REVIEW ARTICLE

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Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes

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Summary Soil-disturbing animals have wide-ranging effects on both biotic and abiotic processes across a number of Australian ecosystems. They alter soil quality by mixing surface soils and trapping litter and water, leading to areas of increased decomposition of organic matter. The foraging pits of indigenous soil-disturbing animals tend to have different soil chemical characteristics, greater levels of infiltration and lower levels of soil density than adjacent areas. Enhanced capture of seeds and water turns disturbance pits into areas of enhanced plant germination. The burrows, pits and mounds of both native and exotic animals provide habitat for a range of vertebrates and invertebrates and contribute to patchiness in the landscape. Given their wide-ranging effects on surface soil and ecological processes, we argue in this review that soil disturbance by native animals has the potential to contribute to restoration of degraded landscapes, particularly in arid and semi-arid areas.

Key words: *biopedturbation, ecosystem engineers, re-introductions, restoration, soil disturbance, soil processes.*

Introduction

Soil disturbance by animals has long been recognized as a significant and substantial landscape and ecological process (Whitford & Kay 1999). Studies of soil disturbances by vertebrates worldwide have documented widespread effects on ecosystem properties and processes including soil formation (pedogenesis), seed entrapment, plant germination and establishment, soil nutrient heterogeneity, water infiltration and storage, soil respiration, microbial activity and litter decomposition. In Australia, these functions have, until recently, been maintained by native soil-disturbing animals.

The loss of soil-foraging, medium-sized mammals over large areas of continental Australia has resulted in substantial declines in ecosystem functions. This is particularly apparent in arid and semi-arid Australia where stability and productivity depend on the maintenance of a range of processes mediated by these animals. Many of the lost species created large soil disturbances in the form of warrens and burrow systems, and smaller disturbances known as foraging pits (Fig. 1) while digging for subterranean food. The loss of soil-disturbing native animals has also been accompanied by an invasion of exotic analogues; animals that also dig in the soil but have, as far as we know, negative effects on soils and landscapes. Exotic animals such as the European Rabbit (*Oryctolagus cuniculus*) and Pig (*Sus scrofa*) have successfully invaded most of the continent and their combined disturbances have had substantial negative ecological consequences (Wood 1988; Mitchell & Mayer 1997; Eldridge & Myers 2001; Eldridge *et al*. 2006). Exotic, soil-disturbing animals are also thought to occupy niches formerly occupied by native diggers. Competition between native and exotic soil-disturbing animals has led to further reductions in native animal populations and hastened the loss of some key ecosystem services formerly provided by native animals while foraging. There are no *a priori* reasons why native animals should have positive effects while exotic animals appear to have negative effects. However, there are a number of possible explanations relating to pit morphology, and amount and location of disturbances. Different shaped pits constructed by rabbits and native animals may differ in the way that they capture and retain resources. Similarly, although some exotic animals such as pigs are known to disturb large areas of soil surface, disturbances by native animals appear to be more dispersed. Exotic animals might dig in areas where plant and invertebrate species are not adapted to disturbance.

Figure 1. These foraging pits of the Burrowing Bettong, concentrated around the edge of a patch of vegetation, lead to an increase in the amount of nutrients in the soil

Although increasing effort has been made to reinstate locally extinct animals across arid Australia (e.g. Moseby & O'Donnell 2003; Mawson 2004; Finlayson *et al*. 2008), little attention has been given to the benefits that accrue from their effects on landscape health or the roles that they might play in the processes of restoration and rehabilitation (Martin 2003). Given the growing awareness of the importance of native animals for maintaining healthy soils and landscapes (e.g. Whitford & Kay 1999; Whitford 2002), we believe that a synthesis of the Australian literature is warranted and timely.

Here we examine the ecological mechanisms whereby soil-disturbing vertebrates create and maintain healthy landscapes in Australia. The review incorporates studies of both native and exotic vertebrates across continental Australia but our focus is on native animals from arid and semi-arid environments where we believe that the effects will be most marked. We use published and unpublished data to describe the effects of vertebrates on soil quality (soil formation, litter capture and decomposition, and soil nutrients), seed germination and establishment, maintenance of habitat, and development of landscape patchiness, and argue that the effects of native, soil-disturbing animals should be considered in any efforts to 'restore' degraded landscapes.

