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Termite activity and decomposition are influenced by digging mammal reintroductions along an aridity gradient

Nicole V. Coggan [a,*], Matthew W. Hayward [b,1], Heloise Gibb [a]

[a] Department of Zoology, School of Life Sciences, La Trobe University, Melbourne, Vic., 3086, Australia
[b] Australian Wildlife Conservancy, PO Box 8070, Subiaco East, W.A., 6008, Australia

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ABSTRACT

Species declines can have broader impacts on ecosystems, particularly when those species act as ecosystem engineers. Ecosystem engineers modify habitats, indirectly shaping biotic communities. Environmental attributes may limit the direct influence of engineers on habitat properties, indirectly affecting other species and ecological functioning. We used three sites differing in abiotic properties, where endangered digging mammals had been reintroduced, and hypothesised that: Reintroduced mammals affect resource consumption and abandonment by termites, and local factors influence termite interactions with reintroduced mammals. We therefore performed two manipulative experiments: first testing the effects of depth on termite consumption of resources, second, testing resource abandonment by termites following simulated disturbances by determining the proportion of termites remaining at disturbed resources relative to undisturbed controls. Experiments were conducted inside reintroduction enclosures and compared against controls. Resource consumption was ~25% lower, and resource abandonment ~50% higher where digging mammals were reintroduced and termite responses were consistent with decreasing aridity. The near-extinction of native digging mammals from much of Australia is likely to have significantly altered termite activity and decomposition, but impacts may be context-dependent, with aridity potentially playing a key role. Our work suggests, counterintuitively, that ecosystem impacts of reintroductions may be lower in resource-poor sites.

1. Introduction

Recent declines in biodiversity have been dramatic (e.g. Colwell et al., 2012; Dunn et al., 2009), resulting in significant changes to species assemblages and to the function of ecological communities (e.g. Silvey et al., 2015). The loss of species can have broad-reaching effects, particularly when those species act as ecosystem engineers (Gibbs et al., 2008). Ecosystem engineers modify habitats through physical activity, such as digging (for shelter construction and food) and herbivory (increasing habitat complexity as a by-product of herbivore actions), (Jones et al., 1996). Digging by vertebrate ecosystem engineers provides refuges for other species (e.g. Davidson et al., 2012), and significantly influences soil processes and patterns of vegetation cover in arid habitats where water and nutrients are limiting (Whitford and Kay, 1999). Previous studies suggest that the loss of digging mammals has significantly altered ecosystems worldwide, with serious consequences for other organisms (Davidson et al., 2012).

Engineering impacts are predicted to provide increasing benefits to biotic communities as abiotic stressors increase (Crain and Bertness, 2006). However the magnitude of an engineer species' impacts can be context-dependent, mediated by factors such as aridity, engineer population density or land use history, which affect interactions between species and their environment by altering resource availability (e.g. Eldridge et al., 2011; Erpenbach et al., 2013). Between 31 and 40% of the Earth's surface is classified as arid (Salem, 1989), and water availability is a key driver of productivity. Few studies have explicitly considered the effects of climate on the role of ecosystem engineers, but there is evidence that increasing precipitation amplifies the positive effects of engineering by termites on plant diversity (Erpenbach et al., 2013). Here, we investigate the influence of climate on interactions between engineers and other animal species. Few reintroduction studies have included site-level replication (e.g. Hayward et al.,

* Corresponding author.
E-mail address: n.coggan@latrobe.edu.au (N.V. Coggan).
[1] Current address: School of the Environment, Bangor University, LL572UW, United Kingdom.

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2015), thus we consider the influence of site-specific factors, particularly that of land-use history, upon termite reactions to mammal reintroduction. The new knowledge will contribute to developing theories of environmental effects on biotic interactions (Schemske et al., 2009), and inform conservation practices which employ reintroduction of ecosystem engineer species (Manning et al., 2015).

Over the past two centuries Australia has suffered the highest rate of mammal extinctions worldwide: 22 species have been driven extinct and a further 21% of species are suffering severe population declines (Woinarski et al., 2015), rendering them ecologically extinct, i.e., too rare to contribute substantially to ecological functions (McConkey and O'Farrill, 2015). These extinctions have largely been attributed to predation by introduced cats and foxes (Woinarski et al., 2015). The implications for habitat quality in Australia's arid ecosystems are severe. In reintroduction sites, native mammalian digging engineers are responsible for soil turnover of between one to six tonnes of soil per hectare every year (Eldridge and James, 2009), and pre-European levels are likely to have been similar. That level of soil engineering is unmatched by other digging vertebrates in Australian ecosystems, and no ecological equivalents have replaced the lost or declining species.

Efforts to conserve threatened mammals in Australia are increasingly centered on reintroduction into fenced sanctuaries, free of introduced predators. While the primary aim of these introductions is to preserve species, a secondary aim is to restore the interactions and ecological engineering functions of species (Manning et al., 2015). Declines in native digging mammals are likely to have resulted in a broad-scale loss of ecosystem function, with quantified impacts upon the current structure of arid habitats and the biota within them (Fleming et al., 2014). These include impacts upon soil (e.g. Clarke et al., 2015), invertebrate (e.g. Silvey et al., 2015), and plant assemblages (e.g. Chapman, 2016). Re-establishment of native mammal assemblages is anticipated to restore impacted ecological processes such as soil turnover (Manning et al., 2015). Populations of digging mammals have been successfully established inside sanctuaries in arid and semi-arid habitats, but the scarcity of accurate historical data needed for these types of conservation projects means that little is known of their potential interactions with, nor their impacts upon pre-existing ecological assemblages.

