Experimental evidence for ecological cascades following threatened mammal reintroduction

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Abstract. Species extinction has reached unprecedented rates globally, and can cause unexpected ecological cascades. Since Europeans arrived in Australia, many endemic mammals have declined or become extinct, but their ecological roles and outcomes of their reintroduction for ecosystems are poorly understood. Using surveys and novel long-term exclusion and disturbance experiments, we tested how digging mammal reintroduction affects predatory invertebrates. Mammal exclusion tended to decrease bare ground. Although scorpion burrow abundance increased with bare ground, mammals also had direct negative effects on scorpions. Increased disturbance alone decreased scorpion abundance, but other mechanisms, such as predation, also contributed to the mammal effect. Despite negative associations between scorpions and spiders, both groups increased and spider composition changed following mammal exclusion. Our long-term research showed that threatened digging mammals drive ecosystem cascades, affecting biota through a variety of pathways. Reintroductions of locally extinct digging mammals can restore ecosystems, but ecosystem cascades may lead to unexpected restructuring.

Key words: arachnids; bilby; digging mammals; ecological extinction; ecological restoration; ecosystem engineers; rewilding; scorpions; spiders; trophic cascades.

Introduction

Species extinction rates are now on par with those of the five mass extinctions, as a result of anthropogenically driven global change (Barnosky et al. 2011). The next tier of species likely to become extinct includes species currently experiencing population declines, resulting in their ecological extinction (Borrvall and Ebenman 2006, Brodie et al. 2014). Complex interactions among and between species and their environments mean that the impacts of species extinctions or declines are difficult to predict (Hagen et al. 2012). For some ecosystems, species loss may result in extinction cascades, leading to the loss of further species and ecological functions (Borrvall et al. 2000, Hooper et al. 2012). Alternatively, ecosystems may be reconfigured through ecological cascades, whereby species assemblages and ecological functions change without further extinctions (Pires et al. 2014).

Island biota is vulnerable to extinction caused by introduced predators and competitors, due to their long evolutionary history of isolation (Burney and Flannery 2005). Since European colonization 230 yr ago, the island continent of Australia has experienced the highest contemporary rate of mammal loss globally (29 species extinct; 21% threatened; Woinarski et al. 2015). The decline of digging mammal populations is a global phenomenon (Davidson et al. 2012) and many of Australia's extinct and threatened mammals are fossorial. Species such as bilbies (*Macrotis* spp.) and bettongs (*Bettongia* spp.) acted as ecosystem engineers, altering soils and vegetation (James and Eldridge 2007, Eldridge and James 2009, James et al. 2009). Digging by vertebrates affects other animals directly, by altering burrow systems (Grossman et al. 2019), and indirectly, by changing habitat structure, particularly in the ground layer (Davidson and Lightfoot 2007, Davidson et al. 2012, Coggan et al. 2016). Habitat disturbance, and associated decreases in ground layer complexity, often leads to a decline in the richness of epigeic species (Gibb et al. 2015).

In addition to their role as ecosystem engineers, threatened mammals were also part of complex networks involving interactions such as predation, competition and parasitism (Gibb 2012, Coggan et al. 2018). Previous studies examining the effects of insectivorous vertebrates on invertebrates suggest that invertebrates

are smaller and less abundant in their presence (Spiller and Schoener 1990, Dial and Roughgarden 1995). In addition, the exclusion of vertebrate insectivores affects above- and belowground insect-driven ecosystem processes, such as herbivory and nutrient cycling (Dial and Roughgarden 1995, Dunham 2008). Recent studies suggest that threatened Australian mammals may drive ecological cascades (Silvey et al. 2015) and lead to altered ecosystem functions (Coggan et al. 2016, Coggan et al. 2018, Decker et al. 2019). However, no studies have attempted to experimentally verify these findings, or to elucidate the mechanisms through which impacts occur.

The impact of species loss on ecosystems is difficult to study, and our knowledge is based largely on mensurative surveys (Coggan et al. 2018). Reintroductions are increasingly used to conserve threatened species (Armstrong et al. 2015), but they also provide an opportunity to study how ecosystems may have operated prior to ecological extinctions. However, locations for reintroductions are selected subjectively, so findings based on inside-outside reintroduction area comparisons may be confounded by differences in habitat quality and by pseudoreplication (Hurlbert 1984). Although experiments are critical for definitively separating correlation from causation, field experiments have only rarely been used to examine the impacts of threatened species on ecosystems (Coggan et al. 2018).

Here, we use paired inside-outside comparisons at two reintroduction sanctuaries, a 9-yr exclusion experiment within a reintroduction sanctuary, and experimental disturbance to investigate the impacts of threatened mammal reintroduction on assemblages of ground-dwelling arachnids. Arachnids are a critical component of terrestrial ecosystems, acting as key predators of other invertebrates and engaging in intraguild predation (Polis and McCormick 1987, Polis et al. 1989, Schoenly 1990, Polis and Strong 1996). Previous surveys suggest that mammal reintroductions may drive ecological cascades among arachnids (Silvey et al. 2015). Understanding how mammals affect these taxa is critical in understanding how ecosystems in Australia may have operated prior to European arrival and how they will change following successful mammal reintroductions. Here, we first definitively test the hypothesis that threatened mammals regulate arachnid assemblages. We predict that mammal reintroduction will be associated with increases in bare ground and declines in abundance, biomass and body size of arachnids, due to predation. Arachnid richness is expected to decline due to decreases in abundance and increases in bare ground. Mammals are expected to alter arachnid assemblage composition by consuming scorpions and spiders, with net positive effects on some spider species due to declines in predation by scorpions, and by differential effects of habitat disturbance on different spider species. Exclusion of mammals from reintroduction areas is expected to have the opposite effects to reintroduction. Second, we explore the mechanisms behind this interaction, by

simulating mammal disturbance to test the hypothesis that the non-trophic effects of mammal disturbance (ecosystem engineering without predation), are sufficient to alter arachnid assemblages. Finally, we use structural equation modelling to test the hypothesis that both direct (predation) and indirect (via disturbance or trophic cascades) effects of mammal reintroduction drive ecological cascades in arachnid assemblages. Our study provides the first long-term, experimental test of the ecological cascades resulting from the loss of digging mammals.