Surface-disturbing animals alter soil quality

Soil turnover and soil formation

Australian soils are highly weathered and characterized by low levels of biologically derived nutrients such as carbon and nitrogen. Physical rates of soil formation are very low, probably <0.5 tonnes/ha/year for more mesic landscapes (Edwards & Zierholz 2000). The greatest impact that animals have on soils is through their effects on soil detachment and transport. Evidence from a number of published and unpublished studies across Australia highlight some consistent themes in relation to soil-disturbing vertebrates (Table 1).

Soil disturbance by animals has many negative effects such as reducing structural stability, burying plants, or inverting the soil profile and allowing finer material to be lost from the site through the action of water and wind. However, soil disturbance is an important pedogenic process, particularly in dry areas where more common abiotic processes such as leaching are limited. Soil disturbance mixes surface soils and creates macropores that increase aeration and water entry into the soil. Disturbance is also critically important for seed and litter capture (see below).

In semi-arid Australia, rates of soil turnover range from 0.1 to 6 t/ha for foraging pits and mounds created by a range of soil-disturbing mammals, to over 87 t/ha for burrow systems of the Southern Hairy-nosed Wombat (*Lasiorhinus latifrons*) (Table 1, Steele & Temple-Smith 1998). Rates of soil disturbance from pits of the Rabbit (0.1–0.6 t/ha, Table 1) are substantially less than those from the pits of native animals such as the Greater Bilby (*Macrotis lagotis*) or Burrowing Bettong (*Bettongia lesueur*) (1.3–6.0 t/ha). When we take into account the per-capita effect of a large number of rabbits constructing foraging pits (Eldridge & Kwok 2008), they are unlikely to ever assume the critical role previously held by these native animals.

Soil movement by the Wedge-tailed Shearwater (*Puffinus pacificus*) (10.5 t/ha per year; Bancroft *et al.* 2004) is almost double that of arid-zone mammals, and disturbances in higher rainfall areas may even be orders of magnitude greater. For example, the Superb Lyrebird (*Menura novaehollandiae*) can move up to 200 t/ha/year of organic-rich soil in rainforest and wet sclerophyll forest in eastern Australia (Adamson *et al.* 1983; Ashton & Bassett 1997). The ecological significance of soil-disturbing activities by the Cassowary (*Casuarius casuarius*) and the Australian Brush-turkey (*Alectura lathami*) is unknown but they may be critical for breakdown of organic matter and mineralization of soil nutrients. Overall, the data presented in Table 1 emphasize the importance of native animals for mixing of surface soils and promoting soil development in Australia.

Litter capture and soil nutrients

Animal foraging pits intercept organic matter transported by wind or water and therefore provide a mechanism for trapping it below ground. This is particularly important in degraded areas where many of the natural sinks for litter, such as perennial shrub hummocks and grass tussocks, have been lost through overgrazing. The literature indicates an overwhelming trend for pits to trap more litter than non-pit surfaces (Table 1) and this is critically important for three reasons. First, organic matter is known to be limiting over large areas of the continent and decomposition rates are greatest where this litter comes into direct contact with the soil and soil microbes (Eldridge & Mensinga 2007). Second, the microclimate of the pits is more conducive to decomposition (more moisture, moderate temperature, differing infiltration). Third, the products of litter decomposition in pits are directly available to plants because the nutrients become part of the soil nutrient pool. Litter that breaks down on the surface, generally through photo-oxidation by ultraviolet light (Whitford 2002), results in fewer nutrients being returned to the soil. Overall, the construction of pits and depressions, and the capture of litter and its decomposition within these pits, is probably the most important process moderated by soil-disturbing animals.

Soil chemical and physical properties

Given that pits contain more litter and promote increased decomposition, concentrations of soil nutrients are generally greater. Unlike the large, organically rich mounds constructed by Megapodes such as the Australian Brush-turkey, mounds associated with foraging pits are typically highly disturbed bare surfaces that are constructed from less fertile subsoil. Therefore, they are likely to be nutrient-poor due to reduced incorporation of organic matter. The results of published work in Australia suggest substantial increases in electrical conductivity, soluble and exchangeable cations, phosphorus, pH and mineralizable nitrogen, and variable effects on nitrogen and carbon on the mounds (Table 1). In arid areas, most nitrogen and carbon occurs in the top few centimetres of the soil, and digging is therefore likely to truncate this nutrient-rich layer, leading to lower concentrations through topsoil erosion.

