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Journal of Arid Environments

DOI:

[10.1016/j.jaridenv.2016.06.005](https://doi.org/10.1016/j.jaridenv.2016.06.005)

Published: 01/10/2016

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Coggan, N. V., Hayward, M., & Gibb, H. (2016). Termite activity and decomposition are influenced by digging mammal reintroductions along an aridity gradient. *Journal of Arid Environments*, 133(October), 85-93. <https://doi.org/10.1016/j.jaridenv.2016.06.005>

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1 **Termite activity and decomposition are influenced by digging mammal**
2 **reintroductions**

3

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9

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11

12 Abstract

13 ~~The decline of species~~ Species declines can have broader impacts on ecosystems, particularly when
14 those species act as ecosystem engineers. Ecosystem engineers modify habitats and therefore indirectly
15 shape plant and animal communities. However, environmental attributes, such as aridity, may influence
16 the direct effect of engineers on habitat properties, indirectly affecting other species and the functions
17 they perform. We used three sites where endangered digging mammals had been reintroduced to test the
18 hypotheses that: 1. digging mammal reintroductions affect resource consumption and abandonment by
19 termites, and 2. locality attributes, such as aridity, influences ~~termite~~ termite interactions with reintroduced
20 mammals. We performed two manipulative experiments to test these hypotheses. First, we tested the
21 effects of burial resource depth on termite consumption of resources (toilet rolls). ~~Here, resource depth~~
22 ~~was a proxy for disturbance intensity by reintroduced mammals, with shallow rolls expected to~~
23 ~~experience more disturbance.~~ Second, we tested resource abandonment by termites in response to
24 simulated disturbances by determining the proportion of termites remaining at disturbed resources
25 relative to undisturbed controls over time. Both experiments were conducted at all three aridity
26 ~~levels~~ sites, inside and outside exotic predator and exotic digging mammal-free reserves. We discovered
27 that: 1. resource consumption was ~25% lower; and resource abandonment ~50% higher where digging
28 mammals were reintroduced; and 2. termite responses to ~~reintroduced digging mammals~~ mammal
29 reintroduction became less pronounced potentially -as aridity increased. ~~We thus showed that the~~ The
30 near-extinction of digging mammals from much of Australia is likely to have significantly altered
31 termite ~~behaviour and termite driven~~ activity and decomposition, but that impacts may potentially
32 depend on aridity. Our work should also be considered in the context of reserve carrying capacities as it
33 suggests, counterintuitively, that ecosystem impacts of reintroductions may be lower in resource-poor
34 sites.

Commented [MH1]: Broader than what? I'd use 'widespread'.

35 **Keywords:** Climatic gradient, Critical weight range mammal, Decomposition, Ecosystem engineer,
36 Interactions, Termite

37 1. Introduction

38 [Recent declines in biodiversity have been dramatic](#) (e.g. Colwell et al., 2012; Dunn et al., 2009),
39 resulting in significant changes to ecosystem functioning and species assemblages (Boyer and Jetz,
40 2014; Brodie et al., 2014; Feer and Boissier, 2015; Silvey et al., 2015). Australia has the fourth- highest
41 record of species loss (IUCN 2015) [and the highest rate of terrestrial mammal extinctions](#) worldwide.
42 [Thirty terrestrial mammal species have been declared extinct since European settlement \(from 1788\)](#) ~~and~~
43 [and a further 21 native mammals are threatened with extinction](#) (Fleming et al., 2014; Woinarski et al.,
44 2015). [Non-native predators are amongst the leading contributors to Australia's mammal extinction](#)
45 [record](#) (Woinarski et al., 2015). [Some of the greatest impacts have occurred in arid and semi-arid](#)
46 [habitats, where species of intermediate body size \(35 g – 5500 g, referred to as 'Critical Weight Range'](#)
47 [species\)](#), (McKenzie et al., 2007), [and greater mass](#) (up to 10 kg, i.e. Hanna and Cardillo, 2014), [have](#)
48 [been more susceptible to regional extinctions or declines. The scale of these species losses has been](#)
49 [mitigated through mammal reintroductions into fenced reserves, from which exotic predators and other](#)
50 [non-native species have been removed](#) (e.g. Hayward and Kerley, 2009; Short and Turner, 2000).
51 [Digging mammals in the critical weight range were almost completely extirpated from Australia's](#)
52 [mainland, where arid and semi-arid habitats comprise up to 70 % of the total terrestrial landscape](#) (James
53 et al., 1995). Desertification is increasing globally (Reynolds et al., 2007), *ergo*, the [cover of arid and](#)
54 [semi-arid habitats is likely to increase in the near future. Australia's native digging mammals are](#)
55 [thought to have functioned as ecosystem engineers](#) (sensu Jones et al., 1996). [Engineering impacts are](#)
56 [generally expected to benefit biotic communities as abiotic stressors increase by providing physiological](#)

