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REVIEW

Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function?

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ecosystem engineers, ecosystem restoration, ecosystem services, foraging pits, inter-fire interval

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ABSTRACT

1. Despite once being described as common, digging mammal species have been lost from the Australian landscape over the last 200 years. Around half of digging mammal species are now extinct or under conservation threat, and the majority of extant species have undergone marked range contractions.
2. Our aim is to identify the role of digging mammals in ecosystem processes throughout Australia. We highlight how the actions of digging mammals are vital for maintaining ecosystem functioning and how their extirpation has led to loss of ecosystem functions.
3. A review of the literature indicates that many aspects of the influence of bioturbation on ecosystem functioning have been studied. The role of digging mammals in arid and semi-arid zones has been previously established. We collate and review a broader scope of studies, including those carried out in the mesic woodlands and forests of Australia. We identify roles of digging mammals in the context of ecosystem functioning and conservation management.
4. Bioturbation significantly alters soil processes, increasing soil turnover and altering the chemical and structural properties of soil. Greater water infiltration and decreased surface run-off and erosion alter soil hydrophobicity and increase soil moisture. Diggings capture organic matter, provide habitat for a diversity of microscopic and macroscopic organisms, and increase nutrient cycling. Mycophagous mammals disperse fungi (e.g. mycorrhizae), while all diggings can create suitable sites for fungal growth. Diggings also capture plant seeds, increasing seedling germination, recruitment and plant growth. The overall effect of mammal diggings is therefore increased plant vigour and resilience, increased biodiversity and consequently improved ecosystem functioning.
5. We propose that the loss of digging mammals has contributed to the deterioration of ecosystems in Australia. Recognising the roles of digging mammals will inform potential management options such as species translocations or reintroductions.

INTRODUCTION

Ecosystem engineers are organisms that influence resource availability for other species by modifying, maintaining or creating habitat (Jones et al. 1994). Bioturbation (the movement and manipulation of soil by living organisms; Whitford & Kay 1999) is a mechanical form of ecosystem engineering that alters physical and biotic processes (Reichman & Seabloom 2002, James et al. 2009), increases soil mixing (Zhang et al. 2003) and has been associated with promoting species diversity (Ceballos 1999, Davidson et al. 2008). Since bioturbation produces multiple benefits to the overall ecosystem (Eldridge et al. 2009), digging mammals have been recognised as playing a significant role in ecosystems, and their importance for environmental conservation has been highlighted (Davidson et al. 2012). However, these animals not only influence the physical properties of landscapes but also influence biological processes through trophic interactions (e.g. by the ingestion and movement of seeds and fungal spores). Digging mammals can therefore also be considered important biotic engineers (sensu Dickman 1999).

Many Australian forest and woodland ecosystems have shown marked declines in health and function over recent decades, with higher background tree mortality rates, episodic die-offs and general declines noted in a number of plant species (Close & Davidson 2004, Allen et al. 2010, Brouwers et al. 2013, Matusick et al. 2012). Although climate change and changing land uses have been identified as leading causes, few researchers have considered the loss of ecosystem functions that would have increased the resilience of woodlands and forests to such changes. Also, most studies of digging mammals have been carried out in arid and semi-arid habitats (see review by Whitford & Kay 1999, Eldridge & Myers 2000, James & Eldridge 2007, Eldridge & Koen 2008, Eldridge & Kwok 2008, Newell 2008, Eldridge & James 2009, Eldridge et al. 2009, James et al. 2009, 2010); few researchers have tested predictions under more mesic forest or woodland conditions.

Most Australian soils are nutrient poor, and long-term weathering has depleted nutrients even at depth (Orians & Milewski 2007). Soil degradation is a major factor implicated in poor ecosystem functioning, and productive soil is recognised as a crucial component of healthy ecosystems (Schoenholtz et al. 2000). Productive soil has nutrients available to plants and also provides food and habitat for a diversity of invertebrate and vertebrate animals. Healthy soil sustains plant and animal growth and maintains or enhances water quality and infiltration (Doran & Zeiss 2000). Thus, soil is arguably one of the most important components in an ecosystem.

Australia supports a diversity of digging mammals that contribute to soil processes and have been important in shaping the ecology of Australian ecosystems. These range from the fossorial marsupial moles *Notoryctes* spp., which spend most of their time tunnelling under the surface of sandy deserts, to animals that dig for food or shelter and therefore have semi-fossorial lifestyles. The majority of diggings by mammals in Australia have been carried out by animals with strong forelimbs and large claws: bettongs *Bettongia* spp., *Aepyprymnus* sp.; potoroos *Potorous* spp.; bilbies *Macrotis* spp.; bandicoots *Perameles* spp., *Isoodon* spp., *Echymipera rufescens*; wombats *Vombatus ursinus*, *Lasiorhinus* spp.; and echidnas *Tachyglossus aculeatus*, *Zaglossus bruijnii* (Martin 2003, Eldridge & Mensinga 2007). Native rodents comprise about a quarter of Australia's terrestrial mammals and virtually all of them dig. For example, pebble-mound mice *Pseudomys chapmani* (Anstee 1996, Anstee et al. 1997) and long-haired rats *Rattus villosissimus* (Predavec & Dickman 1994) create complex underground systems. Rodent burrows are also used extensively by species that do not burrow (Dickman 2006). Digging mammals therefore create a range of disturbances in the form of nose pokes, scratchings, shallow to deep digs, long bulldozing tracts and complex subterranean burrows (Eldridge & Mensinga 2007). They manipulate the substrate and create a variety of disturbances that affect resource availability, contributing to land, soil and water quality (Martin 2003).

In this review, we investigate how the loss of Australian mammalian bioturbators could contribute to declining ecosystem functioning. Over the last 200 years, many of Australia's medium-sized mammals have suffered declines, extirpations, range contractions and extinction. Indeed, Australia has a higher record of extinction of mammal species over the last 200 years than any other part of the world (McKenzie et al. 2007). Species have variously succumbed to a combination of disease, introduced predators and competitors, altered fire regimes, persecution and habitat destruction (Abbott 2008). Today, many species that were once common over large parts of the continent are restricted to small, isolated populations within predator-controlled fenced areas or on offshore islands (Burbidge et al. 2008). Species with body weights between 100 g and 5 kg (termed the 'critical weight range', CWR; Burbidge & McKenzie 1989) are considered most at risk from predation by introduced foxes *Vulpes vulpes* and cats *Felis catus*, especially if they are ground-dwelling species in low-rainfall areas (Burbidge & McKenzie 1989, McKenzie et al. 2007, Johnson & Isaac 2009). Unfortunately, this is also the size range of the majority of Australia's digging mammals (Table 1), many of which have declined in abundance or distributional range (Martin 2003).

