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Restoration potential of threatened ecosystem engineers increases with aridity: broad scale effects on soil nutrients and function

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Species extinctions alter ecosystem services, and the magnitude of this impact is likely to change across environmental gradients. In Australia, soil-disturbing mammals that are now considered ecologically extinct are thought to be important ecosystem engineers. Previous studies have demonstrated microsite-level impacts of reintroduced soil-disturbing mammals on soil functions, but effects are yet to be tested across larger scales. Further, it is unclear how impacts vary across environmental gradients and if the restoration potential of reintroductions changes with climate. We examined the effects of soil-disturbing mammal reintroductions across a large rainfall gradient in Australia to test the hypothesis that ecosystem engineering effects on soil function depend on climate. We compared soil labile carbon, available nitrogen and the activity of four enzymes associated with nutrient cycling in three microsite types with and without soil-disturbing mammals in five sites along a large rainfall gradient (166–870 mm). Soil enzyme activity was greatest in the presence of soil-disturbing mammals and increased with rainfall, but soil available carbon and nitrogen varied across the gradient and among microsites. Microsite effects were often stronger than any effects of soil-disturbing mammals, with soil beneath vegetated patches (shrubs and trees) having greater enzyme activity, carbon and nitrogen than bare soils. However, soil-disturbing mammals homogenised nutrient distributions across microsites. The impacts of soil-disturbing mammals on soil function previously detected at micro-scales was detected at a landscape-scale. However, the overall effects of soil-disturbing mammals on soil functions varied with productivity (rainfall). The context of soil-disturbing mammal reintroductions is thus likely to be critical in determining their effectiveness in restoring soil function.

Keywords: context-dependency, ecosystem engineer, extinctions, rainfall gradient, soil-disturbing mammals, soil functioning

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Introduction

Biodiversity loss often leads to a decline in ecosystem functions (Purvis and Hector 2000, Barnosky et al. 2011, Boyer and Jetz 2014), particularly where species play key roles as predators (Schmitz 2008, Estes et al. 2011) or ecosystem engineers (Coleman and Williams 2002). However, species loss has a complex and context-dependent relationship with ecosystem functioning (Cadotte et al. 2011), whereby the magnitude of change depends on characteristics of the species and the ecosystem (Dobson et al. 2006, Coggan et al. 2016). Returning locally extinct fauna has recently been recognised as a key component of ecosystem restoration because such species may play trophic or engineering roles important for ecosystem structure (Wilmers and Schmitz 2016, Sobral-Souza et al. 2017, Schweiger et al. 2018). However, the value of reinstating species for ecosystem function is also likely to be context-dependent (Coggan et al. 2016, 2018).

Ecosystem engineers physically modify their surroundings and therefore affect coexisting species via direct or indirect interactions and regulate community dynamics (Jones et al. 1996, 1997). These habitat-modifying animals therefore increase landscape heterogeneity by creating unique habitat patches differing from the surrounding landscape (Wright et al. 2006, Davidson and Lightfoot 2008, McKey et al. 2010). Due to their digging and foraging activities, semi-fossorial mammals are considered ecosystem engineers, which modify not only soil physical properties, but also soil nutrient dynamics and invertebrate communities (Whitford and Kay 1999, Davidson and Lightfoot 2007, Silvey et al. 2015, Coggan et al. 2016, Orwin et al. 2016). The degree of modification might change along environmental gradients, but only a few studies have attempted to disentangle the context-dependency of engineering effects (Wright et al. 2006, Coggan et al. 2016). Differences in soil nutrient patterns contribute to landscape heterogeneity and therefore drive species distributions. In deserts, soil-disturbing animals often contribute substantially to the development of landscape heterogeneity by altering soil nutrients (Whitford and Kay 1999). In these systems, soil disturbance by small animals might be the only mechanism that brings up soluble nutrients from the deeper layers of the soil to the surface (Abaturov 1972) or increases soil moisture (Eldridge and Mensinga 2007). In arid and semi-arid systems, these changes drive soil microbial processes (Eldridge et al. 2016), influence invertebrate activity (Riutta et al. 2012) and create resource-rich patches that enhance the productivity and stability of these systems (Brooker and Callaghan 1998, Bruno et al. 2003). However, only few studies have investigated the context-dependency of ecosystem engineering (Coggan et al. 2016).

Given that ecosystem engineering impacts are context-dependent, the consequence of losing semi-fossorial mammals might also be context-dependent. Despite their functional importance, many soil-disturbing mammal species are threatened globally by human activities, including land clearing for agriculture, introduced exotic species and diseases (Davidson et al. 2012). In the 230 yr since European colonisation, Australia has had the highest mammal extinction rate in the world, losing 27 mammal species (Burbidge and McKenzie 1989, Woinarski et al. 2015). Of the extinct mammals 22% are fossorial and are considered ecosystem engineers, playing key roles in soil processes (Fleming et al. 2014). A substantial decline in the abundance of persisting species has resulted in the ecological extinction of soil-disturbing mammals from much of mainland Australia (Johnson and Isaac 2009). Australian soil-disturbing mammals such as echidnas *Tachyglossus aculeatus*, bettongs *Bettongia* spp. and greater bilbies *Macrotis lagotis* increase soil moisture, soil carbon and nitrogen and alter bacterial communities at the scale of individual pits measured within single landscapes (Garkaklis et al. 2000, Eldridge and Mensinga 2007, Eldridge and James 2009, James et al. 2009, Travers et al. 2012), but the question of whether their impacts change with environmental variables or are important at larger spatial scales remains unanswered.

Australian soils are deeply weathered and have low fertility due to the lack of recent geological activity (White 1994, Eldridge et al. 2018), therefore soil disturbance by mammals may be an important driver of microflora and plant establishment (Whitford and Kay 1999). While landscape heterogeneity dictates local nutrient cycling, precipitation is thought to be the driver of productivity at larger scales (Austin and Vitousek 1998, Austin et al. 2002). Ecosystems at different points along an environmental gradient, such as a precipitation gradient, might respond differently to the same disturbance (Shachak et al. 1991, Coggan et al. 2016). Similarly, it is likely that the productivity of the ecosystem will impact the engineering effects of mammals on soils, but only a few studies have explicitly tested interactions between landscape productivity and habitat engineering (McAfee et al. 2016, Coggan et al. 2018). Habitat engineering increases plant-available soil chemicals by enhancing soil microbe activity (Eldridge et al. 2015, 2016), which breaks down and transforms organic material (Hendrix et al. 1986). Consequently, engineered soils are expected to have a more diverse and dynamic microbial community, with higher activity of extracellular enzymes that sequester carbon into the soil (Tardy et al. 2015) and mineralise essential mineral nutrients such as nitrogen, phosphorus or other micro-elements for use by plants (Bardgett and Chan 1999). However, no studies have tested whether this effect is moderated by the environment.

