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Net effects of soil disturbance and herbivory on vegetation by a re-established digging mammal assemblage in arid zone Australia

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Large-scale re-introductions of locally extinct digging mammal assemblages have been implemented at a number of arid zone sites, with the aim of conserving mammal species and restoring ecosystem function. Previous studies have focused on the ways in which foraging pits benefit plants, but the effects of herbivory by digging mammal assemblages are poorly understood.

We used a randomised block design with control, procedural control and exclusion plots (n = 10) to experimentally test the net effect of a re-established mammal assemblage of bridled nailtail wallabies, *Onychogalea fraenata*, greater bilbies, *Macrotis lagotis*, brush tailed-bettongs, *Bettongia penicillata*, and burrowing bettongs, *Bettongia lesueur*, on plants in the Australian arid zone.

We found that the re-established mammal assemblage limited natural seedling abundance and consumed transplanted seedlings. Plant composition between treatments did not differ, but perennial forbs and subshrubs, which are known food items of the re-introduced mammals, were most abundant in mammal exclusions. Furthermore, a landscape-scale survey showed that composition in the re-introduction area differed significantly from an adjacent control.

When conceptualising the role of mammalian ecosystem engineers in arid environments, negative effects on plants from herbivory and soil disturbance must be considered alongside the better studied processes of nutrient cycling and seedling establishment.

1. Introduction

Australia has the worst modern mammal extinction rate in the world: roughly half of global mammal extinctions in the last 200 years are of Australian native species. This has been driven by the introduction of predators (feral cats *Felis catus* and red foxes *Vulpes vulpes* in particular), competition with exotic herbivores (rabbits *Oryctolagus cuniculus*, goats *Capra hircus*, sheep *Ovis aries* and cattle *Bos taurus*), human persecution and changes to land-use and fire regimes (Dickman et al., 1993; Lunney, 2001). The loss of species from an ecosystem can have implications for ecosystem functioning, as well as the persistence of sympatric species (Byers et al., 2006). This is especially true for ecosystem engineers which modify, maintain and create habitats (Jones et al., 1994; Lawton, 1994).

Ecosystem engineering is a ubiquitous process in terrestrial environments (Jones et al., 1994). Engineers may cause substantial disturbance in ecosystems with wide-ranging consequences for species diversity and composition (Romero et al., 2015). Digging mammals are a cosmopolitan example of ecosystem engineers affecting soil nutrient cycles through the creation of foraging pits, burrows and mounds (Whitford and Kay, 1999; Davidson et al., 2012). Foraging pits accumulate litter and seeds, increasing nutrient loads and providing seedling establishment sites (Eldridge and James, 2009). In Australia, the loss of the ecosystem services provided by near-extinct digging mammals such as bettongs, *Bettongia* spp., and bilbies, *Macrotis* spp., has resulted in altered ecosystem functioning in their historic range (Byers et al., 2006; James and Eldridge, 2007; Gibb, 2012).

Changes in ecosystem functioning where digging mammal assemblages have been lost result in changes in plant population dynamics and community composition. Digging mammal assemblages decrease the proportion of grass cover and increase forb abundance in some systems (Korn and Korn, 1989; Martinsen et al., 1990; Heske et al., 1993; Rogers and Hartnett, 2001; Arias et al., 2005; Yoshihara et al., 2009; but see Branch et al., 1996), while in others, foraging pits are required for the persistence of some grass

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species in the landscape (Tilman, 1983).

Many of Australia's arid zone mammal species are considered ecosystem engineers due to the effect of their foraging on soil processes and plants (Whitford and Kay, 1999; Eldridge and James, 2009). Given that much of Australia's digging fauna are also herbivores (Gibson, 2001; Robley et al., 2001; Murphy et al., 2005; Southgate and Carthew, 2006; Bice and Moseby, 2008; Newell, 2008), both the trophic (herbivore) and non-trophic (digging) actions of digging mammals must be considered when attempting to determine their role in shaping plant composition. Herbivory can drive changes in plant composition and survivorship, likelihood of fire, and even vegetation type (Noble et al., 2007; Munro et al., 2009; Leonard et al., 2010; Maher et al., 2010). The loss of digging mammal assemblages native to Australia's arid zone is likely to have affected plant population dynamics and community composition, as both digging and herbivory have a strong influence on plant composition in a variety of ecosystems (Crawley, 1983, 1997; Huntly, 1991).

In recent decades, populations of endangered arid zone mammals have been re-established at various sites in Australia. Typically, these sites have been fenced and feral animals removed as part of the re-introduction program. While conservation of the mammals themselves is usually a primary goal of re-introduction programs, re-introductions also contribute to ecosystem restoration (Eldridge and James, 2009), and re-introduction sites are managed for cross-taxonomic biodiversity conservation (e.g. Arid Recovery, 2014).