Commented [MH2]: Hayward, M. W., Moseby, K. E., Read, J. L. (2014). The role of predator exclosures in the conservation of Australian fauna. In *Carnivores of Australia*: pp 363-379. Glen, A. S., Dickman, C. R. (Eds.). Heidelberg, Melbourne, Australia: CSIRO Publishing.

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57 ~~or physical refuge~~ (Crain and Bertness, 2006). ~~Engineering effects~~ However, their inputs are not
58 adversity. The magnitude of an engineer species' impacts can be context-dependent upon factors
59 including aridity or productivity (hence, resource availability), both of which are important features of
60 arid environments (Fischer and Turner, 1978; Hadley and Szarek, 1981).

61 Prior to their declines from arid habitats, burrowing bettongs (*Bettongia lesueur*) and greater bilbies
62 (*Macrotis lagotis*) were native digging mammals that made prolific contributions to soil turnover,
63 moving between one to six tonnes of soil per hectare every year (Eldridge and James, 2009). The
64 survival record of these species on the Australian mainland since 1788 is mixed. Bilbies persist in
65 isolated populations in north-western Australia and north-central Queensland (e.g. Southgate and
66 Carthew, 2006) but were lost from their central, south and south-eastern Australian range from the
67 1910s to the 1930s (Pavey, 2006). In contrast, bettongs became regionally extinct from mainland
68 habitats by the 1960s (e.g. Short and Turner, 2000). Critical weight range mammal declines (especially
69 of digging mammals) represent a broad-scale loss of ecosystem function, with quantified impacts upon
70 the current structure of arid habitats and the biota within them (Fleming et al., 2014; Manning et al.,
71 2015). These include impacts upon multiple aspects of soil (Clarke et al., 2015; Eldridge et al., 2015),
72 invertebrate (Davidson and Lightfoot, 2007; Read et al., 2008; Silvey et al., 2015), ~~and plant~~
73 assemblages (e.g. Chapman, 2016; Fleming et al., 2014; Verdon et al. in review) ~~and fire regimes~~ Re-
74 establishing native mammal assemblages is anticipated to restore impacted natural ecological processes
75 (James and Eldridge, 2007; James et al., 2009; Manning et al., 2015). Digging mammals have been
76 successfully established inside sanctuaries in arid and semi-arid habitats but the scarcity of accurate
77 historical data needed for these types of conservation projects means that little is known of their
78 potential interactions with, nor their impacts upon pre-existing ecological assemblages (e.g. Nogués-
79 Bravo et al., 2016).

Commented [MH3]: Hayward, M. W., Ward-Fear, G., L'Hotellier, F., Herman, K., Kabat, X. (2016). Could biodiversity loss have increased Australia's bushfire threat? *Animal Conservation* **In press**.

Commented [MH4]: Hayward, M. W., Moseby, K. E., Read, J. L. (2014). The role of predator enclosures in the conservation of Australian fauna. In *Carnivores of Australia*: pp 363-379. Glen, A. S., Dickman, C. R. (Eds.). Heidelberg, Melbourne, Australia: CSIRO Publishing.

80 [Termites are the dominant invertebrate soil engineers and detritivores in Australian arid systems](#)
81 (Morton et al., 2011), and are vitally important to soil health wherever they occur (de Bruyn and
82 Conacher, 1990). [Prior to European colonisation, native digging mammals were likely to have been](#)
83 [important disturbance agents and predators of subterranean termites and other ground-dwelling](#)
84 [invertebrates](#) (Gibb, 2012a; Silvey et al., 2015). [Termite activity is sensitive to disturbances](#) ~~which that~~
85 [affect the availability and suitability of their resources](#) (e.g. Jones et al., 2003). They are therefore likely
86 to respond indirectly [to soil disturbance when mammals are foraging or burrowing](#) (Gibb, 2012a). This
87 may [have cascading influences on factors such as habitat productivity, given their input into the](#)
88 [functioning of arid systems](#). In addition to their functional significance, [termites are](#) consumed by a
89 variety of fauna (e.g. Colli et al., 2006; Morton and James, 1988; Sheppe, 1970). They are [directly](#)
90 [relevant to reintroduced digging mammals as one of their primary food sources](#), as a [number of these](#)
91 [and other threatened critical weight range species are opportunistic dietary generalists and/or](#)
92 [insectivores](#) (e.g. Bice and Moseby, 2008).