Materials and Methods

Study system

This study was conducted at Arid Recovery, in arid northern South Australia (30°33′ S, 136°55′ E) and Scotia Wildlife Sanctuary, in semiarid southwestern New South Wales (33°21′ S, 141°17′ E), Australia (Fig. 1; Appendix S1: Table S1). Both sanctuaries have extensive areas protected by predator-proof fences, allowing a variety of locally extinct native mammals (Burbidge and McKenzie 1989, Short and Smith 1994, Hayward and Somers 2012) to be successfully reintroduced since 2000; several of the reintroduced species consume invertebrates and forage in the soil (Gibb 2012; Appendix S1: Table S1).

Mensurative surveys

Mensurative surveys (natural experiments) were used to compare response variables (foraging pits, bare ground, scorpion burrows and pitfall-trapped spider assemblages) in plots inside the reintroduction area with control plots outside the reintroduction area. At Scotia, mensurative surveys were conducted in February 2009 and February 2015 (Fig. 1). In 2009, plots (20 × 20 m) were arranged to complement a pre-existing vertebrate sampling regime, with four plots in Stage 1, four in Stage 2 and a further eight outside the reintroduction area ($n = 8$ reintroduction; $n = 8$ control). In 2015, we set up a paired design to compare the reintroduction area with paired "control" plots outside the reintroduction ($n = 8$). However, many pitfall traps from reintroduction plots were dug up by mammals, so we used "reintroduction" plots from the exclusion experiment ($n = 10$), which were open simultaneously and were less disturbed, for February 2015 comparisons. The final design for this mensurative component was therefore no longer paired.

At Arid Recovery, we sampled 10 pairs of 20 × 20 m plots in control and reintroduction areas ($n = 10$ reintroduction; $n = 10$ control) in September 2015.

Exclusion experiment

The exclusion experiment was conducted within the fenced reintroduction area at Scotia (Fig. 1; treatments

a) Locations in Australia

b) Mensurative and experimental plots at Scotia Sanctuary

500 m

Stage 2

c) Pitfall trap layout

Stage 1

Mensurative
surveys 2009
○ Control
● Reintroduction
   2015
◇ Control

d) Exclusion plot

Experimental treatments
● Reintroduction
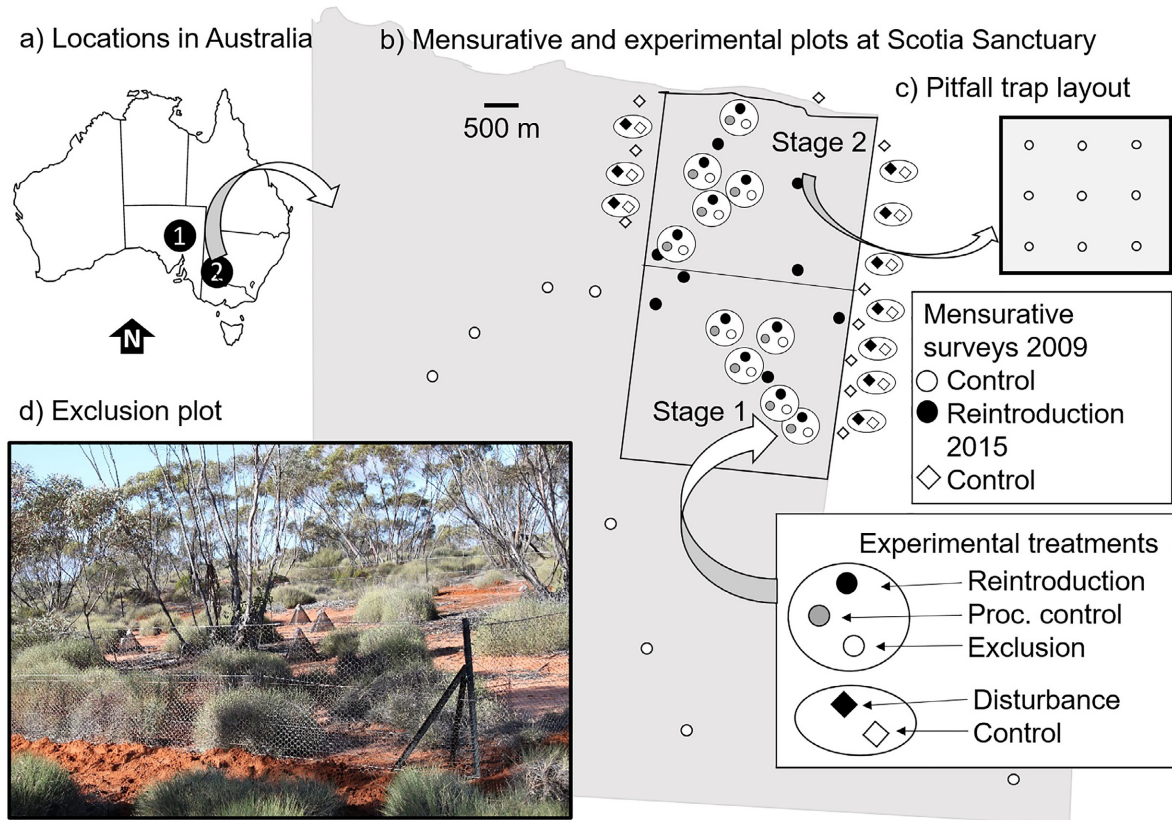◐ Proc. control
○ Exclusion