Conditions in newly constructed pits will be markedly different from those in older pits. Studies of Echidna (*Tachyglossus aculeatus*) pits decomposing over time, demonstrate that levels of labile carbon in

Table 1. Impact of Australian vertebrates from a range of vegetation communities on soil quality as measured by soil turnover (t/ha), litter accumulation, soil nutrient concentrations and soil physical properties

Organism and habitat	Soil turnover (t/ha)	Litter mass	Soil nutrients	Soil physical properties	Vegetation community	Reference
Foraging pits						
Greater Bilby (*Macrotis lagotis*) and Burrowing Bettong (*Bettongia lesueur*)	1.27–5.99	>litter	>C, N, S, LC	>infiltration	Arid shrubland,	James (2004), James & Eldridge (2007)
			>NH_4^+/NO_3^-	>moisture <temp	Semi-arid woodland	James *et al*. (in press), Huang (2007)
Tasmanian Bettong (*Bettongia gaimardi*)	0.38–4.5					Johnson (1994)
Eastern Barred Bandicoot (*Perameles gunnii*)	2.2				Wet sclerophyll	Mallick *et al*. (1997)
Long-nosed Potoroo (*Potorous tridactylus*)	0.34–1.1				Wet sclerophyll	Claridge *et al*. (1993)
Brush-tailed Bettong (*Bettongia penicillata*)	2.6–4.0				Dry sclerophyll	Garkaklis *et al*. (2004)
				>infiltration	Dry sclerophyll	Garkaklis *et al*. (1998)
Long-nosed Bandicoot (*Perameles nasuta*)	0.47		=LC		Coastal heath	Eldridge (unpubl. data)
Short-beaked Echidna (*Tachyglossus aculeatus*)	0.39–2.1	>litter			Semi-arid woodland	Huang (2007)
	0.57	>litter		>erosion	Semi-arid woodland	Eldridge & Kwok (2008)
		>decomp		=runoff, infiltration		Eldridge (unpubl. data)
		>litter	<N, S, P >EC =C, pH	>moisture <infiltration, BD >CO_2, temp	Semi-arid woodland	Eldridge & Mensinga (2007)
	0.1				Dry sclerophyll	Robinson (2003)
European Rabbit (*Oryctolagus cuniculus*)	0.10–0.36	>litter			Arid shrubland	James & Eldridge (2007)
	0.6	>litter			Semi-arid woodland	Huang (2007)
			=LC		Coastal heath	James (unpubl. data)
Pig (*Sus scrofa*)	4.1†				Wet tropics	Mitchell & Mayer (1997)
	2.0–5.0†					Bowman & McDonough (1991)
		=litter	=C, N		Wet tropics	Mitchell *et al*. (2007)
Gould's Sand Goanna (*Varanus gouldii*)	0.07–0.88	>litter			Semi-arid woodland	Huang (2007), Kwok (2005)
	0.26	>litter			Semi-arid woodland	Eldridge & Kwok (2008)
	0.07	>litter	>NH_4^+/NO_3^-		Arid shrubland	James & Eldridge (2007) James *et al*. (in press)
			>avail P =EC, pH, C, N, S		Semi-arid woodland	Eldridge (unpubl. data)
Superb Lyrebird (*Menura novaehollandiae*)	200‡	>decomp	>C, =N	<BD	Wet – dry sclerophyll	Ashton & Bassett (1997)
	44.7–63.0‡				Dry sclerophyll	Adamson *et al*. (1983) Humphreys & Mitchell (1983)
Chowchilla (*Orthonyx spaldingii*)		variable			Wet tropics	Theimer & Gehring (1999)