93 [Understanding the responses of ecological assemblages to the reintroduction of regionally extinct](#)
94 [species is a developing field in ecology. New evidence indicates that critical weight range mammal](#)
95 [reintroductions \(digging mammals included\) have had significant influences on the community](#)
96 [assembly of arthropods by initiating trophic cascades](#) (Silvey et al., 2015), [and on soil microbes through](#)
97 [digging and defecation](#) (Clarke et al., 2015). [However, no previous studies have investigated the effects](#)
98 [of digging mammals on invertebrate activity and its implication for functions such as detritivory.](#)
99 [Understanding the impacts of mammal reintroduction on termite activity is important because of the](#)
100 [significant contribution of termites to food webs and ecological processes](#) (i.e. Bice and Moseby, 2008;
101 Colli et al., 2006; Matthews, 1976; Morton et al., 2011; Morton and James, 1988; Sheppe, 1970),
102 [particularly in arid habitats](#) (Whitford and Kay, 1999).

103 We used replicated comparisons of three reintroduction sanctuaries located in arid/semi-arid southern
104 Australia. Our aim was to quantify the responses of subterranean termite activity inside sanctuaries
105 where native digging mammals have been reintroduced, against controls outside the sanctuaries; where
106 native digging mammals are regionally extinct. We did this by comparing the proportion of a) resources
107 eaten by termites at different depths, and b) termites remaining at experimentally-disturbed resources
108 buried at both reintroduction and control habitats. We hypothesised that soil disturbances generated by
109 reintroduced digging mammals would reduce termite activity, resulting in lower proportions of buried
110 resources consumed, and higher proportions of resource abandonment by termites. Because aridity was
111 one of the major abiotic variables to increase across the sanctuaries, and also because engineering
112 impacts tend to be context-dependent (Crain and Bertness, 2006; McAfee et al., 2015), we also
113 considered whether different aridity levels at each sanctuary could affect the magnitude of termite
114 responses when digging mammals were present. We hypothesised that the effect of digging mammals on
115 termite foraging would be influenced by the level of aridity experienced at each sanctuary.

116

117 **2. Methods**

118 **2.1. Study sites**

119 We compared termite responses to soil disturbance by reintroduced digging mammals at three
120 conservation sanctuaries. These were Arid Recovery (~~30°33'55.38''S, 136°55'3.85''E~~, South
121 Australia), Scotia (-33°8'9.00''S, 145°11'33.00''E, New South Wales), and Yookamurra sanctuaries (-
122 34°31'19.38''S, 139°28'31.91''E, South Australia) (Table 1, Fig. 1a). Scotia and Yookamurra
123 sanctuaries were administered by the Australian Wildlife Conservancy, and Arid Recovery by BHP
124 Billiton. Aridity varied across sanctuaries. The three sanctuaries were located along a gradient of aridity
125 (Table 1). Temperature, precipitation, gross primary production (GPP) and the enhanced vegetation
126 index (EVI) co-varied with aridity. We used aridity indices for each site that were provided by the
127 Australian Virtual Herbarium (Australian Virtual Herbarium 2015). We placed the aridity index value
128 for each sanctuary relative to the others according to the United Nations Food and Agriculture
129 Organization's (FAO) aridity index scale. Aridity indices are calculated as the annual mean ratio of
130 precipitation/potential evapotranspiration (Chiew, Wang, McConachy, James, Wright and deHoedt
131 2002, Tabari and Aghajanloo 2013). 'High' aridity indices closer to 1 are less arid than 'low' indices
132 closer to 0. Thus, Hyper-arid zones have indices <0.05, Arid zones are <0.05 - <0.20, and Semi-arid
133 zones are <0.20 - <0.50 (FAO 2015). Arid Recovery was the most arid sanctuary and Yookamurra
134 sanctuary was the least arid. Aridity indices, annual precipitation, GPP and EVI increased by an average
135 interval of 34.11%, and the mean daily maximum temperature decreased by an interval of 7.25% from
136 Arid Recovery to Yookamurra sanctuary (Table 1). Note: Aridity indices are calculated as the annual
137 mean ratio of precipitation/potential evapotranspiration (Chiew et al., 2002; Tabari and Aghajanloo,
138 2013). 'High' aridity indices closer to 1 are less arid than 'low' indices closer to 0. Thus, Hyper-arid
139 zones have indices <0.05, Arid zones are <0.05- <0.20, and Semi-arid zones are <0.20 - <0.50 (FAO,