◆ Disturbance
◇ Control

FIG. 1. Experimental design, showing (a) location of the study areas at (1) Arid Recovery, South Australia and (2) Scotia, New South Wales; (b) layout of plots at Scotia, showing mensurative surveys from 2009 and 2015 and experimental treatments from the exclusion experiment (commenced in 2009) and disturbance experiment (commenced in 2015); reintroduction plots from the exclusion experiment were used in 2015 mensurative survey analyses as pitfalls in paired reintroduction plots (not shown) were too disturbed; (c) layout of pitfall traps in each plot; and (d) photograph of an exclusion plot. Proc., procedural. [Color figure can be viewed at wileyonlinelibrary.com]

and comparisons outlined in Appendix S1: Table S2). We marked the corners of 30 plots of 20 × 20 m in *Triodia* mallee habitat in October 2009 using star pickets (Gibb et al. 2018). All plots were within the introduced predator-free reintroduction area, one-half in Stage 1 and one-half in Stage 2. We set up 10 blocks of three plots, separated by at least 60 m. Within each block, plots were randomly allocated exclusion, procedural control and reintroduction treatments. We constructed exclusion ($n = 10$) and procedural control ($n = 10$) fences in July 2010. Mammals were fenced out of "exclusion" plots using a 1 m high fence constructed from hexagonal wire mesh with 52 × 40 mm holes. A skirt buried 50 cm below the soil surface prevented mammals digging under the fence. Similar fences were constructed at "procedural control" plots, but they lacked the bottom 50 cm of wire. To control for the disturbance associated with burying the base of the fence at exclusion plots, we made similar excavations along all sides of procedural control plots. Reintroduction plots ($n = 10$) were left undisturbed.

Disturbance experiment

The disturbance experiment was conducted outside the reintroduction at Scotia and in similar habitats on the adjacent property to the east, Nanya. Nanya is also managed for conservation, i.e., no livestock grazing and ad hoc control of introduced animals including rabbits, goats, cats, and foxes. We marked the corners of 20 plots of 20 × 20 m in spinifex mallee in May 2015, again using star pickets. We set up 10 blocks of two paired plots, with pairs separated by at least 60 m. Plots within blocks were randomly allocated to control and disturbance treatments. Control plots were left undisturbed. Disturbance plots were disturbed at two-monthly intervals from May 2015 to February 2019. The disturbance treatment involved digging holes of 16 (length) × 13 (width) × 6 (depth) cm, 48% in bare ground, 32% under trees, 15% under shrubs and 5% in litter. We varied the number of pits among sites to simulate a gradient of mammal densities and among months to simulate seasonal effects. Numbers of foraging pits

were based on data previously collected from Scotia (D. J. Eldridge, *unpublished data*; H. Gibb, *unpublished data*; Appendix S1: Table S3).

Foraging pits and scorpion burrows

We used mammal foraging pits as an index of mammal foraging activity in the plots. We walked two 20 × 2 m east-west band transects in each 20 × 20 m plot. Transects were positioned 6 m from, and parallel to, the north and south edges of the plot. Foraging pits whose center fell within 1 m either side of a central line were counted (i.e., the band transects were each 2 × 20 m = 40 m^2 in area). We counted pits deeper than 2.5 cm and broader than 5 cm. Along these transects, we also counted scorpion burrows that looked "active", i.e., burrows that had recent excavations or held their shape, suggesting recent maintenance. We then conducted a "whole plot" survey of "active" scorpion burrows, i.e., burrows with well-formed entrances, by systematically searching across the entire area of the 20 × 20 m plot to better sample scorpions. A previous study showed that the burrows belonged primarily to the inland robust scorpion, *Urodacus yaschenkoi* (Silvey et al. 2015). We conducted surveys of mammal foraging pits and scorpion burrows in the mensurative surveys in February 2015 at Scotia and September 2015 at Arid Recovery and in the 30 exclusion experiment plots at Scotia in October 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, and 2018 and February 2010, 2011, 2012, 2014, 2015, 2016, 2017, 2018, and 2019. We also conducted pre-treatment surveys in the 20 disturbance experiment plots in May 2015 and post-treatment surveys in February 2016, 2018, 2019, and October 2016, 2017, 2018, and 2019.

Pitfall trapping and invertebrate processing

Pitfall trapping was conducted at Scotia in February 2009 and 2015 for the mensurative surveys and in February 2010 (before exclusion), 2012 and 2015 for the exclusion experiment and February 2017 for the disturbance experiment. We placed nine pitfall traps (7 cm diameter, 8 cm height), filled with 100 mL of propylene glycol in each plot. Pitfalls were set in a 3 × 3 grid pattern, separated by 6 m, with the outer pitfall traps 4 m from the plot boundary or fence (Fig. 1c). Traps were collected after 6 d. Invertebrates were sorted to order, then transferred to ethanol. Spiders were sorted to morphospecies and a reference collection checked by an expert (G. Milledge, Australian Museum). Cephalothorax length was measured for all spiders collected.

Nocturnal arachnid activity

On warm nights in February 2015 (minimum 22°C during sampling), between the hours of 21:30 and 00:30, we conducted 10-minute spotlight surveys of scorpion and ground-dwelling spider activity within the experimental plots using a head torch and a UV torch (A 101-LED, 390-nm ultraviolet torch). When eye shine was observed, the observer approached the eye shine to verify that it was from a spider (usually a wolf spider, Lycosidae, or a prowling spider, Miturgidae) and to identify the microhabitat in which it occurred (bare ground, under spinifex or shrubs, or in leaf litter). Scorpions (*U. yaschenkoi*, *U. armatus*, or *Lychas* spp.) fluoresced clearly under the UV light. All observations were recorded and habitats noted.