We examine the role of Australian digging mammals in providing ecosystem services and in contributing towards

Table 1. Compilation of 29 Australian digging monotremes and marsupials (Van Dyck & Strahan 2008), including their threat status (IUCN and EPBC), whether or not they are within the critical weight range (CWR; see Fig. 3) and their ecological digging activity: foraging and/or burrowing. We have not included rodents, although most species burrow and many have, similarly, shown substantial range contraction over the last 200 years

Species	IUCN status	EPBC	CWR	Digging activity	
				Forage	Burrow
MONOTREMES, Tachyglossidae					
Long-beaked echidna *Zaglossus bruijnii*†	EX¶		N	Y?	N?
Short-beaked echidna *Tachyglossus aculeatus*	LC	–	Y	Y	Y
MARSUPIALS					
Myrmecobiidae					
Numbat *Myrmecobius fasciatus*	EN	VU	Y	N	Y
Chaeropodidae†					
Pig-footed bandicoot *Chaeropus ecaudatus*†	EX	EX	Y	Y?	N?
Peramelidae					
Rufous spiny bandicoot *Echymipera rufescens*	LC	–	Y	Y	Y
Golden bandicoot *Isoodon auratus*	VU	VU	Y	Y	N
Northern brown bandicoot *Isoodon macrourus*	LC	–	Y	Y	N
Southern brown bandicoot *Isoodon obesulus*	LC	–‡	Y	Y	N
Western barred bandicoot *Perameles bougainville*	EN	EN	Y	Y	N
Desert bandicoot *Perameles eremiana*†	EX	EX	Y	Y	N
Eastern barred bandicoot *Perameles gunnii*	NT	VU‡	Y	Y	N
Long-nosed bandicoot *Perameles nasuta*	LC	–	Y	Y	N
Thylacomyidae					
Bilby *Macrotis lagotis*	VU	VU	Y	Y	Y
Lesser bilby *Macrotis leucura*†	EX	EX	Y	Y	Y
Vombatidae					
Northern hairy-nosed wombat *Lasiorhinus krefftii*	CR	EN	N	N	Y
Southern hairy-nosed wombat *Lasiorhinus latifrons*	LC	–	N	N	Y
Bare-nosed/Common wombat *Vombatus ursinus*	LC	–‡	N	N	Y
Potoroidae					
Rufous bettong *Aepyprymnus rufescens*	LC	–	Y	Y	N
Southern bettong *Bettongia gaimardi*	NT	–	Y	Y	N
Boodie/burrowing bettong *Bettongia lesueur*	NT	VU	Y	Y	Y
Woylie/brush-tailed bettong *Bettongia penicillata*	CR	EN	Y	Y	N
Northern bettong *Bettongia tropica*	EN	EN	Y	Y	N
Desert rat-kangaroo *Caloprymnus campestris*†	EX	EX	Y	Y	N
Gilbert's potoroo *Potorous gilbertii*	CR	CR	Y	Y	N
Long-footed potoroo *Potorous longipes*	EN	EN	Y	Y	N
Broad-faced potoroo *Potorous platyops*†	EX	EX	Y	Y	N
Long-nosed potoroo *Potorous tridactylus*	LC	VU‡	Y	Y	N
Notoryctidae					
Northern marsupial mole *Notoryctes caurinus*	DD	EN	N	N	Y
Southern marsupial mole *Notoryctes typhlops*	DD	EN	N	N	Y

IUCN status: International Union for Conservation of Nature Red List of Threatened Species Version 2012.1 http://www.iucnredlist.org (EX †, Extinct; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, near threatened; DD, Data deficient; LC, Least Concern).

EPBC: listing under the Environment Protection and Biodiversity Conservation Act 1999, Australian Government. (EX †, Extinct, CR, Critically Endangered; EN, Endangered; VU, Vulnerable; –, not listed; ‡ indicates that a sub species of the taxa is listed under the EPBC Act 1999).

CWR: Critical Weight Range for Australian mammals according to Johnson and Isaac (2009); Y indicates species has a mass between 0.1–5 kg; N indicates the species is outside of the CWR.

¶ The presence of the long-beaked echidna in Australia is documented by a museum specimen collected in 1901 (Helgen et al. 2012). Its IUCN status is assumed EX.

maintaining ecosystem functioning throughout the continent. We outline the short-term and long-term changes that are likely to occur as a consequence of their extirpation. While many researchers have examined the effects of bioturbators under arid conditions, we also question whether the loss of mammalian bioturbators could contribute to the declines in condition of woodlands and forests currently witnessed.