Termites are the dominant invertebrate soil engineers and detritivores in Australian arid systems (Morton et al., 2011), and are vitally important to soil health wherever they occur (de Bruyn and Conacher, 1990). Prior to European colonisation, native digging mammals were likely to have been important disturbance agents and predators of subterranean termites and other ground-dwelling invertebrates (Gibb, 2012; Silvey et al., 2015). Termite activity is sensitive to disturbances, which affect the availability and suitability of their resources (e.g. Jones et al., 2003). They are therefore likely to respond to soil disturbance resulting from mammal foraging or burrowing (Gibb, 2012). Effects may cascade further through ecosystems, for example by altering termite-driven functions such as nutrient cycling. In addition to their functional significance, termites are consumed by a variety of fauna (e.g. Colli et al., 2006) and are a major food source for reintroduced digging mammals (e.g. Bice and Moseby, 2008), so mammals may also alter termite assemblages through predation.

Recent studies suggest that digging mammals affect not only soil microfauna and vegetation (Clarke et al., 2015; Verdon et al. in review), but also assemblages of invertebrates (Davidson and Lightfoot, 2007; Read et al., 2008; Silvey et al., 2015). However, no previous studies have investigated the effects of digging mammals on invertebrate activity or invertebrate-driven functions. Further, few have considered the role of site context in moderating the influence of ecosystem engineers in terrestrial systems. We tested the effects of reintroduced endangered digging mammals (vertebrate ecosystem engineers) on a key invertebrate ecosystem engineer, termites, by comparing reintroduction and control sites at three reintroduction sanctuaries in arid/semi-arid southern Australia. We hypothesised that soil disturbances generated by reintroduced digging mammals would reduce termite activity, resulting in lower rates of resource consumption (termite-driven decomposition) and higher rates of resource abandonment. Because engineering impacts may be context-dependent (Crain and Bertness, 2006; McAfee et al., 2015), we considered the underlying influences of aridity and historic land-use, which differed among the sanctuaries, on the overall impact of mammal reintroductions upon termite activity.

2. Methods

2.1. Study sites

We compared termite responses to soil disturbance by reintroduced digging mammals at three conservation sanctuaries. These were Arid Recovery (30°33′55.38″S, 136°55′3.85″E), Scotia (33°8′9.00″S, 145°11′33.00″E), and Yookamurra sanctuaries (34°31′19.38″S, 139°28′31.91″E) (Table 1, Fig. 1a). Scotia and Yookamurra sanctuaries were administered by the Australian Wildlife Conservancy, and Arid Recovery by BHP Billiton. The three sanctuaries differed in aridity and land-use history (livestock densities). Temperature, precipitation, gross primary production (GPP) and the enhanced vegetation index (EVI) co-varied with aridity. Arid Recovery was the most arid sanctuary and Yookamurra sanctuary was the least arid (Table 1). All sanctuaries functioned as pastoral land for livestock (sheep and/or cattle) after European settlement and prior to their conversion into sanctuary habitats. Historical stocking data for Yookamurra sanctuary and surrounding properties could not be located in published records, thus an estimated carrying capacity for livestock in South Australia's arid lands was used (Squires and Bennett, 2004). Unlike aridity, there was no clear gradient in historic livestock densities across the sanctuaries. Livestock densities were stocked in response to annual rainfall (higher in wetter years, lower in drier years), and ranged between 0.02 and 0.1 sheep ha^{-1} (Read, 2002; Squires and Bennett, 2004; Westbrooke, 2012). The maximum recommended stocking density for the entire region was 0.1 sheep ha^{-1}, and this was considered to be the carrying capacity of south Australian arid and semi-arid regions as dictated by average annual rainfall (Squires and Bennett, 2004).

The dominant vegetation class for Scotia and Yookamurra sanctuaries was remnant Mallee woodland and shrublands, with climate at Yookamurra classified as 'Mediterranean', while that at Scotia was 'Semi-arid'. Dominant ground cover at Scotia included spinifex (*Triodia* spp.) and chenopod species, and *Westringia rigida* at Yookamurra sanctuary. The dominant trees in Mallee woodlands and shrublands are *Eucalyptus* species, including *E. dumosa* and *E. gracilis.* Arid recovery was classified as Acacia shrubland with a 'Desert' climate. Dominant ground cover at Arid Recovery varied with season: at the time of data collection, the Poached-egg daisy (*Polycalymma stuartii*) and Desert Rattle-pod (*Crotalaria eremaea*) were abundant. Sandhill wattle (*Acacia ligulata)* was the dominant shrub species at Arid Recovery. Scotia and Yookamurra sanctuaries supported a cryptogamic crust, which bound the soil surface at those sanctuaries, but it was absent at Arid Recovery.

2.1.1. Sampling design

All sanctuaries included large (up to ~ 8000 ha) enclosures free of introduced predators and protected by predator-proof fencing.