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140 2015). ~~Previous research suggests that effects of (invertebrate) ecosystem engineers on vegetation~~
141 ~~communities increase with precipitation , and resource scarcity promotes fidelity for termites (Lenz,~~
142 ~~Kard, Evans, Mauldin, Etheridge and Abbey 2009). We therefore hypothesised that termite responses to~~
143 ~~reintroduced mammal disturbance would increase with decreasing aridity.~~

144 The dominant vegetation class for Scotia and Yookamurra sanctuaries was remnant Mallee woodland
145 and shrublands, with climate at Yookamurra classified as ‘Mediterranean’, while that at Scotia was
146 ‘Semi-arid’. Dominant ground cover at Scotia included spinifex (*Triodia spp.*) and chenopod species,
147 and *Westringia rigida* at Yookamurra sanctuary. The dominant trees in Mallee woodlands and
148 shrublands are *Eucalyptus* species, including *E. dumosa* and *E. gracilis*. Arid ~~recovery~~ Recovery was
149 classified as Acacia shrubland with a ‘Desert’ climate. Dominant ground cover at Arid Recovery varied
150 with season: at the time of data collection, the **Poached-egg daisy (*Polycalymma stuartii*) and Desert**
151 **Rattle-pod (*Crotalaria eremaea*)** were abundant. Sandhill wattle (*Acacia ligulata*) was the dominant
152 shrub species at Arid Recovery. Scotia and Yookamurra sanctuaries supported cryptogamic crust which
153 bound the soil surface at those sanctuaries, whereas Arid Recovery did not.

155 2.1.2. Sampling design

156 All sanctuaries included large (up to ~86000 ha) enclosures free of introduced predators and protected
157 by predator-proof fencing. [Reconstruction of native mammal assemblages commenced at Scotia](#)
158 [Sanctuary circa 2004](#) (Finlayson et al., 2008), [at Arid Recovery circa 2000](#) (Moseby et al., 2003), and at
159 [Yookamurra Sanctuary circa 1999](#) (Vieira et al., 2007). [All sanctuaries functioned as pastoral land for](#)
160 [livestock \(sheep and/or cattle\) after European settlement and prior to their conversion into sanctuary](#)
161 [habitats](#) (Grolleau and Peterson, 2012). [All reintroduced mammal species were considered regionally](#)

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162 [extinct from both reintroduction and control areas prior to the establishment of these sanctuaries](#) (Table
163 1). [Rabbits were present at control habitats, but had been eliminated from inside reintroduction](#)
164 [enclosures. The population densities of exotic species in control habitats \(e.g. cats, foxes and rabbits\) are](#)
165 [routinely controlled by sanctuary management using poison baiting, trapping and shooting.](#)

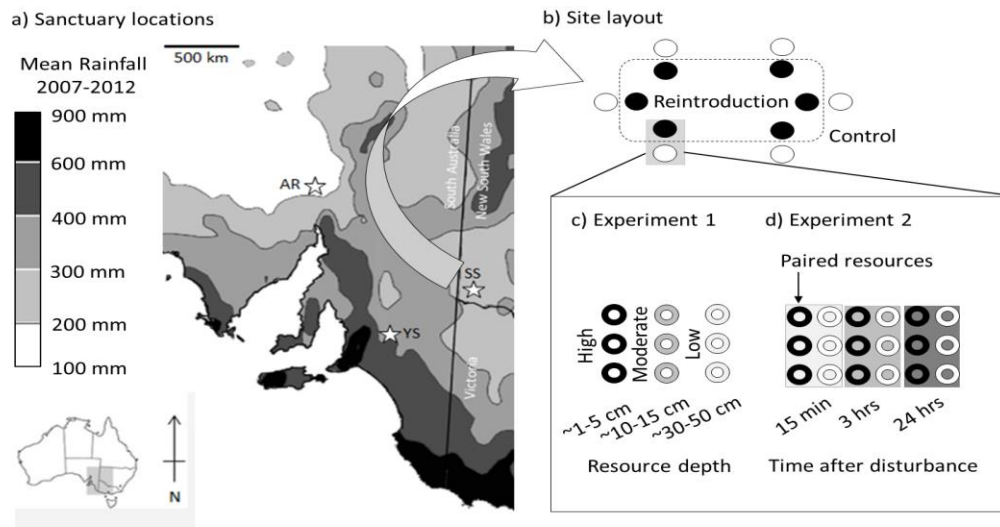
166 To test the effects of [native](#) digging mammals on termite [foraging along the climatic gradient](#)[activity](#), we
167 performed experiments inside (reintroduced [mammalian engineers](#)[digging mammals](#) present:
168 ‘Reintroduction’) and outside the reintroduction enclosure (controls with no native [mammalian](#)
169 [engineers](#)[digging mammals](#): ‘Control’) at each sanctuary (Fig. 1b). We paired sampling sites (n = 6)
170 inside and outside the reintroduction enclosure at each sanctuary. Sites were paired to minimise the
171 influence of spatial autocorrelation of biotic and abiotic characteristics on our response variables.
172 Sampling sites were placed at least 150 m from the fence line (i.e., paired sites were at least 300 m
173 apart) and, where possible, the distance between sites was 1 km (Fig. 1b).