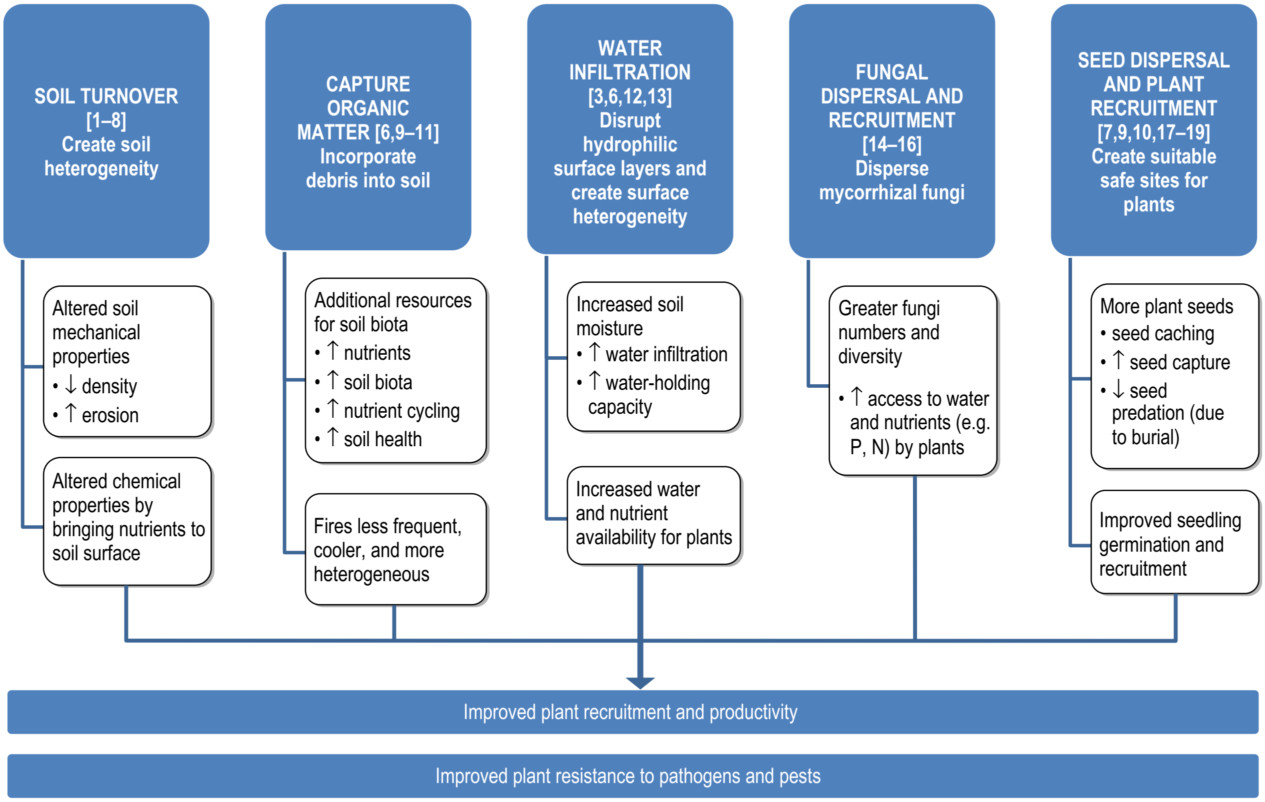


Fig. 1. Flow diagram showing five main ecosystem functions of Australian digging mammals discussed in this review. References: 1. Sheets et al. (1971), 2. Ceballos (1999), 3. Reichman and Seabloom (2002), 4. Eldridge (2004), 5. Garkaklis et al. (2004), 6. Eldridge and Mensinga (2007), 7. Newell (2008), 8. Eldridge et al. (2009), 9. Alkon (1999), 10. Murphy et al. (2005), 11. James et al. (2009), 12. Garkaklis et al. (1998), 13. Garkaklis et al. (2000), 14. Lamont et al. (1985), 15. Hawkins (1996), 16. Tory et al. (1997), 17. Guo (1996), 18. James and Eldridge (2007), 19. Shevill and Johnson (2007). ↑indicates an increase and ↓a decrease.

THE ROLE OF AUSTRALIAN DIGGING MAMMALS IN ECOSYSTEM PROCESSES

In this section, we review published evidence for the role of digging mammals in enhancing soil and ecosystem productivity (Fig. 1 and references therein).

Diggings increase soil turnover

Bioturbation can improve soil health through turnover and organic matter mixing. Digging mammals can move large amounts of soil (Fig. 2). During foraging activities, mammals can turn over around 1.8–3.6 tonnes of soil per kilogram body mass in a year. For example, each woylie *Bettongia penicillata* (~1.3 kg body mass) creates between 20 and 100 diggings per night during foraging (Garkaklis et al. 2004), and each southern brown bandicoot *Isoodon obesulus* (~1.4 kg) can excavate over 3.9 tonnes of soil per year (Valentine et al. 2013). Even more substantial volumes of soil are turned over by mammals that burrow underground: boodies *Bettongia lesueur* (~1.5 kg), greater bilbies *Macrotis lagotis* (~1.5 kg) and northern hairy-nosed wombats *Lasiorhinus krefftii* (~25–40 kg) have soil turnover rates that are an order of magnitude higher (Fig. 2). Although population estimates are not available, given that many of these animals were once described as common (Abbott 2008), their impacts on the environment must have been considerable. In a 275 ha fenced reserve in Western Australia, woylies are present at a density of ~2 individuals ha^{-1} (Australian Wildlife Conservancy, unpublished data), so annual soil turnover due to this species alone is approximately 8.7 tonnes ha^{-1}.

In addition to moving huge volumes of soil, bioturbation by digging mammals increases landscape heterogeneity, creating a spatial mosaic (Davidson & Lightfoot 2008). Digging mammals break through and reduce bulk density of hard soils, which are otherwise impenetrable to plant seedlings. For example, wombats not only generate massive sediment displacement (Borchard & Eldridge 2011) but also burrow through compact soil and thick layers of calcrete. Similarly, boodies preferentially construct warrens in ‘hard red’ soils (Noble et al. 2007) that offer structural integrity for the

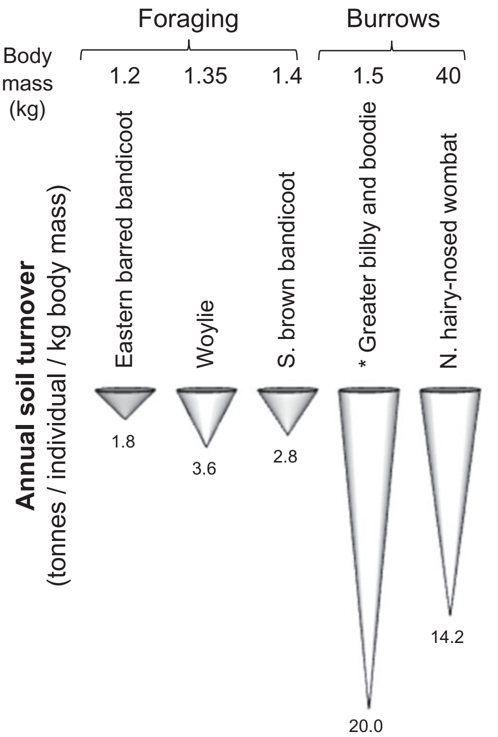


Fig. 2. Soil turnover for six Australian digging mammal species, ordered left to right in sequence of increasing body mass. Values for annual soil turnover are expressed as a function of body mass. References: eastern barred bandicoot *Perameles gunni* (Mallick et al. 1997); woylie *Bettongia penicillata* (Garkaklis et al. 2004); southern brown bandicoot *Isoodon obesulus* (Valentine et al. 2013); greater bilby *Macrotis lagotis* and boodie *Bettongia lesueur* (*combined measurements because both were present at the same site and their diggings could not be distinguished; Newell 2008); and northern hairy-nosed wombat *Lasiorhinus krefftii* (Loffler & Margules 1980).

persistence of burrows in the long term. Diggings by these large mammals therefore break the soil crust and contribute to heterogeneity of soil structure.