We tested the impacts of reintroductions of ecologically-extinct ecosystem engineers along a rainfall gradient on soil nutrients (labile carbon and available nitrogen) and microbial enzyme activities related to organic material breakdown. We targeted the following microbial enzymes: β-glucosidase, N-acetyl-β-glucosaminidase, phosphatase and cellobiosidase, because these enzymes are proxies of the capacity of soils to effectively carry out processes of decomposition that make essential nutrients available to plants. β-Glucosidase and

cellobiosidase are released by bacteria and fungi to convert complex sugars and cellulose-rich plant wall structures, respectively, into lower molecular weight products that are available for plant uptake (Burns 1982). Phosphatase and N-acetyl-β-glucosaminidase are released by microbes to transform phosphorus and organic nitrogen substrates into plant-available inorganic forms. We hypothesised that: 1) soil-disturbing mammals would increase soil nutrient availability and microbe activity; 2) effects of mammals are greater in drier environments; 3) variation among nutrients in microhabitats is lower in the presence of mammals (due to mixing). To test our hypotheses, we conducted replicated surveys inside and outside five mammal reintroduction reserves over a 3337 km rainfall gradient (mean annual precipitation: 166–870 mm) in southern Australia. Further, to experimentally test our first and third hypotheses, we conducted a mammal exclusion experiment inside a reintroduction reserve.

Methods

Study sites

We studied soil attributes in five predator-proof reintroduction areas in southern Australia (Fig. 1a): Arid Recovery in South Australia (independent incorporated charity), Scotia in New South Wales (Australian Wildlife Conservancy – AWC), Yookamurra in South Australia (AWC), Mt Rothwell Conservation and Research Centre in Victoria (privately owned) and Karakamia in Western Australia (AWC). The reserves differed in annual precipitation, vegetation, soil type, area, reintroduced mammal species and densities and had different land use histories (Table 1). Foxes were removed prior to the reserve establishment, and control of rabbit and fox populations at all reserves is ongoing. Most of the soil-disturbing mammal populations have suffered substantial declines in their natural distribution area. Soil-disturbing mammals were locally extinct from our study sites, where they had been reintroduced. Only quenda *Isoodon obesulus fusciventer*, woylie *Bettongia penicillata ogilbyi* and numbat *Myrmecobius fasciatus* populations still occurred in Western Australian remnant woodlands, but woylies were re-introduced to Karakamia. Eastern barred bandicoot *Perameles gunnii* populations still existed in Victoria in low densities prior to their release in fenced reserves, but now are listed as extinct in the wild.

Landscape-scale study of the impact of soil-disturbing mammals

Ten paired 20 m by 20 m plots were established inside ('reintroduction') and outside ('control') the fence line of each reserve (Fig. 1b), hereafter 'landscape-scale study'. We use the term 'reintroduction' throughout because it indicates the treatment imposed at the sites, i.e. the reintroduction of locally-extinct, native, soil-disturbing mammals. We do acknowledge, however, that one site, Karakamia in Western Australia, still supported quendas *Isoodon obesulus fusciventer* prior to its formal establishment (Dundas et al. 2018), but the densities were substantially lower than currently supported by the reserve and much lower than pre-European densities (Driessen and Rose 2015). Plots were selected to represent the dominant vegetation types in each reserve (Table 1) with similar fire and grazing histories. Paired plots (reintroduction and control) were assessed at each site to make sure that the ground cover and the structure of the woody vegetation were similar and the paired plots belong to the same habitat type without major differences which might have occurred before or after the establishment of the reserves (Supplementary material Appendix 1). All plots were located at least 60 m from any road and at least 25 m from any predator-proof fence and were separated by a minimum of 60 m.

Soil sampling was conducted between September 2015 and September 2016 (Table 1). Sites were visited in different seasons, but sampling from each reserve took place during the same visit (i.e. within the same week), so seasonal variation was not expected to affect any reintroduction–control comparisons. Most sampling was conducted in autumn and winter to avoid sampling in the growing season when plants are actively using available nutrients (Chapin 1980), except in Arid Recovery where we went in early September. Although September is in spring, the temperatures were still low early in the month. Three different microsites were sampled within each plot: bare soil from the upper 5 cm (hereafter 'topsoil'); subsurface samples from the deeper layers of the soil and equivalent to the depth of the pits (10–15 cm deep following studies of Eldridge et al. 2009, James et al. 2009, hereafter 'subsurface soil') and soil from under the tallest dominant over storey (hereafter 'vegetation'). Within each plot we collected six subsamples each of bare, subsurface and vegetated soil using two transects, situated 6 m from the edges of the plot. Subsampling points were situated 4 m from each other and the three microsite types were separated by at least 1 m. These six subsamples were then pooled for each plot, resulting in 10 samples for the reintroduction and 10 for the control areas. In total, we sampled five reintroduction sites and five control sites. Within each site, we sampled between eight and 10 plots, depending on the size of the areas (only eight suitable paired plots could be located at Karakamia and Mt Rothwell reserves). In total, we collected 276 soil samples. After collection, the samples were immediately air-dried for 5 d and stored until further analysis.