Data analysis

Mammal foraging pits and scorpion burrows.—Responses of mammal foraging pits and scorpions to treatments were tested in the lme4 package on R (Bates et al. 2014, R Development Core Team 2014), using a generalized linear model with a negative binomial response. For the mensurative surveys, we tested for differences in abundances of mammal foraging pits and scorpion burrows between reintroduction and outside controls (treatments) in the two locations (Arid Recovery and Scotia), using the model: response ~ location + treatment + location × treatment. For the exclusion experiment, we first tested for differences in baseline (pre-treatment) abundances of mammal foraging pits and scorpion burrows among experimental treatments, using the generalized linear mixed model: response ~ treatment + (1|survey) + (1|stage/group/plot), where "stage" was the Stage 1 or 2 mammal enclosure, "group" was the set of three "paired" plots and "survey" was the month and year of the survey. Stage, group, plot, and survey were random factors. Second, we tested the effects of the experimental treatments on numbers of mammal foraging pits and scorpion burrows among treatments separately, using the model response ~ treatment + season + treatment × season + (1|year) + (1|stage/group/plot). For the baseline tests of the disturbance experiment, we used the model response ~ treatment + (1|group/plot), since the disturbance experiment was conducted in the same stage. The post-treatment analyses for the disturbance experiment used the following model: response ~ treatment + season + treatment × season + (1|year) + (1|stage/group/plot). Both exclusion and disturbance treatments were included in the post-treatment analyses for the disturbance experiment, so this might be better termed a "combined analysis". However, this analysis was run separately from the exclusion experiment (only) analyses as the disturbance treatment didn't commence until May 2015.

Spider assemblage composition.—To test the effect of mammal reintroduction on spider assemblage composition, we used simultaneous generalized linear models (ManyGLM; Warton 2011, Wang et al. 2012) conducted in mvabund (Wang et al. 2012) in R, and residual plots were checked to ensure that the selected response

distribution (negative binomial) was appropriate. Tests were performed separately for the mensurative surveys for 2009 and 2015 (response ~ treatment; different sets of sites were used for 2009 and 2015, so between-year differences would have been confounded by location if included in the analysis), the exclusion experiment (response ~ treatment + year + treatment:year + (1|stage/group/plot); 2010, 2012, and 2015 in the same analysis) and the disturbance experiment (response ~ number of foraging pits + (1|group); 2017 only). Where whole assemblage effects were significant, unadjusted post-hoc tests were used to investigate responses of abundant individual species (≥5 individuals for mensurative surveys and the disturbance experiment and ≥10 individuals for the exclusion experiment; we used more individuals for the exclusion experiment as sampling effort was greater). Adjusted post-hoc tests were considered overly conservative for the species-level analysis (Garcia 2004).

We also tested the effects of experimental treatments on spider body size. Spider maximum body size differed among treatments in pre-treatment surveys (spiders in exclusion plots were initially larger), so we tested the effect on change in mean and maximum body size (2012 and 2015 measures compared with pre-treatment baselines) using a repeated measures analysis on JMP (SAS Institute 2007). The model was response ~ treatment + year + treatment:year + (1|stage/group/plot).

For the nocturnal surveys, we compared the abundances of scorpions among experimental treatments using a generalized linear model with a negative binomial response distribution: scorpions ~ treatment + (1|group/plot). For spiders, which were more common, the model was linear and accounted for habitat type: spiders ~ treatment + habitat + treatment × habitat + (1|group/plot). Weather conditions were uniform across nights, so survey night was not included in analyses.

Direct and indirect effects of mammals on spiders.—We used piecewise structural equation modelling (SEM; PiecewiseSEM in R, Lefcheck 2016) to examine direct and indirect effects of mammal reintroduction on spider richness for exclusion (February 2010, 2012, 2015) and disturbance experiments (February 2017), analyzing each year separately. For the exclusion experiment, we combined the reintroduction and procedural control treatments into a single treatment as these had similar effects on counts of mammal foraging pits. Because imposed disturbance levels (number of artificial pits) varied among plots in the disturbance experiment, we treated disturbance as a continuous variable. We used the boot estimator (Smith and van Belle 1984, Chao 1987, calculated using the R package Vegan Oksanen et al. 2010) as our measure of the number of species. Piecewise SEM allows incorporation of multiple linear equations, which are evaluated individually, and allows greater flexibility in distributions and sampling designs and lower replication than traditional SEM (Shipley 2009). It also helps disentangle direct and indirect effects. We specified four equations (Fig. 3): the first predicted the percentage of bare ground cover from mammal treatment (experimental treatments for the exclusion experiment and simulated mammal density for the disturbance experiment). The second equation predicted the number of scorpion burrows from the mammal treatment and bare ground cover. The third equation predicted the abundance of spiders from mammal treatment, scorpion burrows and bare ground and the fourth equation predicted spider richness from spider abundance and bare ground cover. We did not include the random factors in this analysis to avoid problems with singularity, which may be resolved by avoiding fitting overly complex models (Matuschek et al. 2017). In addition to testing for multi-collinearity, we calculated the variance inflation factor (VIF) for each predictor in the piecewise SEM using the package usdm (Naimi 2015). The VIF indicates the proportion of variance in each predictor in the model that is explained by other predictors. No predictors in the model had a VIF greater than 2 (as recommended by Zuur et al. 2010). The fit of the piecewise SEM was evaluated using Fisher's C statistic, where $P > 0.05$ indicates a good fit of the model to the data. We report standardized effect sizes for variables with significant relationships in the piecewise SEM and R^2 values for each of the four paths. Standardized coefficients for the GLM component of the piecewise SEM (not provided by PiecewiseSEM) were calculated using the latent theoretic approach (Lefcheck 2019).

RESULTS

Mensurative study

In the mensurative surveys, the density of mammal foraging pits was considerably greater in reintroduction than control areas at both sanctuaries (Table 1, Fig. 2a). An interaction between location and treatment (reintroduction vs. control) indicated more extreme differences at Scotia: a greater density of foraging pits at Scotia than Arid Recovery for reintroduction plots, but lower density for controls.

The density of scorpion burrows was lower in reintroduction than control plots at both Scotia and Arid Recovery in mensurative surveys (Table 1, Fig. 2c). No scorpion burrows were detected inside sanctuaries during these surveys (although they were present in low densities outside the plots). Abundances were much lower at Arid Recovery than Scotia during the surveys, but this might again be a result of seasonal, rather than locational, differences.