Various studies demonstrate that mammalian bioturbation affects soil texture, structure, bulk density, mixing, erosion and surface run-off (Reichman & Smith 1990, Meadows & Meadows 1991, Butler 1995, Kinlaw 1999, Whitford & Kay 1999, Borchard & Eldridge 2011). Digging activity results in soil mixing due to the formation of mounds or spoil heaps, where subsurface soil is deposited on the surface, burying undisturbed surface soil (Wilkinson et al. 2009). In addition to causing mechanical changes, digging also changes soil composition: fertility, distribution of inorganic constituents and mineralisation rate (Sheets et al. 1971, Reichman & Smith 1990, Meadows & Meadows 1991, Butler 1995, Kinlaw 1999, Whitford & Kay 1999). Soil turnover brings deep soils and their nutrients to the surface. In deserts, mammalian burrowers may well provide the most important mechanism for moving insoluble materials and soluble nutrients from deep soil layers (10–200 cm) to the soil surface (Whitford & Kay 1999).

Diggings alter soil–water relations

Diggings alter soil texture, and thereby influence the infiltration rate of rain water, soil moisture content and the rate of diffusion of gases in and out of the soil matrix (Bond 1964). Soils can form a hydrophobic crust-like layer on the surface preventing the penetration of water, contributing to non-wetting properties of the soil. This effect is particularly marked in Australian habitats where *Eucalyptus* spp. trees and sandy soils dominate. As an adaptation to nutrient-poor soils and arid environments (Orians & Milewski 2007), the sclerophyllous leaves of eucalypts are high in resins, waxes and aromatic oils that deter herbivory (Doerr et al. 2000). Decay of their leaf litter causes highly water-repellent topsoil compared with deeper soil layers (Umbrello 2010). Disturbance of the soil surface (e.g. via digging) generally reduces soil water repellency and increases water infiltration. Additionally, soil surface heterogeneity (Eldridge & Mensinga 2007) provides sites for water to enter the soil (Bond 1964, Eldridge & Mensinga 2007). Increased porosity and soil organic matter content improve soil water holding capacity (Wilkinson et al. 2009), although diggings may also become sites of increased water repellency due to trapped organic matter (e.g. fungal hyphae, soil microbes, decomposing plant matter; Roberts & Carbon 1972, King 1981).

The effects of bioturbation by echidnas and woylies on soil hydrology have been closely examined. In eastern Australia's semi-arid eucalypt woodlands, foraging pits produced by echidnas capture more water than undisturbed soil: sorptivity and steady-state infiltration are approximately twice as great in the pits as in undisturbed soils (Eldridge & Mensinga 2007). Woylie diggings can significantly reduce soil water repellency in eucalypt-dominated habitats (Garkaklis et al. 1998). Subsurface soil exposed through digging (including that forming the spoil heaps) is hydrophilic (Umbrello 2010). By contrast, within diggings, soil water repellency increases dramatically after only a week due to accumulation of organic matter and fungal growth (Garkaklis et al. 2000, Umbrello 2010). In the long term, however, this organic matter makes the digging more hydrophilic (Garkaklis et al. 2003). Thus, increases in soil water repellency are transient.

Increased water infiltration also reduces surface run-off, and therefore decreases soil erosion, although breaking the soil crust layer also allows for easier soil transport (Alkon 1999, Borchard & Eldridge 2011). Soil water increases nutrient availability to plants, and therefore plant growth, since nutrients in solution are most readily absorbed by plants (Chapin 1980).

Diggings capture organic matter and affect nutrient cycling

Effective infiltration and water-holding capacity in soil increases suitable conditions for decomposers and detritivores (soil biota such as bacteria, fungi, protists and invertebrates) and therefore leads to higher decomposition rates and nutrient cycling (Eldridge & Mensinga 2007). The presence of diggings increases the heterogeneity of the soil surface, effectively capturing and retaining seeds and leaf litter, which would otherwise be removed by the wind. For example, echidna pits capture around twice as much litter and debris (37.2 ± 6.0 g over 0.04 m^2) as equivalent areas on the soil surface (18.0 ± 3.6 g; Eldridge & Mensinga 2007). Bandicoot foraging pits trap greater amounts of organic matter than undug areas of equivalent size, and contain a larger proportion of fine litter material (<0.05 mm in diameter) that contributes towards soil organic matter over time (Bretz 2012). James et al. (2009) noted that in three paddock areas (with and without predator-proofed fences and therefore with varying densities of digging mammals and reptiles), litter was almost exclusively restricted to the pits of digging animals, and more litter was captured in larger pits.

The mechanical action of soil turnover also traps organic matter below the soil surface. On the surface, litter breakdown by photo-oxidation is relatively slow, and most nutrients are lost from the ecosystem through comminution by the wind, rather than being returned to the soil (Eldridge & James 2009, James et al. 2009). By capturing litter and bringing it into direct contact with soil invertebrates and microbes through burial, the release of soil nutrients and nutrient cycling is greatly enhanced (Eldridge & Mensinga 2007). Furthermore, the microclimate of pits, characterised by greater moisture and lower temperature (Eldridge & Mensinga 2007, James et al. 2010, Bretz 2012), is conducive to decomposition. For example, respiration of echidna pit soils is about 30% higher than non-pit soils (Eldridge & Mensinga 2007). Mixing of soil with organic matter creates a rich medium promoting growth of soil biota, including micro-invertebrates, bacteria, fungi, actinomycetes, nematodes and protozoa (Killham 1994) – the building blocks of productive soil (Eldridge & Mensinga 2007). Bioturbation therefore affects resource availability (nutrients, carbon, water, electron donors and acceptors) for microbes, or provides abiotic conditions (soil moisture, temperature, pH, redox potential) that affect rates of microbial processes (Gutiérrez & Jones 2006). Pits may become foci of micro-invertebrate and microbial activity, with high rates of decomposition and nutrient cycling (Eldridge & Mensinga 2007, Fig. 1). This may increase nutrients available for plants. James et al. (2009) recorded three times the concentration of total carbon and twice the nitrogen content in pits, either in surface soils or in soils at depth, while Eldridge and Mensinga (2007) recorded lower carbon, nitrogen and sulphur in echidna diggings.