Experimental exclusion study of the reintroduced soil-disturbing mammals

To experimentally test the effect of soil-disturbing mammal activity, we performed a plot scale study inside the reintroduction area at Scotia, hereafter 'experimental exclusion study' (Fig. 1c). We used 10 areas in eucalypt woodland with spinifex *Triodia scariosa* understorey on dune tops as these habitats are associated with high activity of soil-disturbing mammals (James and Eldridge 2007, Finlayson et al. 2008). In each

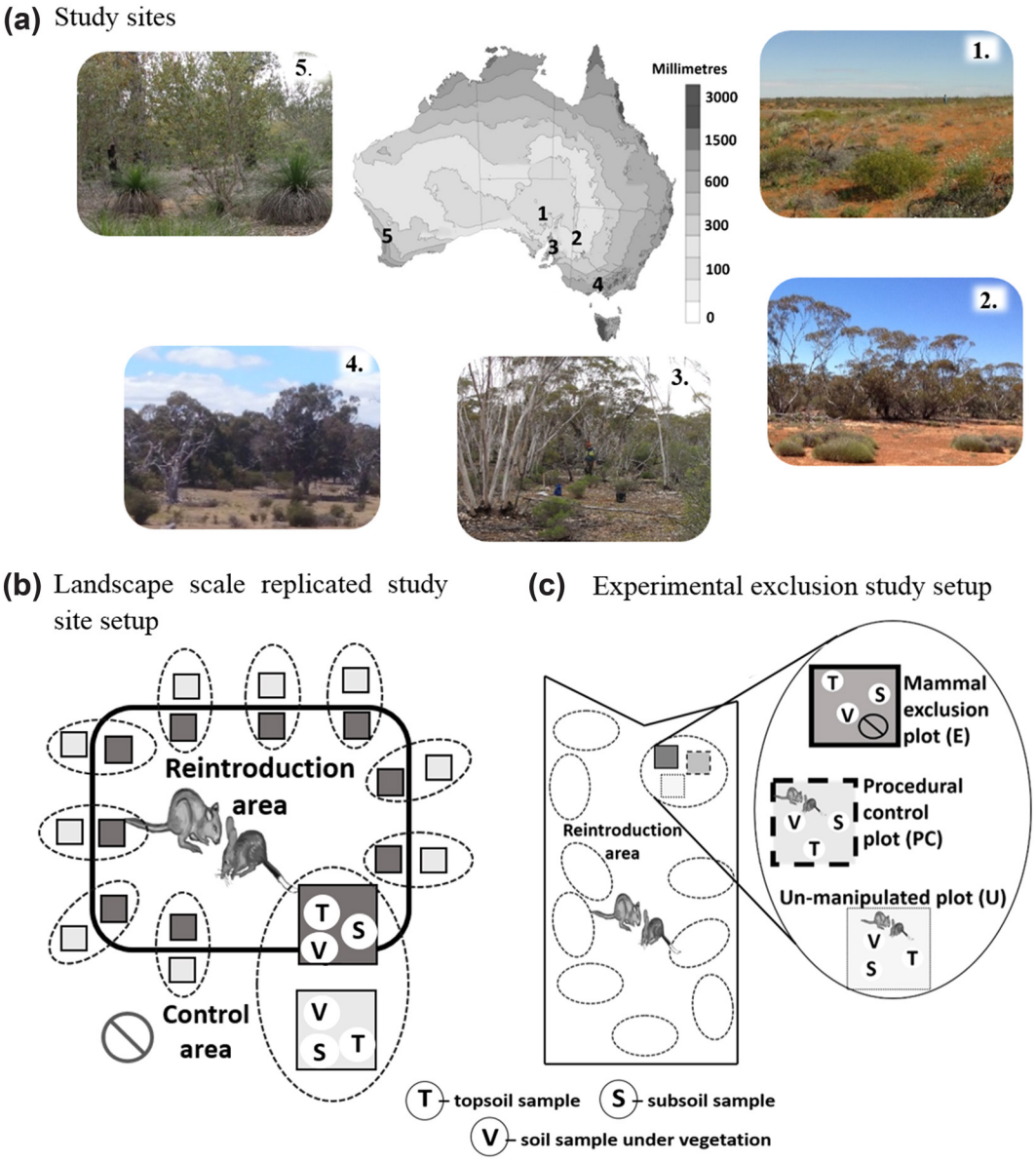

Figure 1. (a) The study sites; in order of increasing average annual rainfall: 1. Arid Recovery (166 mm), 2. Scotia (233 mm), 3. Yookamurra (285 mm), 4. Mt Rothwell (468 mm), 5. Karakamia (877 mm), with photographs demonstrating the dominant vegetation type at each site; (b) sampling design showing paired plots with native soil-disturbing mammals present (dark grey) and absent (light grey) from study plots. Soil samples were taken from 3 microsites: topsoil samples (T); subsoil samples (S) and under vegetation (V); (c) the setup of the experimental plot scale study, where native mammals are excluded from the exclusion plot (E), but allowed inside the procedural control (PC) and un-manipulated (U) plots.

area, a set of three plots, each 20 m by 20 m and separated by greater than 60 m, was set up in October 2009. The following treatments were applied in July 2010: 1) exclusion treatment: medium-sized mammals were prevented from entering these plots using a complete 1 m tall 'chicken wire' (hexagonal mesh with 52 × 40 mm holes) fence with a 'rabbit-proof' skirt dug-in 60 cm deep at the base of the fence; 2) procedural control treatment: these plots had a similar 1 m high fence, but the bottom 50 cm of wire was removed and the disturbance of digging-in the rabbit-proof skirt was simulated; and 3) un-manipulated treatment: an unfenced plot, marked only with metal star pickets. Exclusion plots were successful in excluding reintroduced mammals and contained only a few goanna foraging pits from one year after exclusion, while procedural control and control plots supported similarly large numbers of foraging pits (Gibb et al. 2018). Six soil subsamples from each of the targeted microsites were taken from each plot in May 2015 using the methods described for the landscape scale study. Subsamples were pooled at the plot level, resulting in 10 replicates of each microsite type from

Table 1. Biotic and abiotic attributes of the study sites: climatic and vegetation details, reintroduced species and reserve description. Sources: climate: Bureau of Meteorology, Australia; vegetation: personal observation/study data; soil type: Soil and Landscape Grid of Australia, CSIRO (<www.clw.csiro.au/aclep/soilandlandscapegrid>); EVI: TERN AusCover (<data.auscover.org.au>); reserve attributes: pers. comm. with Katherine Moseby (Arid Recovery), Helen Crisp (Yookamurra), Felicity L'Hotellier (Scotia), Jacqui Young (Mt Rothwell) and Bryony Palmer (Karakamia). MAP = mean annual precipitation, MAT = mean annual temperature, R = reintroduction area, C = control area.