174 **2.1.3. Reintroduced [mammalian engineer species](#)[mammals](#) and presence of reintroduced** 175 **[termitivores](#)**

176 We focused on soil disturbances caused by two reintroduced digging mammal species, burrowing
177 bettongs, *Bettongia lesueur*, and greater bilbies, *Macrotis lagotis* (Table 1). [These species were](#)
178 [important ecosystem engineers prior to their regional extinction from the Australian mainland \(James](#)
179 [and Eldridge 2007\)](#). Bettongs and bilbies are omnivorous and include termites in their diet, although
180 bettongs tend to consume more plant material, while bilbies are more insectivorous (Gibson, 2001;
181 Navnith et al., 2009; Robley et al., 2001). Both species move substantial amounts of soil, within the
182 range of 1.27-5.99 t.ha⁻¹ per year (Eldridge and James, 2009), suggesting that termites experience
183 markedly greater levels of soil disturbance inside sanctuaries. Numbats (*Myrmecobius fasciatus*) were

184 also reintroduced at Scotia and Yookamurra sanctuaries (Vieira et al., 2007). ~~Although this species is not~~
185 ~~considered an ecosystem engineer, it is exclusively termitivorous.~~ Numbats are exclusively
186 termitivorous (Calaby, 1960), but are not digging mammals and do not function as ecosystem engineers
187 (Table 1). Interactions with numbats were not included in our hypotheses, but were acknowledged as a
188 potential influence on termite behaviour.

189



190

191 Fig.1 a) Map showing location of study sanctuaries [relative to the precipitation gradient](#); b) Simplified diagram of sampling sites at each
 192 sanctuary. Dashed line represents the fence dividing habitats. Comparisons of termite responses [to reintroduced to engineers-digging mammals](#)
 193 were made between habitats where digging mammals were reintroduced (Reintroduction: closed circles), or regionally extinct (Control: open
 194 circles); c) Resource (toilet roll) layout for Experiment 1 showing resource depth [\(disturbance level\)](#); d), Resource layout for Experiment 2,
 195 showing 'disturbed' (black) and 'control' (white) resources and layout of blocks by observation time (shaded rectangles). AR: Arid Recovery,
 196 SS: Scotia Sanctuary, YS: Yookamurra Sanctuary.

197 2.1.4. Vegetation Surveys

198 We performed vegetation surveys in September 2011, prior to commencing experiments. We
199 established twelve 5 m x 5 m quadrats at each of the six paired sites in each sanctuary. In every
200 quadrat, we estimated the percentage cover of four habitat characteristics: bare ground, ground
201 cover, leaf litter and canopy. We also calculated the average volume of logs (lying dead wood)
202 with a diameter ≥ 5 cm in every quadrat (c.f. Gibb and Cunningham, 2010). Standing stems were
203 not measured. Log volume was estimated as the volume of a cylinder in cubic centimetres, using
204 log length and diameter measured at the mid-point of the log. Vegetation cover was predicted to
205 decrease with increasing aridity because precipitation restricts resource availability (Oksanen et
206 al., 1981). It was also expected to decrease where ~~ecosystem engineers~~ digging mammals were
207 present, because persistent soil disturbance limits opportunities of for plants to establish (e.g.
208 Gurney et al., 2015). Climate was expected to regulate the impact of digging mammals on
209 vegetation cover in more-arid habitats by limiting the amount of vegetation available for
210 manipulation ~~by engineers~~.

