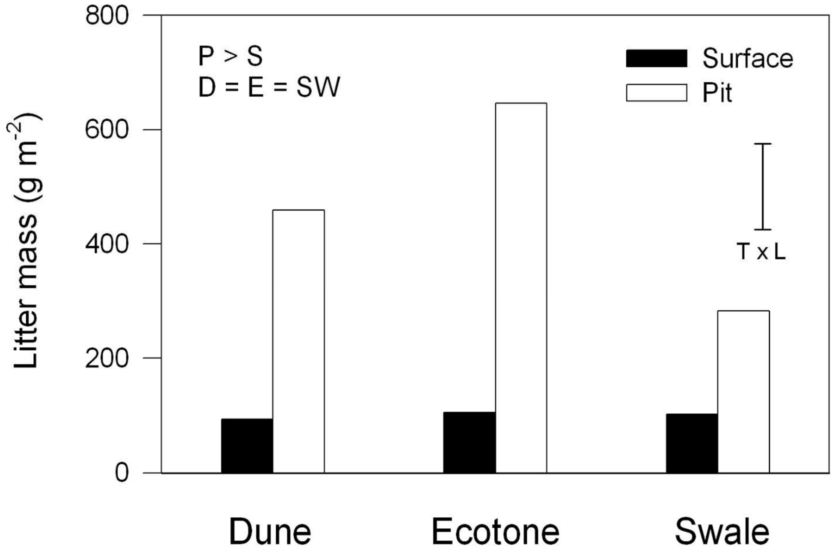

Figure1. Mean litter mass (g/m^2) in pits and surface soils in the dunes, ecotones and swales. The 5% LSD bar for the treatment (pit vs. surface) by landscape (dune, ecotones, swale) interaction is shown. P= pit, S= surface, D= dune, E= ecotones, SW= swale.

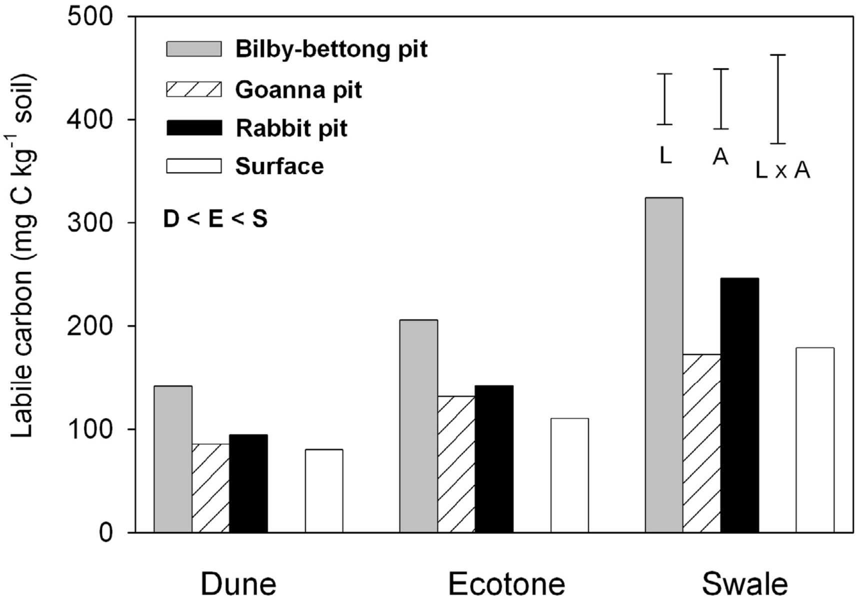

Figure 2. Labile carbon concentrations (mg C/kg of soil) of soil from pits of three groups of animals and an adjacent soil surface, across three landscapes. Bars indicate the 5% least significant difference for different animal (A), landscape element (L) and the landscape element by animal interaction (LxA). Significant differences between the three landscapes (D= dune, E= ecotones, S= swale), summed over animal groups, are indicated.

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