	Attribute	Arid Recovery	Scotia	Yookamurra	Mt Rothwell	Karakamia
Location	Latitude	−30.5653	−33.1358	−34.5220	−37.8894	−31.8230
	Longitude	136.9177	145.1925	139.4755	144.4402	116.2430
Climate	MAP (mm)	166	233	285	468	877
	Aridity index	0.077	0.132	0.158	0.367	0.803
	MAT (°C)	26.35	24.4	22.6	20.3	22.6
	Climate	Arid	Semi-arid	Semi-arid	Temperate	Mediterranean
	Vegetation	*Acacia* shrub land	Mallee woodland	Mallee woodland	Open woodland	Jarrah forest
Biotic attributes	Main overstorey	*Acacia ligulata*, *Dodonea viscosa*	Mallee eucalyptus	Mallee eucalyptus	*Eucalyptus melliodora*	*Eucalyptus marginata*, *Corymbia calophylla*
	Main understorey	*Crotalaria eremea*, *Polycalymma sturtii*, Chenopodiaceae	*Triodia scariosa*, Chenopodiaceae	*Westringia rigida*, *Olearia muelleri*, *Cratystylis conocephala*, Chenopodiaceae	*Acacia paradoxa*	*Banksia sessilis*, *Banksia grandis*, *Xanthorrhea preissii*
	Soil type	Calcarosols	Calcarosols/Rudosols	Calcarosols	Sodosols/Tenosols	Tenosols/Chromosols
	EVI	0.1173	0.1719	0.2216	0.2828	0.3314
Re-introduced soil-disturbing mammals	Potoroidae spp. (ind. ha^{-1})	*Bettongia lesueur* 1.09	*Bettongia lesueur* 0.23	*Bettongia lesueur* 0.22	*Aepyprymnus rufescens* 0.71	
			Bettongia penicillata 0.10	*Bettongia penicillata* 0.10		*Bettongia penicillata* 1.10
	Macrotis lagotis (ind. ha^{-1})	0.16	0.17	0.03	0.00	0.00
	Myrmecobius fasciatus (ind. ha^{-1})	0.00	0.03	0.03	0.00	0.00
	Peramelidae spp. (ind. ha^{-1})		0.00	0.00	*Isoodon obesulus obesulus* 0.71	*Isoodon obesulus fusciventer* 1.00
		Perameles bougainville 0.20			*Perameles gunnii* 2.38	
Reserve attributes	Predator-proof area (ha)	6000	8000	1092	420	275
	First reintroductions (date)	1999	2005	1992	2002	1994
	Livestock grazing ended	1998	1994	1950s	2000	1991
Soil sampling	Date	September, 2015 (spring)	May, 2015 (autumn)	March, 2016 (autumn)	May, 2016 (autumn)	August, 2016 (winter)

each experimental exclusion treatment plot. This resulted in a total of 90 soil samples.

Laboratory analysis of soils

We tested the activity of four enzymes: β-glucosidase (BG), which plays an important role in carbon cycling; N-acetyl-β-glucosaminidase (NAG), which is important in nitrogen cycling; phosphatase (PHOS), which plays a role in phosphate cycling; and cellobiosidase (CB), which is important in breaking down cellulose. One gram of air–dried soil was mixed with 33 ml of sodium acetate buffer (pH > 7.5) using an orbital shaker for 30 min at 200 rpm. Then 800 µl of the soil slurry was pipetted into a well on a deep welled plate and 200 µl of the substrate of each enzyme was added to the slurry. Substrates used for the BG, NAG, PH, CB enzymes, respectively, were: 4-methylumbelliferyl β-D-glucopyranoside, 4-methylumbelliferyl-N-β-D-glucosaminide, 4-methylumbelliferyl-phosphatase, 4-methylumbelliferyl-β-D-cellobioside. The soil–substrate solution was incubated at 25°C for 3 h and the activity (nmol activity g^{-1} dry $soil^{-1}$ h^{-1}) was measured at 365 nm excitation wavelength and 450 nm of emission wavelength in a microplate reader (CLARIOstar, BMG Labtech, Germany).

Labile carbon (C) content was measured by the change of absorbance of $KMnO_4$: the alkaline $KMnO_4$ reacts with the most readily oxidisable forms of carbon to convert Mn(VII) to Mn(II) (Weil et al. 2003). Available nitrogen (N) was assessed from soil samples following an extraction with 0.5 M K_2SO_4 in a 1:5 ratio. Extractions were placed on an orbital shaker at 200 rpm for an hour at 20°C then filtered using 0.45 µm Millipore filter (Delgado-Baquerizo et al. 2010). Nitrate and nitrite content was measured using flow injection analysis (QuickChem 8500; Lachat Instruments, Milwaukee, WI, USA). Given that the soil samples were from a wide range of habitat types, it was only possible to determine soil total nitrate (NO_3^-) and nitrite (NO_2^-) content without changing the extraction methods for each soil type (hereafter available nitrogen). Soil nitrate is an important compound for plants and bacteria (Forde 2000), so was used to assess soil available nitrogen content.

Statistical analysis

We tested for correlations among annual rainfall, site and sampling characteristics using Pearson's correlation test. We did this to ensure that effects attributed to precipitation patterns were not due to co-varying factors. We tested only those site characteristics that were not directly limited by rainfall: sampling season, reserve 'age', reserve size, years since mammal reintroduction, years since grazing by domestic livestock, soil clay percentage as an indicator for soil type, foraging pit density and average pit volume. 'Season' was the number of days between the hottest day of the year at each site and the actual sampling day at each site. None of the characteristics, except reserve size, were correlated with rainfall (correlations > 0.6). It is unlikely that reserve size affected soil function because our plots were situated on the edges of the reintroduction areas, so none represented a core area of habitat occupied by reintroduced mammals. Thus, no other site characteristics are likely to have confounded our interpretation of the impacts of annual precipitation on soil nutrients and function.

All statistical analyses were conducted using the R Statistical Computing Environment (R Core Team). For both studies we used linear mixed models on the lme4 package (Bates et al. 2015) to test if soil nutrients and microbial enzymes differed between control and reintroduction along the rainfall gradient in the landscape-scale study or to test the differences between treatments in the experimental exclusion study. For all modelling analyses, soil nutrients (labile carbon, available nitrogen) and the microbial enzymes were used as response variables. Data were transformed, where necessary, to meet the assumptions of our models. We used a natural log transformation for soil carbon and nitrogen data. Our global model included the fixed factors annual mean precipitation (only the landscape-scale study), soil-disturbing mammal presence/absence and microsite type and all two-way and three-way interactions among these factors. Precipitation was included in the models of the landscape-scale study with a coupled transformation: logarithmical transformation to linearize the spread of the rainfall gradient and a polynomial term to optimize the fit to the data points. Random effects were specified as paired plots (reintroduction and control) within sites for the landscape-scale study.