211 2.2. Termite responses

212 2.2.1. Experiment 1: Resource consumption ~~under increasing soil disturbance intensity~~.

213 We performed an experiment using resources buried at three depths to test the effect of soil
214 disturbance by reintroduced ~~ecosystem engineers~~ digging mammals on termite ~~foraging across~~
215 ~~the climatic gradient~~ activity. ~~We used resource depth as a surrogate for disturbance intensity.~~ A
216 longitudinal study of soil disturbance indicated that the average foraging pit constructed by
217 bilbies and bettongs is 10-20 cm (Travers, 2013). We therefore expected that resource
218 consumption by termites would be affected most by ~~reintroduced ecosystem engineers~~ soil

219 [disturbance](#) at depths less than 10 cm, moderately affected at depths less than 20 cm and not
220 affected at depths greater than 20 cm.

221 In February 2012, we buried nine unscented toilet paper rolls ('resources') in a 3 [m](#) x 3 [m](#) grid at
222 each of the 6 paired sampling sites in each sanctuary (Fig. 1a-c). We used toilet rolls as resources
223 because they were attractive to common soil and wood-feeding termite genera (*Coptotermes*, and
224 *Heterotermes*), whose ranges intersected all of our study sites (French and Robinson, 1981;
225 Watson and Abbey, 1993). A row of three resources was buried at each of the three depths,
226 ~~where depth was a surrogate for disturbance~~. Treatments were: 1) intensely disturbed resources
227 ('High disturbance'), 1-5 cm below ground (these represented the zone of highest resource
228 exposure to soil disturbance); moderately disturbed resources ('Moderate disturbance'), 10-15
229 cm below ground (these were close to the average maximum depth of [engineer](#) [diggings](#)); and
230 least disturbed resources ('Low disturbance'), 30-50 cm below ground, where the majority of
231 ~~engineer-disturbancedigging~~s should be avoided (Fig. 1c). In August/September 2012, we
232 unearthed the resources and visually estimated the proportion of each resource that termites had
233 consumed: 0% consumption indicated that the resource remained intact, and 100% consumption
234 indicated that the resource was completely consumed.

235 **2.2.2. Experiment 2. ~~Effect of intense soil disturbance on resource abandonment by~~** 236 **~~termites~~ [Resource abandonment](#).**

237 We hypothesised that disturbance would ~~increase the rate of~~ [affect](#) resource abandonment [by](#)
238 [termites](#). Disturbance caused by reintroduced digging mammals was expected to expose termite
239 foragers to threats such as desiccation or [to](#) attack by termite predators, which also include the
240 reintroduced mammals themselves (Table 1). We tested the effects of disturbance ~~on termites~~ [by](#)

241 comparing [termite](#) abundances on experimentally disturbed resources with those on controls
242 (undisturbed resources) over 24 hours (Fig. 1d).

243 In February 2012, we buried nine resources in pairs within a 3 [m](#) x 3 [m](#) grid at each of the six
244 paired sites at each sanctuary (Fig. 1d). Resources were buried approximately 5 cm below
245 ground, within the range of highest soil disturbance intensity by reintroduced mammals (see
246 Experiment 1). Resource pairs were separated by 5-10 cm and rows were 1 -2 m apart ([Fig. 1d](#)).
247 Termites were allowed to colonize resources until August/September 2012, when we applied our
248 disturbance treatment. For each pair, we disturbed one resource by unearthing it and leaving it
249 unburied in its hole, and one resource, the ‘control’, undisturbed. The purpose of the control
250 resource was to estimate the number of termites using undisturbed resources. We disturbed
251 termite resources between 0900h-1000h to standardize temporal conditions at our sampling sites.
252 Resource abandonment in response to our disturbance was measured by comparing the number
253 of termites in the ‘disturbed’ and ‘control’ resources. We examined each row separately at 15
254 minutes, 3 hours and 24 hours after our initial disturbance treatment. Each replicate resource was
255 examined only once, i.e. termites inside resources from row 1 were collected and counted after
256 15 minutes, from row 2 after 3 hours, and from row 3 after 24 hours following resource
257 disturbance. For each pair, we counted the number of termites remaining in the disturbed
258 resource and its control. For tests of the effect of digging mammals ~~and climate~~ on resource
259 abandonment, we standardised each response by the total number of termites at the pair (Control-
260 Disturbed)/(Control+Disturbed). We identified termite species whenever soldiers were found
261 (soldiers were required for identification). We also noted predation by ants on termites, i.e., ants
262 carrying termites away (~~Fig. 1d~~), at the disturbed resources. Finally, we calculated the proportion
263 of disturbed resources that were attended by ants and photographed ants for later identification to
264 genus.