Table 1. *Continued*

Organism and habitat	Soil turnover (t/ha)	Litter mass	Soil nutrients	Soil physical properties	Vegetation community	Reference
Burrows and mounds						
Southern Hairy-nosed Wombat (*Lasiorhinus latifrons*)	2.6–87.5					Steele & Temple-Smith (1998)
Common wombat (*Vombatus ursinus*)	1.72			>BD	Dry sclerophyll	Borchard (unpubl. data), Evans (2008)
	2.8–9.8				Continental	Triggs (1996)
Burrowing Bettong (relict) (*Bettongia lesueur*)			>pH, OC =N	<BD >infiltration	Semi-arid woodland, Spinifex grassland	Noble *et al*. (2007), Burbidge *et al*. (2007)
European Rabbit (*Oryctolagus cuniculus*)	1.4–29.4	<litter	>pH, EC, Ca, K, Al, Bo, Mn, Fe, sol Na <C, S; =N	>clay, bare =BD, silt <aggregation¶ <cryptogam	Semi-arid woodland	Eldridge & Kwok (2008), Vine (1999), Eldridge & Myers (2001), Eldridge & Koen (2008)
	88.2				Continental	Butler (1995)
			>N, C	>infiltration $=CO_2$	Semi-arid woodland	Birnbaum (2007)
				=compaction	Dry sclerophyll	Milner *et al*. (unpubl.data)
				>temp, RH	Continental	Myers *et al*. (1994)
	0.83				Arid woodland	Wood (1985)
Australian Brush-turkey (*Alectura lathami*)	1.94§					Jones (1988)
Malleefowl (relict) (*Leipoa ocellata*)		>litter	$>NH_4^+/NO_3^-$		Semi-arid woodland	Noble (1993)
Superb Lyrebird	0.2‡	>litter >decomp		>soil moisture	Dry sclerophyll	Adamson *et al*. (1983)
Wedge-tailed Shearwater (*Puffinus pacificus*)	10.5‡		$>NO_3^-$, P, NH_4^+, S, K; <OC, Fe; >EC	<moisture >BD	Coastal heath	Bancroft *et al*. (2004, 2005)
Resting forms						
Western Grey Kangaroo, Red Kangaroo (*Macropus* spp.)	0.74–2.7	>litter	>C, N, S, ex Ca, Mg, Na, =pH	<infiltration =BD	Semi-arid woodland	Eldridge & Rath (2002), Eldridge & Kwok (2008)
Latrines						
European Rabbit			>EC, OC, N, K, P, Mg =pH		Semi-arid woodland (Spain)	Willott *et al*. (2000)
			>pH, EC, N, P, ex Na <OC, ex Mg, K =C:N, ex Ca		Dry forest	Campbell (1978)

LC, labile (active) carbon; OC, organic carbon; EC, electrical conductivity; BD, bulk density; RH, relative humidity; temp, temperature; decomp, litter decomposition; ex, exchangeable; sol, soluble; >, greater than; <, less than; =, no effect; †, percentage of area affected; ‡, annual rate; §, mass per mound; ¶, dry and wet aggregate stability.

mineral soil exposed by foraging remain depressed for more than 12 months following excavation (D. J. Eldridge, unpubl. data). However, as pits are traps for organic matter, they will develop a nutrient profile over time and nutrient levels of older pits typically exceed the background levels at the soil surface (James & Eldridge 2007).

A number of studies indicate consistently lower soil density, and therefore greater infiltration of water, and greater soil erodibility, at least in the short-term, due to soil disturbance (Table 1). These effects are likely to be more significant in arid and semi-arid areas where primary production is limited by soil moisture (and nutrients). Unlike arid Australia, it is difficult to draw general conclusions about the effects of animals on soil chemistry for more mesic environments simply due to a lack of information. However, we predict that in more mesic environments the effects of animals on soil chemistry will be less marked because water is not limiting, and soil turnover and litter breakdown rates are greater.

In general, greater erodibility, particularly of subsoil from mounds, will result in a redistribution of sediment to other landscape positions, including the pits themselves. In highly mobile soils such as dune sands, this may be a mechanism for trapping litter in the pits (James *et al.* in press). Runoff water is known to deposit seeds and eroded sediment in microsites where seeds have a greater chance of germination (D. J. Eldridge, unpubl. data).

Soil disturbance, plant germination and establishment

Animal disturbances may support plant communities of differing composition or biomass from surrounding areas because they are either enriched (pits) or depleted (mounds) in litter, seed and nutrients. Larger disturbances such as rabbit, wombat and bettong warrens tend to have extensive areas of bare soil. The soils on rabbit warrens are resource poor (Eldridge & Koen 2008) while the calcareous soils on the warrens of the Burrowing Bettong are known to support a high biomass of perennial grasses and annual forbs (Burbidge *et al.* 2007; Noble *et al.* 2007). Little is known, however, about the effects of wombat warrens on soils and vegetation.

Exotic animals such as the Rabbit and Pig generally have negative effects on vegetation and soils. Vegetation on rabbit warrens is generally dominated by unpalatable, weedy, exotic species (Eldridge & Myers 2001; Eldridge & Simpson 2002). Digging by pigs is responsible for the loss of native plant seedlings and changes in species composition (Mitchell *et al.* 2007). Disturbances by pigs has been shown to lead to a dominance by disturbance-tolerant plants such as Blackberry (*Rubus fruticosus*) (Alexiou 1983) and Paspalum (*Paspalum dilatatum*) (Pavlov & Graham 1985).