For the experimental exclusion study, the model included the fixed factors soil-disturbing mammal presence/absence, microsite and their two-way interaction, as well as the random factor 'block' (treatments were blocked in triplets). Significant interactions were disentangled using Tukey's tests with adjusted p values for multiple comparisons using the lsmeans package (Lenth 2016). Model predictions were plotted using AICmodavg (Mazerolle 2017) and effects (Fox 2003) packages to further investigate the nature of interactions and extract model predictions. Our models were validated using diagnostic tools: checking the structure of residuals for model fit and normal quantile–quantile tests for data distribution. All graphs shown were made using the 'ggplot2' package (Wickham 2009).

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6hj0824> (Decker et al. 2019).

Results

Landscape-scale replicated study of the impact of soil-disturbing mammals

Microbial enzyme activity differed between reintroduction and control sites for three of the four enzymes, and there were significant interactions between rainfall and microsite

Table 2. Effects of native mammals, rainfall and microhabitat types and their two- and three-way interactions on soil enzyme activities, labile carbon and available nitrogen for the two studies. Soil-disturbing mammals: P = present, A = absent. Microhabitat: V = vegetated, T = topsoil, S = subsurface soil. Rainfall: I = increasing, D = declining. Experimental treatments: E = mammal exclusion, PC = procedural control, U = un-manipulated plot with native mammal present. Significant differences are highlighted in bold, ns = not significant.

	β-Glucosidase (BG)	Cellobiosidase (CB)	N-acetyl-β-glucosaminidase (NAG)	Phosphatase (PHOS)	Labile carbon (C)	Available nitrogen (N)
	χ^2 (p)	χ^2 (p)	χ^2 (p)	χ^2 (p)	χ^2 (p)	χ^2 (p)
Landscape scale						
Mammals	1.662 (0.2)	5.83 (**0.01**)	1.44 (0.23)	4.81 (**0.03**)	12.5 (**< 0.001**)	3.9 (**0.04**)
	ns	P > A	ns	P > A	P > A	P > A
Microsite	35.8 (**< 0.001**)	11.9 (**0.003**)	33.9 (**< 0.001**)	11.1 (**0.003**)	28.7 (**< 0.001**)	192.0 (**< 0.001**)
	V > (T = S)	V > (T = S)	V > (T = S)	V > (T = S)	V > (T = S)	V > (T = S)
Rainfall	10.2 (**0 .01**)	4.6 (0.09)	9.2 (**0.01**)	72.5 (**< 0.001**)	115.2 (**< 0.001**)	44.3 (**< 0.001**)
	I	ns	I	I	I	I
Mammals × Microsite	7.91 (**0.02**)	0.99 (0.60)	3.24 (0.19)	2.21 (0.33)	9.83 (**0.007**)	1.32 (0.51)
Mammals × Rainfall	0.74 (0.69)	2.09 (0.35)	0.62 (0.73)	2.56 (0.28)	5.08 (**0.07**)	7.59 (**0.02**)
Rainfall × Microsite	13.40 (**0.01**)	10.46 (**0.03**)	25.64 (**< 0.001**)	11.00 (**0.03**)	6.15 (0.18)	74.91 (**< 0.001**)
Mammals × Rainfall × Microsite	3.19 (0.52)	1.79 (0.77)	4.53 (0.34)	2.15 (0.71)	3.22 (0.52)	3.55 (0.47)
Experimental scale						
Treatment	7.5 (**0.02**)	1.05 (0.59)	0.03 (0.98)	0.65 (0.72)	0.99 (0.61)	0.18 (0.91)
	PC > (E = U)	ns	ns	ns	ns	ns
Microsite	57.8 (**< 0.001**)	45.3 (**< 0.001**)	119.6 (**< 0.001**)	42.6 (**< 0.001**)	69.8 (**< 0.001**)	63.8 (**< 0.001**)
	V > T > S	V > T > S	V > T > S	T > V > S	V > (T = S)	V > (T = S)
Treatment × Microsite	0.32 (0.99)	2.04 (0.73)	1.09 (0.89)	2.52 (0.64)	12.99 (**0.01**)	10.33 (**0.03**)

type. An interaction between precipitation and microsite showed that microbial enzyme activity was higher in vegetation microsites, but that this effect varied with precipitation. Phosphatase increased monotonically with precipitation, but relationships among β-glucosidase, cellobiosidase and N-acetyl-β-glucosaminidase were not linear (Table 2, Fig. 2). Both cellobiosidase and phosphatase activity were higher in reintroduction areas, independent of precipitation and microsite (Fig. 2c, f) while β-glucosidase activity was greater in reintroduction areas, but only in vegetated microsites (Fig. 2a). An interaction between precipitation and microsite was detected to determine the activity of all microbial enzymes: activity was higher in vegetation microsites, but only in some levels of precipitation. Phosphatase increased monotonically with precipitation, but relationships among β-glucosidase, cellobiosidase and N-acetyl-β-glucosaminidase were not linear (Table 2, Fig. 2).

Labile carbon concentration was highest in the presence of soil-disturbing mammals in the subsurface and topsoil microsites. Where mammals were present, differences in labile carbon among microsites were obliterated (Table 2, Fig. 3a). Positive effects of soil-disturbing mammals on labile carbon were greatest at low precipitation, although this interaction was marginally non-significant ($\chi^2 = 5.08$, $p = 0.07$, Table 2).

Available nitrogen content differed only between reintroduction and control areas between ~160 and 400 mm yr^{-1}, peaking at intermediate levels of precipitation (~350 mm, Table 2, Fig. 3c). Available nitrogen was greater under vegetated microsites than bare microsites, but this impact declined with increasing rainfall, irrespective of the presence of soil-disturbing mammals. Soil nitrogen content was greatest in vegetated microsites in areas between ~160 and 600 mm annual rainfall, after which values declined to levels much lower than in the topsoil (Table 2, Fig. 3d).

Experimental exclusion study of reintroduced soil-disturbing mammals

Our exclusion experiment at Scotia showed that excluding soil-disturbing mammals alone did not have a significant impact on microbial enzymes or soil nutrients (Table 2) within 6 years at the scale of the 20 × 20 m plots. Microsite effects were greater than mammal effects. Although interactions between these factors were significant predictors of soil available carbon and nitrogen, post-hoc tests showed similar trends across microhabitats among treatments (Fig. 4).