Most research on the ecosystem restoration role of re-established mammal assemblages has focused on the effects of digging in enhancing plant establishment and growth. The role of herbivory by these mammals in shaping vegetation has thus far received little attention (though see Noble et al., 2007; Munro et al., 2009). Better understanding of the herbivory effects of re-established mammal assemblages would contribute to effective management of re-introduction sites, as well as enhancing general understanding of arid systems. We aimed to ascertain the net effects of trophic and non-trophic disturbance by a re-established mammal assemblage on arid zone vegetation, rather than focusing on the positive effects of foraging pits only. We used a manipulative approach at a large-scale re-introduction site to investigate mammal herbivory of planted seedlings and the effect of re-introductions on naturally established seedling abundance and plant composition. We then undertook a landscape-scale survey to compare the plant composition of the re-introduction area to an adjacent control with an exotic herbivore assemblage. This was done to investigate the potential longer-term plant composition effects from re-establishing a digging mammal assemblage and removing exotic species. We hypothesised that, despite the well documented provision of seedling establishment sites in the form of foraging pits, the combined effects of herbivory and digging would negatively affect seedlings, leading to altered plant composition in the presence of a digging mammal assemblage.

2. Materials and methods

2.1. Study area

We conducted experiments in Scotia Sanctuary, a 65,000 ha conservation property in western New South Wales, Australia (Latitude 33.21°S, Longitude 141.16°E) owned and managed by the Australian Wildlife Conservancy (Fig. 1). Within the property is a large area comprised of two 4000 ha mammal re-introduction 'Stages' surrounded by a feral animal-proof fence. Stage 1 was feral-free in 2005 and bridled nailtail wallabies, *Onychogalea fraenata*, greater bilbies, *Macrotis lagotis*, brush tailed-bettongs, *Bettongia penicillata*, burrowing bettongs, *Bettongia lesueur*, numbats, *Myrmecobius fasciatus*, and greater stick-nest rats, *Leporillus conditor*, were released into the fenced area (Hayward et al., 2012). The same fencing and eradication process was carried out in Stage 2 and, beginning in 2008, bridled nailtail wallabies, greater bilbies, brush-tailed bettongs and numbats were released (Hayward et al., 2012). The suite of species in each Stage consists of a mix of digging and herbivorous species (Table 1). A small number of individuals (<5) of western grey (*Macropus fuliginosus*) and red (*M. rufus*) kangaroos were also present in both re-introduction Stages.

Scotia Sanctuary is in the arid zone (mean annual rainfall: 250 mm) and is characterised by stable east-west running sand dunes of red sand and sandy solonised brown soil over clay (Westbrooke et al., 1998). Hot summers (>30 °C), cooler winters (<17 °C) and aseasonal rainfall characterise the site (Westbrooke et al., 1998). Experimental plots were established in mixed mallee open woodland (*Eucalyptus socialis*, *E. oleosa*, *E. dumosa* and *E. gracilis*) with *Triodia scariosa* understorey (botanical nomenclature throughout follows the Australian Plant Census database).

2.2. Experimental design

Manipulative study: We used a manipulative study to determine the extent to which the assemblage of digging mammals act as herbivores of transplanted seedlings and the net effect of digging and herbivory on seedling establishment and plant composition. The study comprised ten sets of three 20 × 20 m experimental plots (five sets in Stage 1 and five in Stage 2) in a randomised block design (Fig. 1). Each set of three plots included three treatments: mammal exclusion, procedural control and control. Exclusion fences were constructed in July 2010 and consisted of a 1 m high chicken wire fence (40 mm diameter openings) with a buried "rabbit-proof" base to prevent digging mammals accessing the plots. The procedural control was used to account for any unintended effects of the fence structure, beyond the intended effect of excluding re-introduced mammals. This was identical to the exclusion, except that the bottom portion of the fence was removed to allow re-introduced mammals to access the plot. Here, the disturbance of burying the exclusion treatment fence was mimicked by clearing any vegetation along the fence perimeter and turning over the soil in the same area. Control plots had star pickets to mark their corners. Plots within a set of three were less than 70 m apart whereas sets were no less than 400 m apart.

The density of mammal diggings within experimental plots was surveyed prior to fence construction (October 2009) and each October thereafter. These surveys consisted of counting the number of mammal-produced pits within two 2 m wide belt transects running parallel to each other, 6 m apart, across each plot (80 m^2 per 400 m^2 plot). This count was converted to number of pits per hectare for analysis.

Five seedlings of *Enchylaena tomentosa* and three of *Acacia wilhelmiana*, common species at Scotia Sanctuary, were planted in each manipulative study plot in late July 2011. Twelve weeks after planting, seedlings were revisited and herbivory (cropped foliage and/or stems) was recorded as a presence/absence. In each plot, the proportion of planted seedlings with herbivory was calculated and used for analysis. A survey of naturally established seedlings was also performed, recording the species, number of individuals and height of all shrub and subshrub seedlings less than 50 cm in height in each manipulative study plot. In all plots, all plants were identified to species and the number of individuals of each species was recorded.

Landscape scale survey: For the landscape-scale plant composition survey, ten 20 m × 20 m plots were selected in each re-introduction Stage and a further ten in an adjacent control