Small-scale disturbances such as foraging pits of the Greater Bilby and Burrowing Bettong (Sparkes 2001; James & Eldridge 2007), Superb Lyrebird (Ashton & Bassett 1997) and Echidna (D. J. Eldridge, unpubl. data), and the resting sites of kangaroos (Eldridge & Rath 2002) support greater levels of plant germination after rainfall than surrounding soils. This is likely due to their ability to capture more seed and water after rainfall. Small depressions in arid landscapes intercept and concentrate scarce resources such as water and litter, providing sufficiently fertile patches to promote plant germination (James & Eldridge 2007). Foraging pits may also be important for maintaining small-scale vegetation patchiness in mulga woodlands (Whitford 1998) and may even provide refugia for plants requiring higher levels of moisture with declines in rainfall through global climate change.

Although seed caching has rarely been reported for Australian animals, it may be more widespread than currently recognized. For example, seeds of Sandalwood (*Santalum spicatum*) are known to be cached and dispersed by the Brush-tailed Bettong (*Bettongia penicillata*) in woodlands in Western Australia, possibly enhancing its regeneration (Murphy *et al.* 2005). Similarly, Anangu elders in central Australia maintain that the Burrowing Bettong buries Quandong (*Santalum acuminatum*), Turpentine (*Eremophila sturtii*) and Pituri (*Dubosia hopwoodii*) seeds (Noble *et al.* 2001), and the Spinifex Hopping Mouse (*Notomys alexis*) caches Spinifex (*Triodia* spp.) seeds (Copley *et al.* 2003). Seed caching has the potential to alter the spatial distribution of seeds, thereby altering plant community structure.

Soil disturbance creates habitat for animals

The most obvious effect of soil disturbance on animals is through the creation of burrows, which provide habitat or shelter for both the burrower and other animals. A large number of arid-zone animals use burrows, either their own or those of other animals (Read *et al.* 2008). Burrows provide refuge against predators and help to moderate extremes of heat and cold (Kinlaw 1999).

Some of the most conspicuous and widespread warren systems belong to the Burrowing Bettong, which constructs large warrens in soils that are too hard for other species to dig. This species was once widespread across arid Australia and may have facilitated the invasion of the Rabbit into areas where hard soils would otherwise have prevented their survival (Parer & Libke 1985). The Rabbit and Burrowing Bettong are known to co-habit warrens (Robley *et al.* 2002; Read *et al.* 2008). Relict Burrowing Bettong warrens in the Gibson Desert are known to have also harboured varanids, the Western Quoll (*Dasyurus geoffroii*) and Brushtail Possum (*Trichosurus vulpecula*) (Burbidge *et al.* 1988; Burbidge *et al.* 2007).

The Echidna, Broad-banded Sand-swimmer (*Eremiascinus richardsonii*), hempiterans and coleopterans are known to occupy Burrowing Bettong warrens in South Australia (Read *et al.* 2008), and ants of the genera *Melophurus*, *Rhytidoponera*, *Iridomyrmex* and *Camponotus* have been shown to be more abundant on rabbit warrens (Turner 2004; Read *et al.* 2008). Rabbit warrens are potentially important parasite transition zones for ticks, mites and fleas, and higher arthropod abundances in warrens may provide a valuable food source for small vertebrates. Similarly, higher populations of small mammals and reptiles in warrens may provide an accessible food source for larger predators such as goannas and snakes. Rabbit warrens are also used extensively by the Echidna (Wilkinson *et al.* 1998; Read *et al.* 2008) and Mulga Snake (*Pseudechis australis*), along with pythons, skinks, geckos (Heard *et al.* 2004; Read *et al.* 2008) and even birds (Read *et al.* 2008). The warrens may also be enlarged into dens by the House Cat (*Felis catus*), Red Fox (*Vulpes vulpes*) or Dingo (*Canis familiaris dingo*) (Read *et al.* 2008). Widespread elimination of rabbit warrens, without replacement by warrens of native species, is likely to be detrimental for several arid zone vertebrates and many invertebrates.

The large, conspicuous warrens of wombats that are widespread across Australia provide habitat for the Echidna, Rabbit, Fox, Cat and Dingo (McIlroy *et al.* 1981; Crossman 1988). Common Wombat (*Vombatus ursinus*) burrows have been shown to contain the Mountain Possum (*Trichosurus caninus*) and Bush Rat (*Rattus fuscipes*) (McIlroy *et al.* 1981), while there is evidence that burrows of the Northern Hairy-nosed Wombat (*Lasiorhinus krefftii*) have been used by the Striated Pardalote (*Pardalotus striatus*), Rufous Bettong (*Aepyprymnus rufescens*), Swamp Wallaby (*Wallabia bicolor*) and Black-headed Python (*Aspidites melanocephalus*) (Crossman 1988).