Due to the capture of organic matter in the soil and the acceleration in nutrient cycling, digging mammals have the potential to reduce litter and biomass accumulation. The mixing of organic matter into the soil layer (either litter trapped in pits or litter buried under spoil heaps), coupled with increased rates of litter decomposition, may reduce the amount of combustible plant material within a landscape, possibly altering fire regimes (Martin 2003).

Bioturbation can also influence the largest pool of actively cycling carbon in terrestrial ecosystems – that present in the top layers of the soil (up to ~1 m). This soil contains about 1500–2000 Pg C in various organic forms (together termed ‘soil organic carbon’), including recent plant litter, charcoal and very old, humified compounds (Janzen 2004). This is more carbon than there is in the atmosphere (720 Pg C as CO_2) and biosphere (600 Pg C) combined. Soil biota plays a significant role in soil carbon dynamics and, given the size of this carbon pool, by contributing to maintaining healthy soil biota and trapping organic matter in the soil, the actions of digging mammals therefore have implications for climate regulation (Wilkinson et al. 2009).

Digging mammals increase fungi dispersal and recruitment

Mycophagous bioturbators influence the dispersal of mycorrhizal spores that are important for soil-plant associations in an ecosystem. Australia’s ancient landscapes with infertile, weathered, nutrient-poor soils (especially deficient in phosphorous and nitrogen) are associated with high epigeous and hypogeous fungi diversity (Orians & Milewski 2007). The vast majority of native plants (e.g. *Eucalyptus* spp.) have evolved symbiotic relationships with mycorrhizal fungi (Brundrett 2009). Mycorrhizae are specialised structures arising from the association of roots and fungi, which allow plants greater access to limited soil nutrients and water (Johnson 1996, Van Der Heijden et al. 1998, Egerton-Warburton et al. 2008). Mycorrhizal hyphae may extend meters into the soil from plant roots, and access additional chemical pools of nutrients such as P; they may then release phosphatases or carboxylates that enhance the availability of organic P, or sparingly soluble P, respectively (Landeweert et al. 2001, Van Hees et al. 2006). In return, the fungi are provided with photosynthates from the plant. Fungi also have high nitrogen content, so stimulation of fungal growth (e.g. within pits of burrowing marsupials) represents a major contribution to plant nitrogen sources (Christensen 1980).

Many ectomycorrhizal species form spore-filled underground (hypogeous) fruiting bodies (truffles). Bioturbators that consume these influence the dispersal of mycorrhizal spores. For mycophagous specialists (potoroos and bettongs), hypogeous fungi form 50–90% of their diet (reviewed by Claridge & May 1994, Johnson 1995, McIlwee & Johnson 1998, Vernes et al. 2001, Nguyen et al. 2005). These digging mammals spread mycorrhizal spores, which pass intact through their digestive tracts and are deposited in their faeces (thus providing additional nutrition for spore germination, Johnson 1996). For some fungi, passing through the gut can break spore dormancy, leading to increased germination (Lamont et al. 1985, Reddell et al. 1997). By disseminating spores in their scats, mycophagous mammals help maintain fungal diversity within their home range (Maser et al. 2008, Danks 2012). This fungal diversity increases nutrient availability (especially limiting nutrients, e.g. P, N), ultimately improving plant vigour and resilience to root pathogens (Marx 1972, Malajczuk 1988). Mycophagous animals therefore indirectly influence vegetation assemblages.

Using olfactory cues to locate food sources, mycophagous potoroids focus their digging activity around roots of host plants where the pungent fungal sporocarps are concentrated (Donaldson & Stoddart 1994), adjusting activity patterns over short periods of time to exploit fungal resources (Johnson 1995). This discriminatory foraging behaviour generates a mosaic of small-scale disturbances resulting in a heterogeneous distribution of fungi and nutrients throughout the landscape. The digging behaviour of mammals, therefore, may also influence spatial patterns of plant growth.

Digging mammals alter plant community composition and structure through altered seed dispersal and seedling recruitment

As well as by improving nutrient turnover and availability, digging mammals may also alter the plant community through affecting seed dispersal and seedling recruitment. Seed caching, accidental seed capture in foraging pits or active dispersal of seeds can lead to increased seedling germination and growth (e.g. Guo 1996, Alkon 1999, Murphy et al. 2005, James & Eldridge 2007, Newell 2008). Hoarding and caching food (e.g. in burrows) markedly influences distribution and germination of plants involved (e.g. Whitford & Kay 1999, Midgley et al. 2002). Australian native rodents (Forget & Vander Wall 2001) and marsupials (Dennis 2003, Murphy et al. 2005) exhibit seed-caching behaviour, playing a critical role in dispersing plant seeds. For example, woylies are the key dispersers of large sandalwood *Santalum spicatum* seeds, carrying the seeds away from mature plants and burying them at an optimal depth for seed germination (Murphy et al. 2005). Many studies have shown that pits can increase seedling germination and plant recruitment (Table 1, Fig. 1, and references therein). Diggings may bring buried seeds close to the soil surface (Dickman 2006) while pits may also protect seeds already present at the surface from wind and granivores. By collecting animal faeces, litter and seeds, diggings can generally lead to enhanced seed germination compared with non-pit soils (although litter-filled pits may also retard seed germination by inhibiting soil–seed contact, Rotundo & Aguiar 2005). The shape and altered microclimate of pits additionally confer advantages to germinating seeds: since nutrients are only available to plants in solution, greater water infiltration and more efficient nutrient cycling are likely to contribute positively to plant growth (Martin 2003). Breaking up the hard soil crust is essential for many plants to survive, and increasing surface heterogeneity, trapping rainfall run-off and organic matter, leading to nutrient-rich soil, vegetation recruitment and growth, may consequently be increased by the presence of bioturbation.