The activity of all four enzymes differed among the three microsites (Table 2). Activities of β-glucosidase, cellobiosidase and N-acetyl-β-glucosaminidase were lowest in sub-surface soils and greatest in vegetated microsites (Fig. 4a–c). Phosphatase activity, however, was greatest in the surface soils followed by soil under vegetation (Fig. 4d).

Soil labile carbon and available nitrogen levels were significantly greater under vegetation, irrespective of treatment (Fig. 4e–f). Soil labile carbon content was significantly higher

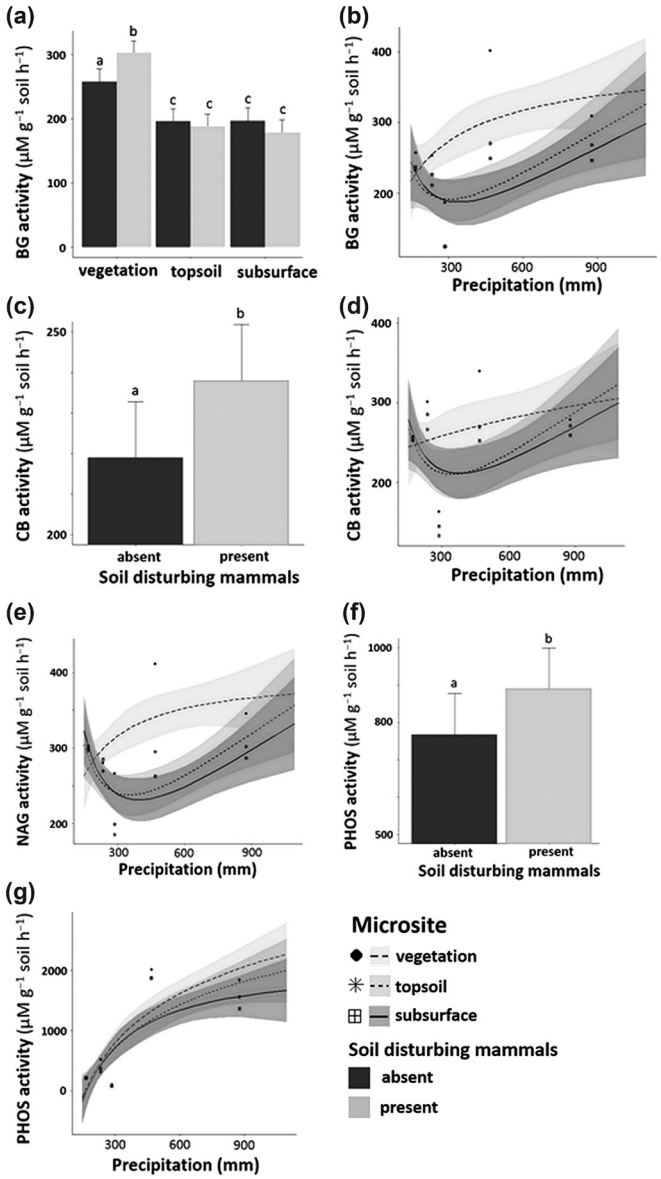

Figure 2. Microbial enzymes in the landscape-scale study: (a) β-glucosidase (BG) enzyme activity in the three microsites with and without soil-disturbing mammals and (b) in relation to annual precipitation (±95% CI); (c) cellobiosidase (CB) activity with and without soil-disturbing mammals and (d) in relation to annual precipitation (±95% CI); (e) N-acetyl-β-glucosaminidase (NAG) activity in relation to annual precipitation (±95% CI); and (f) phosphatase (PHOS) activity in relation to soil-disturbing mammals and (g) annual precipitation (±95% CI). Mean values are plotted of microsite types at each study site.

in soils beneath vegetation in both the procedural control and exclusion treatments, but any microsite differences vanished in the un-manipulated treatment (Table 2, Fig. 4e). Available nitrogen content was significantly greater in soils beneath vegetation in all treatments, but was higher in the subsoil than the surface soil in the un-manipulated treatment, where mammals had access (Table 2, Fig. 4f).

Discussion

Species extinctions may lead to a loss of ecosystem function. Although soil-disturbing mammals are known to alter soil functions at small scales (James et al. 2009, Valentine et al. 2017), no studies have previously tested landscape-scale effects or how they are influenced by environmental gradients. Our study of the effects of reintroduced animals on soil processes showed that soil enzyme activity was greatest in the presence of soil-disturbing mammals, but that this effect was sometimes regulated by microsite. Soil available carbon and nitrogen were both greater in the presence of soil-disturbing mammals, but the magnitude of the mammal effect varied across the rainfall gradient and among microsites. Microsite effects were often stronger than mammal effects, with soil beneath vegetated patches (shrubs and trees) having greater enzyme activity, carbon and nitrogen, than bare soils. Finally, soil disturbance altered the pattern of nutrients across some microsites, but again this effect varied across the rainfall gradient. Together, our results suggest that soil-disturbing mammals increase soil enzyme activity and nutrients, but the impact is strongly context-dependent, and varies with both the physical structure of particular reintroduction sites (make-up of the dominant microsites) and relative site productivity (using precipitation, our proxy for productivity).

Soil disturbance by mammals is associated with increasing enzyme activity, independent of precipitation

In our landscape-scale study, we detected significantly greater enzyme (β-glucosidase, cellobiosidase, phosphatase) activity in reintroduction compared to control areas, irrespective of rainfall. β-Glucosidase activity was only greater in the presence of soil-disturbing mammals within the vegetated microsites, but N-acetyl-β-glucosaminidase only responded to precipitation. The extent to which microbes produce extracellular enzymes for decomposition depends on surface disturbance (Caldwell 2005) and environmental factors such as soil moisture and pH (Knelman et al. 2017), but there is some evidence that soil-disturbing animals also influence enzyme activities. For example, Eldridge et al. (2016) showed that cellobiosidase activity was highly correlated with the size of foraging pits constructed by short-beaked echidnas *Tachyglossus aculeatus*, suggesting that greater per-capita activity of soil-disturbing animals is associated with greater processing of cellulose (Bell et al. 2013). This effect could be due to a greater capture of organic matter in the foraging pits, or more likely, admixing of litter and surface soils through animal activity, bringing microbes and organic matter into contact with moisture (Eldridge and Mensinga 2007, James et al. 2009). Foraging pits occupied only ~2% of the soil surface (Decker unpubl.), but we showed that the effect of digging carried over to undisturbed soils, indicating a previous legacy effect of animals that extends far beyond the contemporary distribution of their disturbances.