Spider assemblage composition differed between control and reintroduction areas in 2009 and 2015 mensurative surveys (Table 2, Appendix S1: Fig. S1, Species list, Appendix S1: Table S4). Three species of ant spiders (Zodariidae) in the genus *Habronestes* were responsible for differences, with *H. bicornis* and *H. hebronae* more

TABLE 1. Test statistic, degrees of freedom, *P* values, and outcomes of contrast tests following generalized linear mixed models testing effects of "treatment" and other factors on mammal foraging pits and scorpion burrows in the mensurative surveys and exclusion and disturbance experiments (pre- and post-treatment analysed separately).

Source	df	Mammal foraging pits			Scorpion burrows		
		χ^2	*P*	Contrasts	χ^2	*P*	Contrasts
Mensurative surveys							
Treatment	1	25.0	**<0.001**	R > C	49.5	**<0.001**	C > R
Location	1	15.2	**<0.001**		10.2	**0.001**	SS > AR
Treatment × Location	1	8.3	**0.004**	R: SS > AR; C: AR > SS	0.0	1.000	
Exclusion experiment							
Pre-treatment (October 2009–February 2010)							
Treatment	2	5.9	0.052	*(E > P)*	0.3	0.872	
Post-treatment (October 2010–February 2019)							
Treatment	2	383.5	**<0.001**	E < PC, R	8.5	**0.014**	E > R
Season	1	0.7	0.413		35.3	**<0.001**	Summer > Spring
Treatment × Season	2	10.0	**0. 007**	Spring and Summer: E < PC, R	2.0	0.359	
Disturbance experiment							
Pre-treatment (May 2015)							
Treatment	1	1.0	1		2.1	0.152	
Post-treatment (October 2015–February 2018) (includes exclusion and disturbance experiment plots)							
Treatment	4	246.7	**<0.001**	Spring: R, P > D > C, E	126.2	**<0.001**	Spring: C, D > R, E, PC
Season	1	1.3	0.254	Summer: D, P, R > C, E	17.1	**<0.001**	Summer: C, D > R, E, PC; E > R
Treatment × Season	4	20,267	**<0.001**		31.9	**<0.001**	

Note: AR, arid recovery; C, control; D, disturbance; E, exclusion; PC, procedural control; R, reintroduction; SS, Scotia Sanctuary.
Bolded *P*-values are significant at *P* < 0.05.

abundant outside reintroductions and *H. driscolli* more abundant inside (Table 2, Appendix S1: Fig. S1).

Exclusion experiment

Pre-treatment analyses of the experimental plots revealed a marginally nonsignificant difference in foraging pits between treatments: exclusion plots initially contained more foraging pits than reintroduction or procedural control plots (Table 1, Fig. 2b). Following fencing, the density of foraging pits in exclusion plots declined dramatically, and was close to zero 1 yr after (Table 1, Fig. 2b), indicating that plot fences were effective in excluding digging mammals. Foraging pit density was higher in spring than in summer (Fig. 2b). Although a few foraging pits continued to be observed in exclusion plots, their structure was similar to that of pits constructed by goannas (Gibb et al. 2018).

Prior to fencing, the density of scorpion burrows did not differ among treatments (Table 1, Fig. 2d). Following fencing, exclusion plots supported more scorpion burrows than reintroduction plots, independent of season, with procedural control plots intermediate (Table 1, Fig. 2d). Scorpion burrow densities were highest in summer (Fig 2d).

For spiders in the exclusion experiment, the interaction between year and treatment was significant for the exclusion experiment, with several species differing among treatments in univariate post-hoc tests (Table 2). Of these species, positive effects of the exclusion were clearest for *H. hebronae* (Appendix S1: Fig. S1f) and *Eilica* sp. 1, while negative effects were observed for Lycosidae sp. 1.

The maximum body size of spiders in experimental plots declined more (relative to 2010 baselines) in exclusions than other treatments (Treatment $F_{2,26} = 4.2$, $P = 0.032$; Year $F_{1,26} = 1.3$, $P = 0.272$; Interaction $F_{2,26} = 0.2$, $P = 0.827$; Appendix S1: Fig. S2a). Mean body size changed similarly among treatments (Treatment $F_{2,26} = 0.1$, $P = 0.936$; Year $F_{1,26} = 0.22$, $P = 0.646$; Interaction $F_{2,26} = 1.68$, $P = 0.205$). One plot was removed from analyses because no spiders were present in 2015.