LOSS OF AUSTRALIAN DIGGING MAMMALS

Australian mammals appear to lack resilience to certain threatening processes, particularly introduced predators, disease and changed fire regimes – processes that have contributed to the high rate of extinction. A quarter of Australian mammalian species are now listed as extinct, critically endangered, endangered or vulnerable (McKenzie et al. 2007). Marsupials with body weights between 100 g and 5 kg (CWR) are considered most at risk from fox predation, particularly if they are ground-dwelling, non-arboreal species in low-rainfall areas (Burbidge & McKenzie 1989, McKenzie et al. 2007, Johnson & Isaac 2009). Of the 160 Australian marsupial and monotreme species, 29 species are considered diggers (broadly defined here as those species that dig for food or burrow for shelter; Fig. 3). Of these 29 digging species, 23 are within the CWR and nearly 70% have an International Union for Conservation of Nature listing (Fig. 3; Table 2). Several species have suffered drastic declines in mainland populations and substantial range contractions (Burbidge et al. 2008; Fig. 4). It is concerning that the majority of Australian marsupial diggers (e.g. the bettongs, potoroos, bilby and bandicoots) are at risk (Figs 3 and 4).

Digging mammals that were once common in ecosystems are now rarely observed or entirely absent (Fig. 4; Box 1). The only species that has not demonstrated a range contraction may be the echidna (Figs 4 and 5). The echidna is a ground-dwelling monotreme within the CWR, but it has persisted throughout its range in the pre-European settlement era. A combination of protective integument and effective anti-predatory behaviour (Fig. 5) means that its shelter requirements are independent of vegetation

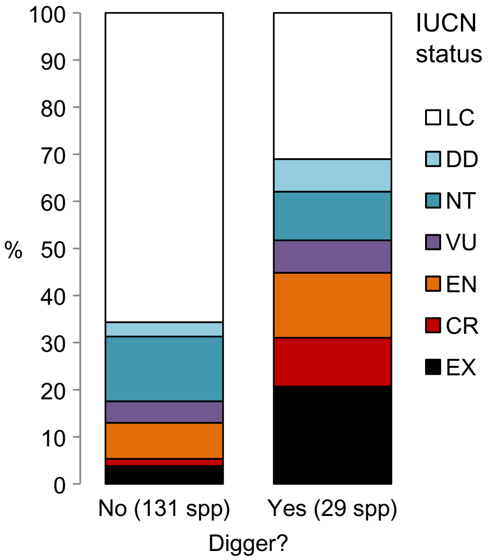


Fig. 3. Status of Australian marsupials and monotremes, separated by whether they dig or not. Of 29 digging species, 23 are within the critical weight range (CWR – body weights between 100 g and 5 kg, and particularly vulnerable to introduced predators; Burbidge & McKenzie 1989), and 6 are extinct. International Union for Conservation of Nature (IUCN) status indicates the conservation status of each species according to the IUCN Red List of Threatened Species category (June 2012): EX, Extinct; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; DD, Data Deficient; LC, Least Concern.

and consequently there is minimal predation on adults (Abensperg-Traun 1991). In addition, echidnas are habitat generalists, specialising on an abundant and reliable food source (termites and ants) for which there is little competition (Abensperg-Traun 1991).

What would happen without Australian digging mammals?

Bioturbation manipulates the substrate and creates a variety of disturbances that have multiple benefits to the overall ecosystem (Eldridge et al. 2009). The significant decline of the majority of Australia's digging marsupials, once common across the continent, has meant that important ecosystem processes these ecosystem engineers contributed towards have been lost (Fig. 6). These losses have probably resulted in a cascade of deleterious impacts, although the time lag before these impacts can be perceived may vary. There may be immediate consequences of the loss of digging mammals (e.g. changes in soil properties, Bretz 2012) as well as long-term effects (e.g. changes in floristic community, Dickman 2006). Some obvious changes may be relatively easy to measure; however, other processes (e.g. loss of plant dispersal and recruitment, distribution of mycorrhizae) may take longer to become evident.

In the absence of bioturbation, ecosystem functioning is likely to decline (Fig. 6). For example, the capture of surface water plays an important role in Australia's arid environments, and water infiltration is likely to become increasingly important under current and future climate scenarios where soil profiles are drying out (Dundas et al. 2012). The loss of digging mammals leads to decreases in the amount of water infiltration, and therefore loss of these animals may contribute to the risk of profound drought and induced tree collapses, as have been witnessed over recent years (Close & Davidson 2004, Brouwers et al. 2013, Matusick et al. 2012).

Although introduced species may contribute towards some of the ecosystem processes identified (e.g. Vernes & McGrath 2009, James et al. 2011), their actions are unlikely to match those of native species that have a long evolutionary history with the land. For example, despite functional similarities, European rabbit *Oryctolagus cuniculus* diggings in Australia support fewer plant seedlings than diggings of native mammals, perhaps because rabbits dig shallower pits than native bilbies and bettongs (James et al. 2011). Feral pigs *Sus scrofa*, similarly, create large, shallow diggings, destroy vegetation (the pigs target the roots of key species) and therefore create clearings. Their actions open up dense vegetation, and therefore reduce habitat for riparian-specialist species (e.g. the quokka *Setonix brachyurus*, Dundas et al. 2010).

CAN WE REINTRODUCE DIGGING MAMMALS TO RE-ESTABLISH ECOSYSTEM PROCESSES?

Where ecosystems have lost digging mammals, key processes (e.g. soil turnover, organic matter mixing and seed recruitment) are likely to have changed or been lost also (James & Eldridge 2007). This may lead to deteriorating ecosystem functioning (Fig. 6). Restoration projects may therefore need to consider the reintroduction of digging mammals (Crain & Bertness 2006, James & Eldridge 2007). For example, 'Arid Recovery' (centred around a 123 km^2 fenced reserve) has been hailed as successful: four species of locally extinct mammals have been reintroduced, and the digging actions of bilbies and bettongs have been demonstrated to restore the arid landscapes through increasing seedling capture and germination (Newell 2008). Introductions and reintroductions (e.g. of bilbies, woylies, boodies, bandicoots) at other sites have had varying success, highlighting the necessity of controlling introduced predators (e.g. through baiting or predator-proof fencing) if projects are to be successful (Short et al. 1992, Finlayson et al. 2010, Dickman 2012).