265 2.3. **Data Analysis**

266 We used a generalized linear model (GLM) and Tukey's post-hoc tests with Bonferroni
267 corrections to test the effect of [ecosystem engineer digging mammal](#) reintroduction on vegetation
268 cover. We also used GLMs to compare termite and ant responses to soil disturbance in habitats
269 with and without reintroduced digging mammals. We used the Gaussian response distribution [for](#)
270 termite activity in both experiments. In experiment 2, note that we used the binomial distribution
271 for ant data, [as these described either the presence or absence of ants](#). Tukey's post-hoc tests with
272 Bonferroni corrections were used to determine differences among interacting factors. All
273 analyses were conducted using [R](#) (R Core Team, 2015).

274

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275 **3. Results**

276 **3.1. General**

277 *3.1.1. Habitat Surveys*

278 Habitat cover differed among sanctuaries, with habitat structure decreasing [with aridity from](#)
279 [Yookamurra to Arid Recovery, and Scotia intermediate between the two](#) (Table 2). Yookamurra
280 had the greatest volume of logs, m^{-2} , the densest canopy, and the least bare ground (Table 2 Post-
281 hoc). At the opposite end of the scale, Arid Recovery consistently had the lowest percentage
282 cover of all recorded habitat types, and had very few logs with a diameter >5 cm, with wood
283 resources concentrated at patches of dead Sandhill wattle (Table 2, Post-hoc). Scotia was similar
284 to Arid Recovery in terms of bare ground and canopy cover, but closer to Yookamurra in terms
285 of ground cover. Leaf litter and logs at Scotia were intermediate between Arid Recovery and
286 Yookamurra sanctuaries (Table 2).

287

Commented [MH12]: Global change required

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288 3.1.2. Termites

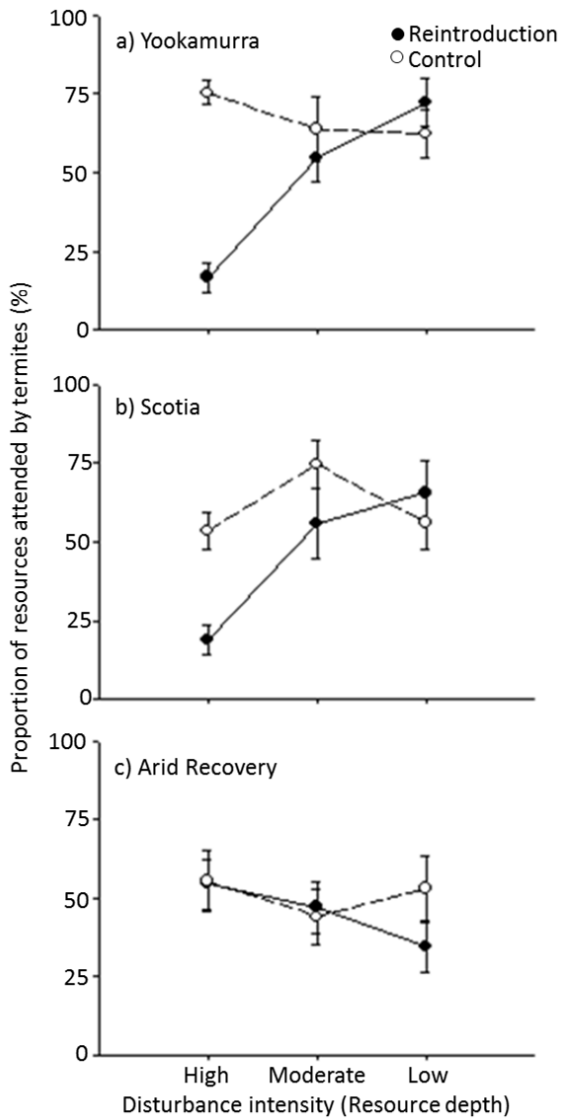
289 Species of *Heterotermes* comprised the overwhelming majority of termites collected in both
290 experiments; *Coptotermes* were collected in very small numbers. [Trench surveys from a related](#)
291 [experiment estimated the average density of *Heterotermes* and of *Coptotermes* as follows:](#)
292 [Heterotermes: Arid Recovery \(AR\) \$87 \pm 22\$ termites.m⁻², Scotia \(SS\) \$137 \pm 21\$ termites.m⁻²,](#)
293 [Yookamurra \(YS\) \$112 \pm 19\$ termites.m⁻². *Coptotermes*: AR \$63 \pm 42\$ termites.m⁻², SS \$120 \pm 47\$](#)
294 [termites.m⁻², YS \$36 \pm 34\$ termites.m⁻².](#)