Nocturnal surveys showed that scorpions were more active in procedural control than control or exclusion plots ($\chi^2_{(2)} = 16.6$, $P < 0.001$). This pattern was driven mainly by *Lychas* spp. scorpions observed in trees, which might be favored by the procedural control fences. Nocturnal spiders were more active in exclusion than control or procedural control plots (Treatment: $\chi^2_{(2)} = 7.84$, $P = 0.020$; Appendix S1: Fig. S2b) and were observed more often on bare ground and leaf litter than under spinifex (Habitat $\chi^2_{(2)} = 55.8$, $P < 0.001$). A marginally nonsignificant
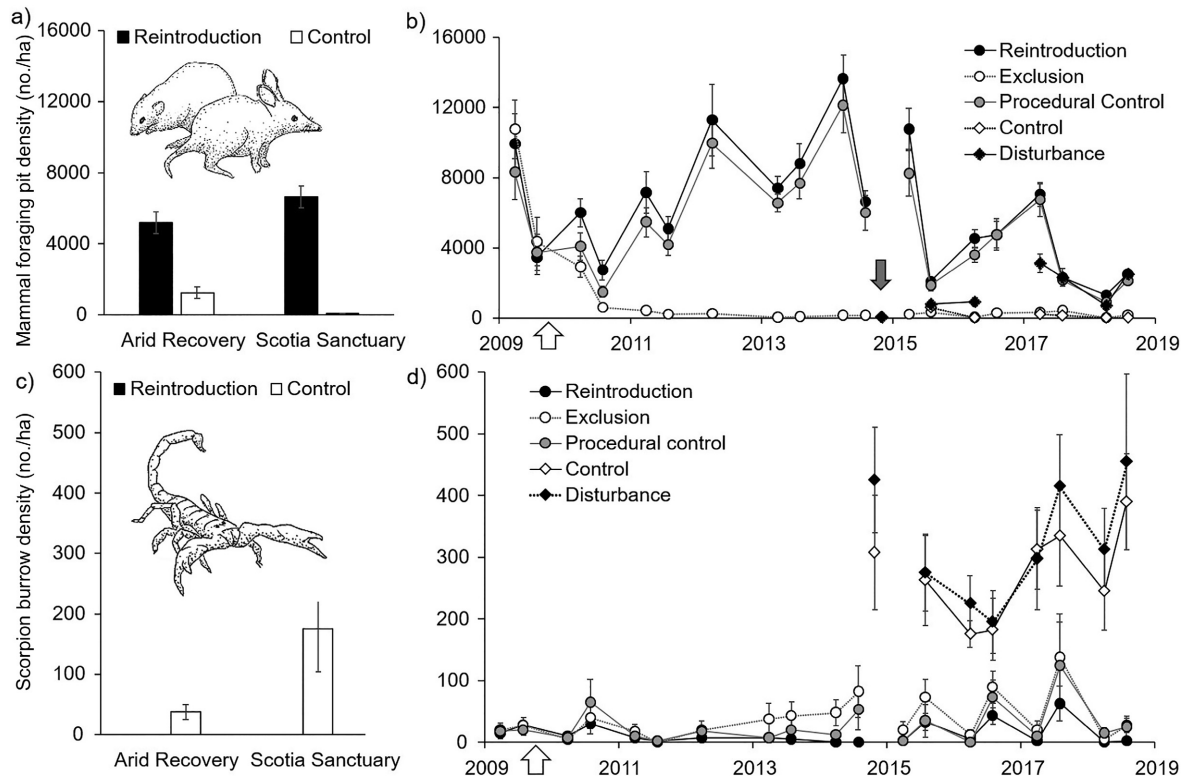
Fig. 2. Density (mean ± SE) of (a, b) mammal foraging pits and (c, d) scorpion burrows from paired plot counts inside and outside the reintroduction area at (a, c) Arid Recovery (*n* = 10) in September 2015 and Scotia (*n* = 8) in February 2015 and (b, d) in each treatment in the experimental plots over time (b, d); arrow indicates the point at which treatments were initiated.

TABLE 2. Generalized linear model analysis comparing spider assemblages (1) inside and outside the reintroduction at Scotia in 2009 and 2015; and (2) among experimental treatments before and 2 yr after experimental exclusion of mammals†.

Source	df	Deviance	*P*	Species
Mensurative survey				
Treatment (2009 data)	15, 1	77.8	**0.011**	*Habronestes driscolli* , **H. hebronae**
Treatment (2015 data)	17, 1	55.7	**0.021**	**H. bicornis**†, **H. hebronae**
Exclusion experiment (2010–2015)				
Treatment	87, 2	220.1	1.000	
Year	86, 1	291.6	**0.001**	*Eilica* sp. 1, *H. driscolli*, *H. hebronae*, Hadrotarsinae sp. 5, Lycosidae sp. 1, Miturgidae sp. 14, *Steatoda* sp. 1
Treatment × Year	84, 2	103.2	0.079	**Eilica sp. 1**, **H. hebronae**, Hadrotarsinae sp. 5, Lycosidae sp. 1
Disturbance experiment				
No. foraging pits	18, 1	123.8	**0.043**	Miturgidae sp. 3, *H. driscolli*†

Note: Species with abundances of ≥5 individuals (mensurative survey and disturbance experiment) and ≥10 individuals (exclusion experiment) showing significant effects (*P* < 0.05) in uncorrected post-hoc tests shown. Species showing negative effects of mammals are presented in boldface type, those showing positive effects are underlined; others showed inconsistent responses.
†0 < *P* < 0.10.

interaction suggested that patterns were clearest on bare ground (Treatment × Habitat $\chi^2_{(4)}$ = 8.14, *P* = 0.087).

The piecewise SEM was a good fit to observed data for species richness in the exclusion experiment (Fig. 3a–c, Appendix S1: Table S5). In all models,

spider abundance was positively correlated with spider richness. Prior to initiation of the exclusion experiment (2010), abundance of scorpion burrows was positively associated with spider activity, perhaps due to shared habitat preferences. In 2012, almost 2 yr after mammal exclusion, we observed no effects of mammals on bare ground or arachnids. Five years after mammal exclusion, we detected a direct negative effect of mammals on scorpion burrows and spider activity and a marginally nonsignificant direct positive effect on bare ground. Bare ground was positively associated with scorpion burrows. The indirect weak positive effect of mammals on spider activity, through decreased scorpion burrow abundance, was not sufficient to offset their direct negative effects.

Disturbance experiment

The density of artificial foraging pits in the disturbance treatment was greater than that in the control and exclusion treatments (Table 1, Fig. 2b) and similar to the density of foraging pits in the reintroduction and procedural control treatments in summer (but less than these treatments in spring). Scorpion burrows did not differ between disturbance and control plots either before or after treatments were imposed (Table 1, Fig 2d). The density of simulated foraging pits affected spider assemblage composition, with the abundance of

Miturgidae sp. 3 and *H. driscolli* positively associated with the abundance of pits (Table 2).

The piecewise SEM was a good fit to the data for spider species richness in the disturbance experiment (Fig. 3d, Appendix S1: Table S5). The density of simulated mammal foraging pits was negatively associated with the abundance of scorpion burrows; spider activity again correlated with spider richness. The relationship between simulated mammal foraging pits and spider activity (positive) was marginally nonsignificant, suggesting weak positive responses to increased disturbance in the absence of predation.