While reintroductions may be required to protect vulnerable animal species, a case also needs to be made to support reintroductions of non-threatened mammal species to

Table 2. Possible mechanisms of action that may explain why mammal diggings lead to increased plant recruitment and growth, and the experimental designs that have been used to test each of these in research examples or case studies

	Possible mechanism of action:				
Examples/case studies	Seed caching	Surface heterogeneity captures more seed	Bring buried seeds to the soil surface	Collapsing diggings bury seed, reducing predation	Biotic (mycorrhizae) and abiotic (nutrients, water, temperature) conditions
Increased numbers of seeds					
due to seed burial					
• Significantly more seeds trapped in bilby *Macrotis lagotis*/boodie *Bettongia lesueur* diggings – seeds sieved out from soil samples (Newell 2008)		✓		✓	
• Artificial diggings retain up to 70–90% of glass beads (seed surrogate) over 18 weeks (Newell 2008)		✓		✓	
due to seed caching					
• Glass beads (seed surrogate) moved from plots in the presence of bilbies/boodies (Newell 2008)	✓				
• Reduced sandalwood dispersal and recruitment in the absence of woylies *Bettongia penicillata* (Murphy et al. 2005)	✓				
Increased seed germination rates and recruitment					
in the presence of pits					
• Greater germination of hand-broadcast seed for sites with a high density of artificial diggings compared with plots with a low density of natural bandicoot *Isoodon obesulus* diggings or matched plots without any diggings (Bretz, Valentine, Ruthrof, Hardy, Fleming)		✓		✓	✓
of existing seed bank					
• For artificial diggings (protected from further seed rain; James et al. 2010)			✓		✓
from the soil seed bank in greenhouse trials					
• For soil collected from bilby/boodie diggings (James et al. 2009)	✓	✓	✓	✓	✓
• For soil collected from echidna *Tachyglossus aculeatus* diggings (Travers et al. 2012)	✓	✓	✓	✓	✓
Increased plant growth, species richness and diversity					
• Boodie warrens contribute to 2% of total plant biomass and 2.5% of palatable nutritious perennial grasses despite comprising only 0.6% of study area, while biomass of forbs and palatable grasses is 227% greater on warren sites than off sites (Noble et al. 2007)	✓	✓	✓	✓	✓
• Plant cover, plant and seed species richness are greater on disturbed soil near long-haired rat *Rattus villosissimus* burrows (Dickman 2006)	✓	✓	✓	✓	✓

restore lost ecosystem functions. For example, southern brown bandicoots *Isoodon obesulus* removed from encroaching urbanisation sites could be released at sites where digging processes have been lost. Protection of existing digging mammal species, recognising their important role and apparent resilience to urbanisation (Bateman & Fleming 2012), is also warranted.

CONCLUSION

Studies compiled globally suggest that some of the world's forested ecosystems may already be responding to increased warming and drought, highlighting the potential for forests to become increasingly vulnerable to higher background tree mortality rates and die-off (Allen et al. 2010). Digging

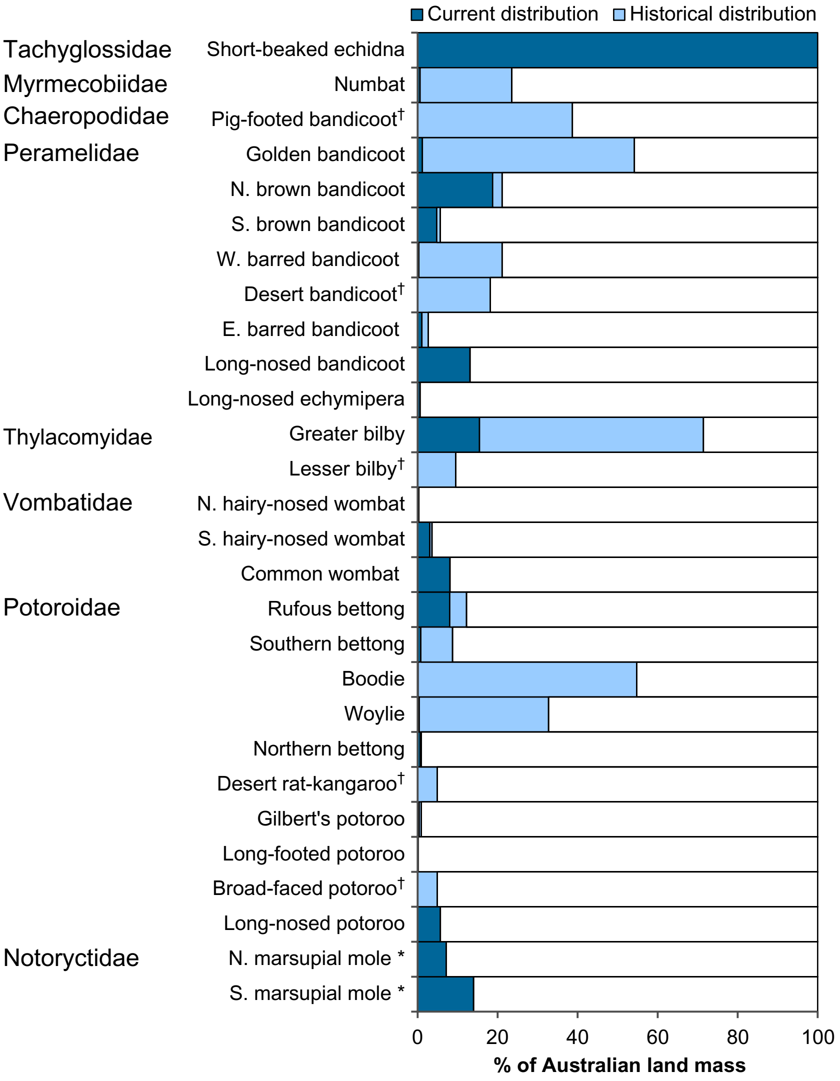


Fig. 4. Changes in geographical ranges of Australian monotreme and marsupial digging species. See Table 1 for full species names. Data extracted from Van Dyck and Strahan (2008). Historical distribution (light blue/cross hatched) includes recent fossil distribution and former distribution (since settlement of Australia by Europeans). Current distribution is shown as dark blue/black. † species extinct, * data deficient. We have not included *Zaglossus bruijnii* because we have no comparable information. Values are expressed as a percentage of the total Australian land mass.

Box 1. The plight of some key digging species in Australia (Fig. 4).