Phosphatase activity was greater in the reintroduction than in control areas, consistent with studies of short-beaked

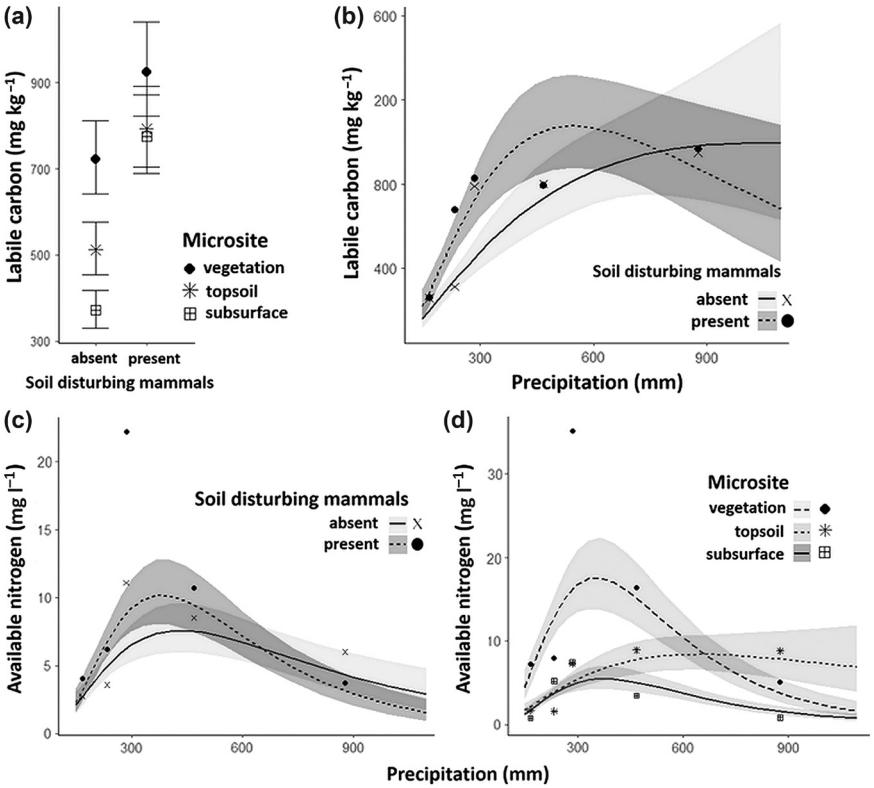

Figure 3. Soil nutrients in the landscape-scale study: (a) mean (±SE) soil labile carbon content with and without soil-disturbing mammals for three microsites; and (b) modelled concentrations of soil labile carbon and (c) available nitrogen in relation to rainfall. Lines indicate mean (±95% CI); (d) soil available nitrogen in three microsites across the precipitation gradient. Mean values of study sites are plotted in relation to soil-disturbing mammal presence or absence and microsite types.

echidnas on dryland soils (Eldridge et al. 2016). Australian soils are extremely low in phosphorus (Lambers et al. 2011), which is derived from the weathering of parent material and the deposition of atmospheric dust (Walker and Coventry 1976). Once inorganic phosphorus is exposed to the soil, it can only be assimilated by organisms in a dissolved form, therefore microbial enzymes play a fundamental role in phosphorus cycling. Phosphorus is unlike carbon and nitrogen, and is under abiotic control derived mainly from subsoils and P-rich parent material (Vitousek et al. 2010). Thus our results suggest that soil-disturbing mammals expose subsoils and distribute them across the landscape.

Finally, the experimental exclusion study showed that enzyme activity did not decline in plots where animals were excluded. The most parsimonious explanation is that positive legacy effects of mammals persist for many years after their local extinction (Noble et al. 2007). Alternatively, leaching from the surrounding area into the exclusion plots might have homogenised soil properties if plot size was too small.

We also detected a general increase in enzyme activity in our landscape-scale study with increasing precipitation: β-glucosidase, cellobiosidase and N-acetyl-β-glucosaminidase activities peaked at intermediate levels of productivity (~300–800 mm rainfall) and depending on microsite. These microbial enzyme activities under vegetated microsites increased rapidly along the rainfall gradient, becoming clearly different from other microsites at high rainfall. This trend was not unexpected as rainfall drives soil microbial biomass through increasing plant productivity (Zak et al. 1994, Waldrop et al. 2017). Shrubs were present at the driest site, but there were no trees, so lowered organic material input from vegetation might explain the similarity among microsites (Whitford 2002).

Context-dependent effects of soil-disturbing mammals on soil available nitrogen and carbon

Surface disturbance resulted in a significant increase in labile carbon, and there was a trend for the effect of mammals to be regulated by rainfall, as indicated by the results of our landscape-scale study. Labile carbon represents the fraction of the total carbon pool most available to soil biota and vegetation: it has the most rapid turnover and comprises amino acids, simple carbohydrates, and the most readily mineralizable fraction of microbial biomass (Zou et al. 2005). Plant cover and biological production are low in drylands, where increases in soil disturbance lead to increased soil heterogeneity (Davidson and Lightfoot 2008, Eldridge et al. 2009). In more mesic (~900 mm rainfall) systems, however, the matrix is dominated by vegetation, and biological activity is high. In these systems, rainfall drives the decomposer community (García-Palacios et al. 2013), whose effects may swamp