Discussion

Digging mammals are reported to enhance biodiversity and drive ecosystem function through ecosystem engineering and trophic roles (Davidson et al. 2012, Fleming et al. 2014, Romero et al. 2015, Mallen-Cooper et al. 2019). Ecological extinction or successful reintroduction of digging mammals is therefore expected to alter ecosystems. However, this knowledge is largely based on short-term mensurative surveys of areas with and without engineers (Coggan et al. 2018), which are potentially confounded by the choice of location. Using plot-scale mammal exclusion and soil disturbance experiments, we provide a robust test of the impacts of, and mechanisms underpinning, the effects of threatened
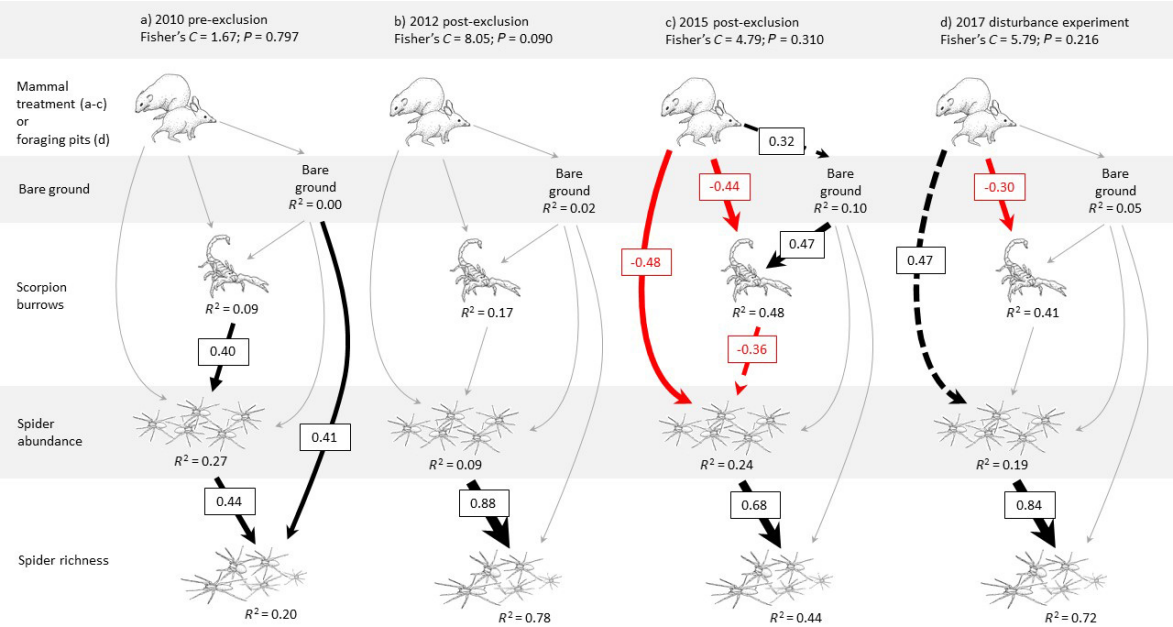

FIG. 3. Piecewise structural equation model showing relationships among experimental treatments and measured variables before and after (two times) instigation of the exclusion experiment. Arrows indicate unidirectional relationships among variables. Black lines indicate significant positive relationships; red lines indicate significant negative relationships; dotted lines indicate marginally nonsignificant relationships (0.05 < P < 0.1); gray lines indicate nonsignificant relationships included in the model. The thickness of significant paths is scaled, based on the magnitude of the standardized regression coefficient (in box). [Color figure can be viewed at wileyonlinelibrary.com]

digging mammals on a key group of predatory invertebrates. Threatened mammal reintroduction was associated with changes in the activity, richness, species composition and body size of arachnids. Structural equation modelling revealed that interactions were complex, with ecological cascades becoming evident after 5 yr of experimental exclusion of mammals. Both direct and indirect effects of digging mammals were important in driving changes. We discuss the paths and mechanisms through which these impacts occur and their implications for ecosystems in the context of species reintroductions.

The importance of digging mammals as ecosystem engineers is well known (Davidson et al. 2012). Excluding digging mammals tended to decrease bare ground cover, consistent with previous studies showing that they increase soil turnover, and bury ground cover vegetation and litter (Davidson et al. 1999, 2012, Davies et al. 2019, Decker et al. 2019). Herbivorous digging mammals also consume ground cover vegetation, further increasing bare ground (Davidson et al. 2012, Verdon et al. 2016). Bare ground was positively associated with scorpion burrow abundance by the third year of the exclusion experiment, consistent with evidence that *U. yaschenkoi* rarely builds burrows in deep leaf litter (Shorthouse and Marples 1982). Despite this indirect positive effect, digging mammals also had direct negative effects on scorpions.

Mensurative and experimental approaches were congruent in finding reduced abundances of scorpion burrows in the presence of reintroduced digging mammals. Mensurative surveys suggested that mammal reintroduction has severe impacts on scorpion populations: despite abundances outside the fence reaching an average of 175 burrows/ha (Scotia, 2015 data), no scorpion burrows were detected inside the fence in paired mensurative surveys at Arid Recovery or Scotia. These differences are consistent with those previously observed for scorpions counted through UV spotlighting and collected in dry pitfall traps (Silvey et al. 2015). Similar patterns were observed in the exclusion experiment, although scorpion burrows were less abundant overall and almost as abundant in the procedural control as the exclusion treatment. The low abundance in the experiment is not surprising as it was based inside the reintroduction sanctuary, where exclusion plots were generally more than 300 m from the edge of the reintroduction area and surrounded by a sea of habitat supporting potential predators, making it difficult for scorpions to recolonize. However, where exclusion plots were colonized, we found up to 375 burrows/ha (15 burrows in a single plot), indicating that scorpions may have reproduced in some plots. The relatively high success of scorpions in procedural controls was surprising, but might indicate that the half fences impeded movement through the plots for mammals in pursuit of fast-moving prey.