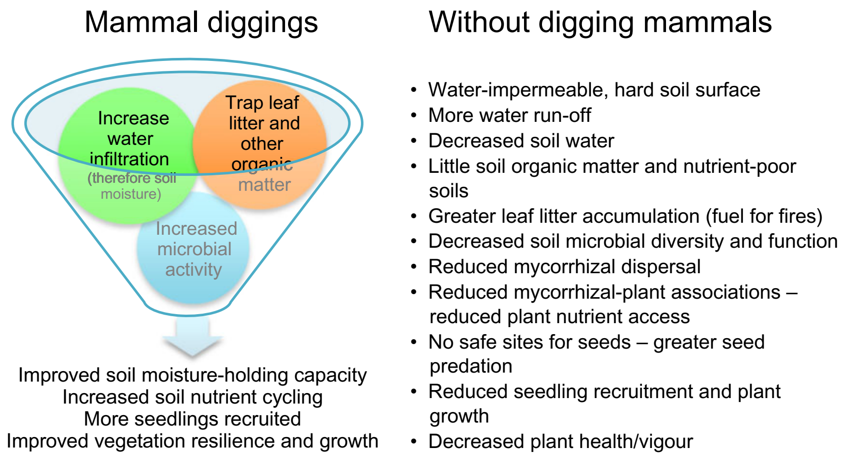
- The woylie was once abundant across ~35% of mainland Australia (Van Dyck & Strahan 2008). The species was described as 'very plentiful', with 'tens of thousands' recorded around some towns (Abbott 2008). Due to disease, habitat loss and introduced predators, the range of the woylie has drastically declined, and it now occupies much less than 1% of its original range (Abbott 2008, Van Dyck & Strahan 2008) where it is largely confined to predator-proof enclosures (Short & Smith 1994).
- Boodies were once widespread and abundant across ~60% of mainland Australia (Short & Turner 1993). They were 'present in their hundreds', and it was necessary to build fences to keep them away from newly sown seed or poison them to control numbers (Abbott 2008, Finlayson et al. 2010 and references therein). Today, apart from reintroductions, boodies are extinct on the mainland.
- The eastern barred bandicoot *Perameles gunnii* and western barred bandicoot *Perameles bougainville* once occurred on mainland Australia, but they are now restricted to Tasmania and offshore islands in Western Australia, respectively (Van Dyck & Strahan 2008).
- Historically, bilbies were once one of the most plentiful Central Australian CWR mammals (Southgate 1990). Bilbies were once so bountiful that their highly prized furs were reasonably available (Abbott 2008). Bilbies were once found across ~70% of the Australian mainland. Today, the lesser bilby is extinct and the greater bilby occupies less than 20% of its former range (Southgate 1994); it is present in northern parts of its former range (Van Dyck & Strahan 2008), possibly due to the absence of red foxes in northern Australia.

Fig. 5. Attempted predation of a short-beaked echidna *Tachyglossus aculeatus* by a red fox *Vulpes vulpes*. The short-beaked echidna is one of the only digging mammal species that has not undergone a massive range contraction over the last 200 years (Fig. 4). Its ability to withstand predation pressures, presumably due to its protective integument, may contribute towards its survival. Photo David Graham, Mukinbudin Western Australia.

and burrowing mammals are clearly extremely important in ecosystems, as they directly and indirectly affect ecosystem functioning. Without these animals, the services they perform are lost also (Fig. 6). The role of these animals is largely unrecognised (Orians & Milewski 2007), and research and management targeting these species need to be undertaken as a matter of some urgency.

In Australia, we are currently managing ecosystems that have relatively recently undergone a massive loss of ecosystem processes. It is quite likely that the effects of lost tree recruitment have yet to be felt under many systems. For example, it has only recently been recognised that in the absence of woylies, there is reduced sandalwood dispersal and recruitment (Murphy et al. 2005). Without digging mammals to break up the hydrophobic surface crust of the soil and create a heterogeneous surface, seeds are less likely to find suitable sites for germination. Also, established trees may already have hypogeous mycorrhizal associations to supply essential nutrients, but what about new plants being recruited in the absence of the animals that spread the spores of these fungi?

The role of fauna in the turnover of organic matter has important implications for how we burn forests. We use past records to inform decisions regarding the appropriate inter-fire interval for controlled burning to prevent wildfires. However, we need to acknowledge that the Australian continent once teemed with medium-sized mammals that dug organic matter into the soil, reducing fuel loads by speeding up breakdown of organic matter, as well as by locking leaf litter away from flames beneath soil. Fuel loads are likely to be much higher now than in the past. Therefore, if we currently burn at similar inter-fire intervals, we may generate fires of greater intensity that may consequently be less patchy and leave fewer unburnt areas for fauna that requires long unburnt habitat. More trees are also likely to succumb due to hotter fires. We also manage fire regimes assuming that the woodlands and forests will respond as they have in the past. It is becoming increasingly obvious, however, that these systems lack some of the resilience that they had before. For example, substantially dropping water tables has meant that even fully grown trees may not have access to resources required to recover from



- Water-impermeable, hard soil surface
- More water run-off
- Decreased soil water
- Little soil organic matter and nutrient-poor soils
- Greater leaf litter accumulation (fuel for fires)
- Decreased soil microbial diversity and function
- Reduced mycorrhizal dispersal
- Reduced mycorrhizal-plant associations – reduced plant nutrient access
- No safe sites for seeds – greater seed predation
- Reduced seedling recruitment and plant growth
- Decreased plant health/vigour

Fig. 6. Digging mammals mix soil and organic matter together while foraging. Organic matter creates a potential substrate for a variety of soil biota (e.g. bacteria, fungi, actinomycetes, nematodes and protozoa) to grow (Killham 1994). This soil biota, which forms the building blocks of productive soil (Eldridge & Mensinga 2007), decomposes the organic matter, accelerating nutrient cycling (Brussaard 1997) and consequently plant recruitment and growth.

disturbance (e.g. Matusick et al. 2012). Has the loss of important services contributed by digging fauna played a role in the decreasing resilience of our ecosystems?

This review highlights the vital roles that digging mammals play in ecosystem processes, which go beyond simply turning over soil, extending to nutrient cycling, enhancing plant recruitment and growth, providing habitat and potentially altering fire regimes. While there has been some success in reintroducing threatened species to predator-controlled areas such as islands or fenced reserves (Short et al. 1992, Finlayson et al. 2010, Dickman 2012), it needs to be recognised that management on a larger scale may be needed. Translocation of species that are still relatively common (e.g. bandicoots) may allow us to re-establish some ecosystem processes. At present, these animals are often moved out of the way of encroaching development with little heed of the valuable role that they can play, under appropriate conditions. If we cannot re-establish lost ecosystem processes, then we at least need to acknowledge their loss and consider it when planning and implementing conservation management. Understanding the critical linkages between digging mammals and their environment is fundamentally important as we work to protect and manage Australia's ecosystems and the biodiversity they support.

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