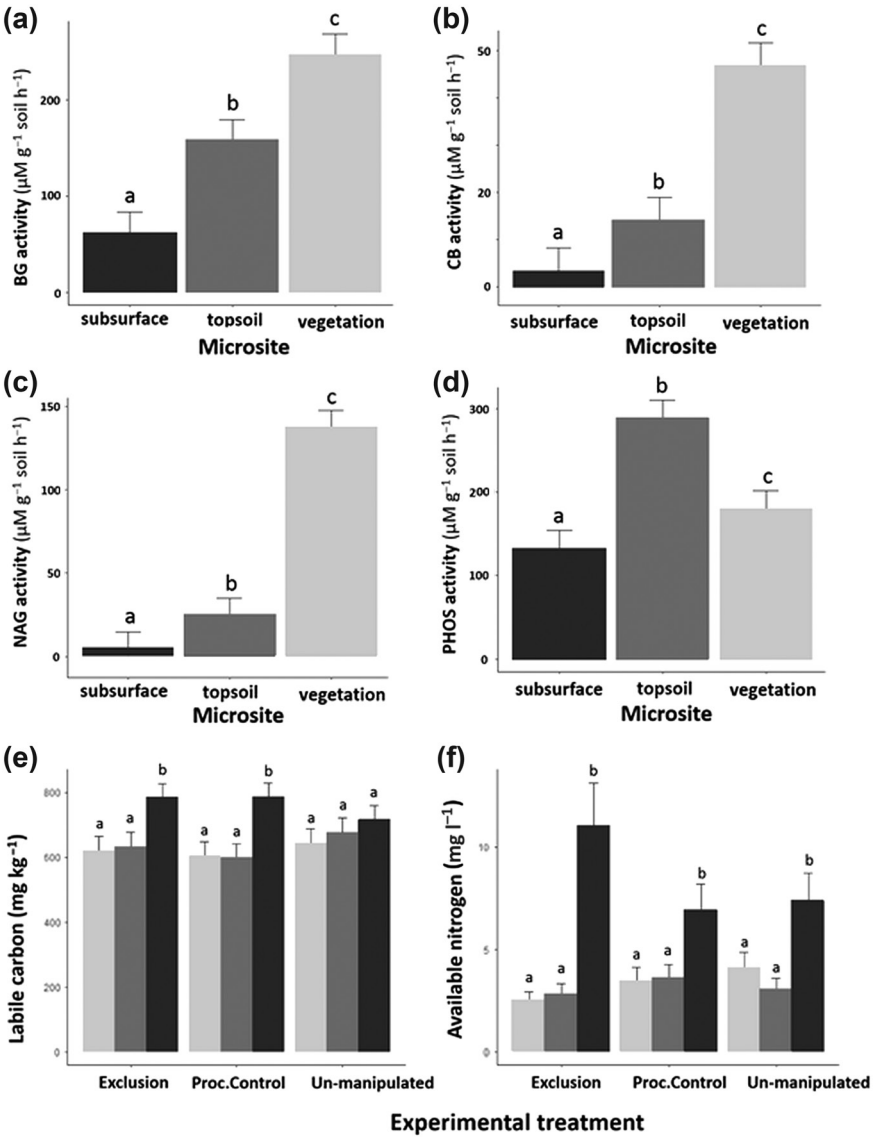

Figure 4. Microbial enzymes and soil nutrients in the experimental exclusion study: (a) mean (+SE) β-glucosidase enzyme activity in relation to microsites; (b) mean (+SE) cellobiosidase (CB) activity in relation to microsites; (c) mean (+SE) N-acetyl-β-glucosaminidase (NAG) and (d) mean (+SE) phosphatase (PHOS) enzyme activities in different microsite types. Mean (+SE) (e) available soil carbon and (f) nitrogen in relation to microsites.

those of soil-disturbing animals at higher rainfall. Soil carbon, therefore, increases in wetter environments irrespective of soil-disturbing mammals, as decomposition processes are more rapid (Hättenschwiler and Gasser 2005, Aerts 2006). This might not be the case for soil nitrogen: at higher rainfall, the positive effect of mammals might be overwhelmed by the impacts of rainfall-driven leaching of nitrogen from the soils (Radulovich and Sollins 1991, Domínguez et al. 2004).

Microsite effects predominate, but vary under soil-disturbing mammal reintroduction

Soil nutrient pools and enzyme activities were more strongly related to microsite than the presence of soil-disturbing mammals, and this trend was consistent for both the landscape-scale and experimental exclusion studies. For example, β-glucosidase and nitrogen were greater under vegetated, perennial microsites than in the open, consistent with the extensive body of literature on patterns of nutrient and moisture accumulation, and microbial and invertebrate communities beneath the canopies of woody plants (Schlesinger and Pilmanis 1998, Ochoa-Hueso et al. 2018). Without soil disturbance and resource distribution by mammals, nutrients can be limited to the canopies of perennial vegetation with increased biological activity (Stock et al. 1999, Whitford 2002).

We found that the process of nutrient accumulation in the soil beneath vegetation patches, or differences within a

given site, were mediated by the activity of soil-disturbing mammals. For example, soil labile carbon differed among microsites in the control, but in the reintroduction area, total values increased, and microsite-level differences vanished in both landscape-scale and experimental exclusion studies. This finding shows that, in addition to driving broad-scale increases in soil nutrients, soil-disturbing mammals homogenise nutrient distribution among microsites. The most parsimonious explanation is the translocation of subsoil to the surface horizons by animals during their digging activities, a process that has been observed in other semi-fossorial animals such as pocket gophers *Geomys* spp. (Kerley et al. 2004). Soil nutrients in foraging pits belowground increase largely through the accumulation of litter (James et al. 2009). Soils from older disturbances will have more labile carbon, and, with the continuous bioturbation of the soil over many years, some subsurface samples may begin to resemble surface soils in their carbon and nitrogen signature. This may then be detected in soils across the entire area occupied by soil-disturbing mammals and not only in their foraging pits.

Conclusions

Accurate prediction of the benefits of animal reintroductions for restoring ecosystem functions may depend on knowledge of species interactions and environmental factors at large and microsite-scales (Nogués-Bravo et al. 2016). However, it is clear that reintroductions of ecologically extinct soil-disturbing mammals provide an opportunity to ameliorate declines in soil function, particularly in the drier parts of Australia. Although mammal reintroductions are conducted primarily for species conservation and, in Australia, are largely confined to predator-free areas, their value in ecosystem restoration provides an additional incentive for conservation.

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Author contributions – HG and OD designed the study. OD collected the data. OD analysed the data and wrote the manuscript in collaboration with HG and DE.
Conflicts of interest – There is no conflict of interest.
Permits – Permits from the reserves and land owners of control areas were given by the reserve ecologists, land owners and local shire councils to work on their land.

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Supplementary material (available online as Appendix ecog-04259 at <www.ecography.org/appendix/ecog-04259>). Appendix 1.

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