While many digging mammals are voracious predators of invertebrates, including scorpions (Silvey et al. 2015, Coggan et al. 2016), they are also agents of disturbance,

which can be disruptive for ground-dwelling invertebrates. In the disturbance experiment, we simulated soil disturbance without the predatory effects of mammals. Structural equation models showed that scorpions declined as the density of simulated mammal foraging pits increased. This suggests that, even without the impacts of predation, increasing densities of digging mammals will lead to declines in scorpions, a key food resource. The experimental disturbance was not targeted at scorpion burrows and did not increase the area of bare ground. It may have affected scorpions by changing the surface structure of plots, vibrational signals, or the landscape of fear. Increased soil surface complexity, such as that caused by foraging pits, reduces invertebrate foraging success due to slipping and increased path tortuosity (Radnan and Eldridge 2017, Radnan et al. 2018), potentially affecting the locomotion of scorpions. Further, scorpions use compressional and surface waves in sand to detect prey (Brownell 1977) and more complex surfaces with more loose sand might make vibrations more difficult to interpret. Alternatively, increased digging activity may have increased scorpion fear of predation, making them more willing to relocate their burrows to disturbance-free areas (landscape of fear concept; Laundré et al. 2010, Matassa and Trussell 2011, Michalko et al. 2019).

In addition to impacts on scorpions, mammal reintroduction was associated with complex changes in the composition of spider assemblages, probably based on variation in spider traits, such as time of activity and sensitivity to disturbance. *Habronestes hebronae* (Zodariidae), *H. bicornis*, and the ant-feeding *Eilica* sp. 1 (Gnaphosidae) were less abundant inside the reintroduction sanctuary or increased in abundance following mammal exclusion. Spiders might decline in the presence of mammals if they are sensitive to disturbance or vulnerable to direct predation by mammals, either while active at night or if resting in exposed locations. In contrast, other spiders did better in the presence of mammals: *Habronestes driscolli* and a wolf spider (Lycosidae) tended to decline and less spider eye shine was observed where mammals were absent, possibly indicating sensitivity to predation by scorpions. Further, *H. driscolli* and Miturgidae sp. 3, increased with increased abundances of simulated foraging pits, suggesting they prefer more disturbed habitats.

Structural equation modelling supported the hypothesis that mammals affected spiders both directly and indirectly, with mammal impacts on scorpion burrow abundance and bare ground cascading weakly through to affect spider abundance and richness by the fifth year of exclusion. This suggests a role for intraguild predation among arachnids (Polis et al. 1989, Michalko et al. 2019) that may be weak due to the opportunistic nature of foraging and generalist diet of scorpions (Polis 1979). However, the relationship among spiders and scorpions might depend on scorpion abundance. At low abundances (in the pre-mammal exclusion surveys), a positive

relationship between scorpion burrow abundance and spider activity may indicate a shared habitat preference. For example, spiders and scorpions both show positive associations with bare ground in at least one of the models. Shared habitat preferences may have become less important following mammal exclusion if scorpions had become sufficiently abundant to suppress spiders, leading to a negative relationship 5 yr after exclusion. At very high abundances in the disturbance experiment, we found no relationship with spiders, perhaps because spiders sensitive to scorpion predation were rare in the scorpion-rich environments outside the mammal reintroduction sanctuary.

Spider abundance increased in response to mammal exclusion and with the density of simulated mammal foraging pits. The weak positive response to the disturbance treatment suggests that some spider species were favored by disturbances, such that direct predation by mammals on spiders is likely to be the key driver of activity declines in the presence of mammals. Spiders have previously been reported in the diets of bilbies and bettongs, although not in large abundances (Gibson 2001, Southgate and Carthew 2006, Bice and Moseby 2008). Sand goannas (*Varanus gouldii*), which were common inside the fence (and present outside), also prey on burrow-forming wolf spiders (Whitford 1998). Goannas accessed our exclusion plots, despite the fence, but might still have been in lower abundance than in reintroduction and procedural control plots. Spider activity was closely associated with spider richness, suggesting a broad effect of mammal predation on spiders, i.e., although some species appeared to be affected more than others, mammals may not select strongly among spiders of similar species. Increased abundance and richness of spiders following exclusion of vertebrate insectivores is consistent with findings from exclusions of vertebrate insectivores (Spiller and Schoener 1994, Dial and Roughgarden 1995, Dunham 2008). Although previous studies have shown increases in spider body size following vertebrate exclusion, we found a decline in maximum (but not mean) body size in exclusion plots. The mechanisms driving this change are unclear, but decreased bare ground cover in mammal exclusion plots may make them less attractive for larger spiders, as foraging of larger invertebrate species is impeded by high habitat complexity (Gibb and Parr 2010).

Conclusions

Our long-term study revealed substantial and complex ecological cascades following the reintroduction of locally extinct mammals. There has been much discussion of the value of "rewilding" in restoring ecosystems (Nogués-Bravo et al. 2016) and it is unclear whether digging mammal reintroductions reconstruct the pre-European state or a create a novel ecosystem (sensu Chapin and Starfield 1997). Reintroductions have a range of potential ecological benefits, but we highlight the problem that the original densities of reintroduced species are unknown and reintroduced species often exist in an environment free of mammalian predators, so impacts on other species may be greater than historically (Moseby et al. 2018). Our disturbance experiment showed that increasing just the soil disturbance associated with increasing densities of mammals was enough to drive declines in a key invertebrate predator and food resource. In the absence of sound knowledge of historical population densities, it is critical that we carefully track the impacts of threatened species reintroductions on ecosystems and do not neglect the "little things that run the world" (Wilson 1987). While many of the smaller ground-dwelling spiders examined in this study might have life histories that lend themselves to rapid recovery, other invertebrates, such as *Urodacus* scorpions and many mygalomorph spiders, are long-lived and dispersal-limited and may therefore be more vulnerable to local extinction (Shorthouse and Marples 1982, Harvey et al. 2011, Mason et al. 2018). Reintroductions of locally extinct digging mammals provide an opportunity to restore ecosystems, but it is important to consider that ecological cascades following reintroduction may result in unexpected consequences for ecosystem structure.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3191/suppinfo

DATA AVAILABILITY

Data associated with this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sqv9s4n22