Small desert mammals may use burrows of other species to increase their ability to exploit patchy resources by allowing them to be more nomadic without having to expend energy in creating their own burrow (Dickman 1996). Dunnarts (*Sminthopsis* spp.) for example, use the burrows of spiders, scorpions, rodents and lizards (Dickman 1996). Burrow use has also been observed in the Sandy Inland Mouse (*Pseudomys hermannsbergensis*), the Lesser Hairy-footed Dunnart (*Sminthopsis youngsoni*) (Letnic 2002), Bolam's Mouse (*Pseudomys bolami*) (Moseby & Read 1998) and Stick-nest Rat (*Leporillus conditor*) (Bolton & Moseby 2004).

Disturbances, such as pits and scrapes created during foraging, may also provide habitat by creating areas of differing resource availability. For example, old disturbances of pigs may be suitable habitat for the Corroboree Frog (*Pseudophryne corroboree*, Bloomfield & Parsonson 1977) and foraging pits of the Echidna and Superb Lyrebird are known to support more invertebrates due to their increased levels of leaf litter (Adamson *et al.* 1983; Eldridge & Mensinga 2007). The large nest mounds created by Megapodes are known to harbour frogs. The Giant Banjo Frog (*Limnodynastes interioris*) has been found in the mounds of Malleefowl (*Leipoa ocellata*) (Priddel 1993) and the Brown-striped Frog (*Limnodynastes peronii*) has been recorded in the mounds of the Australian Brush-turkey (Jones & Goth 2008).

Soil disturbance increases patchiness across the landscape

Although individual disturbances may affect soil fertility and provide habitat for plants and animals, they also increase landscape patchiness (heterogeneity). Animal disturbances create a mosaic of modified, unmodified and regenerating patches that provide habitats of differing resource availability and physical characteristics (Wright *et al.* 2006). This increase in spatial heterogeneity can lead to positive effects on species richness by increasing the diversity of microhabitats and allowing a greater number of plant or animal species with different resource requirements and colonizing abilities to co-exist (Huston 1994; Schooley *et al.* 2000; Wright *et al.* 2002). For example, there may be differential invertebrate or microbial populations associated with pits, which then influence rates of litter decomposition, water flow and plant germination. Thus, the presence of re-introduced soil-disturbing animals could have flow-on effects to other species that may modify habitat and affect ecosystem function. Ultimately, we would expect positive feedback processes on those animals creating the pits, allowing populations of native animals to be self-supporting, while maintaining the functionality of surrounding landscapes.

A role for soil-disturbing animals in monitoring and habitat restoration

The extent and distribution of animal disturbances may be a useful non-invasive method of assessing habitat quality and preference for foraging sites. For example, Hone (1988) showed that the number of diggings by pigs was indicative of their densities, and Mallick *et al.* (1997) showed that diggings were an efficient method for monitoring change in Eastern Barred Bandicoot (*Perameles gunnii*) populations. Research currently underway in the semi-arid woodlands is examining the links between animal densities and their foraging activities.

Despite the many positive effects of soil-disturbing animals on ecosystem processes, relatively little is known about the exact mechanisms involved (Byers *et al.* 2006), although the greatest effects are thought to be in arid and semi-arid environments. Studies of wild, reintroduced populations at Scotia Sanctuary in western New South Wales and at the Arid Recovery Reserve in South Australia have been providing valuable insights into how degraded ecosystems may have functioned before the loss of native species, and consequently, before degradation (James & Eldridge 2007). Studying ecosystem changes over time should give us information on the role played by re-introduced species such as the Greater Bilby and Burrowing Bettong in the restoration of ecosystem function and the likely flow-on effects to other biota and processes such as shrub encroachment in arid and semi-arid environments.

Sufficient knowledge is already available, however, to inform land managers of the value of native soil-disturbing animals and therefore the importance of adopting measures, such as the control of exotic predators, that are likely to enhance their survival prospects outside of fenced exclosures. This review has demonstrated that existing native and locally extinct, soil-disturbing animals have many ecosystem values ranging from the maintenance and restoration of soil processes such as litter decomposition and nutrient creation to increased germination and establishment of native grasses and forbs. It is only logical that their conservation and reintroduction should have positive effects on ecosystem processes.

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