295 **3.2. Experiment 1: Resource ~~consumption under increasing soil disturbance intensity and~~**
296 **~~increasing aridity~~consumption.**

297 Average resource decomposition by termites was ~~53.25-3~~ $\pm 2.09-1$ % ~~upon observation~~ after 6
298 months' burial. We found a significant three-way interaction between the presence of digging
299 mammals, depth and [aridity-sanctuary location](#) (Table 3). There was no difference in resource
300 consumption with resource depth (~~disturbance intensity~~) where ~~engineers-digging mammals~~ were
301 excluded (Fig. 3, post-hoc: $P > 0.05$). However, when reintroduced ~~engineers-digging mammals~~
302 were present, resource consumption at the low disturbance treatment (1-5 cm) was greater than at
303 the high disturbance treatment (30-50 cm) (Fig. 3).

304 At 1-5 cm depths, the effect of reintroductions of digging mammals on resource consumption by
305 termites (i.e., the difference inside and outside the sanctuary) increased with decreasing aridity
306 (Fig. 3a-c, post-hoc: $P < 0.0001$).

307



308

309 Fig. 3: Mean \pm SE proportion of resources consumed by termites exposed to increasing levels of

310 soil disturbance in Experiment I. Graphs for each sanctuary are presented in order of aridity,

311 from least arid (a, Yookamurra), to most arid (c, Arid Recovery).

312

313

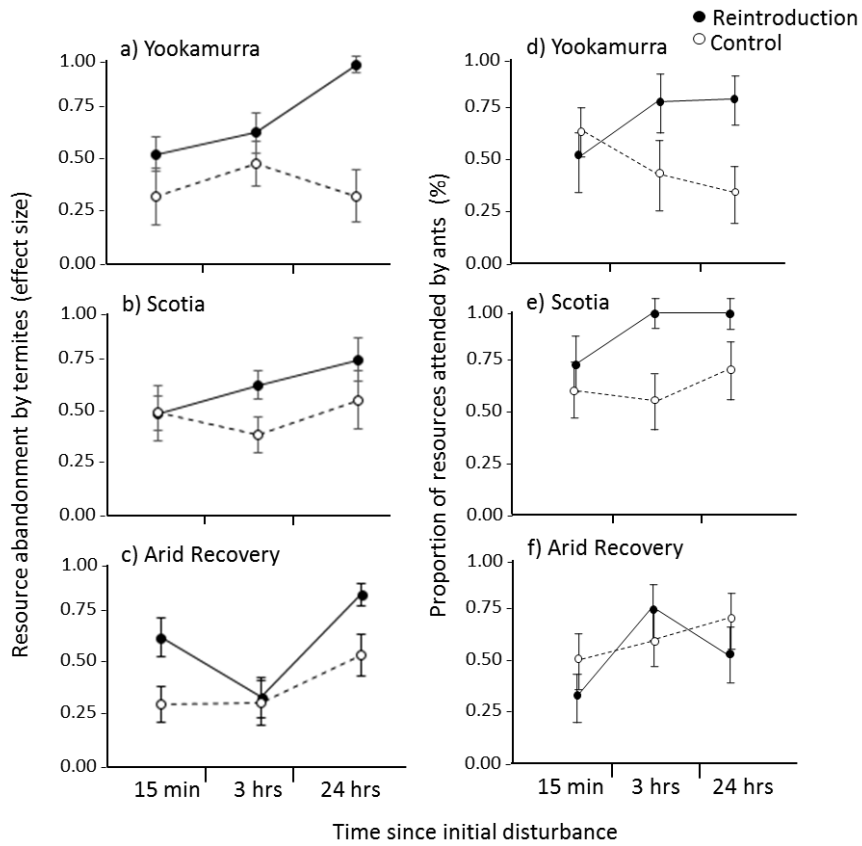
314 **3.3. Experiment 2: Resource abandonment following soil disturbance.**

315 ~~Soil disturbance~~ Experimentally- disturbing buried resources significantly increased ~~rates of~~
316 resource abandonment by termites over time, ~~and rates of Resource~~ abandonment ~~were was~~
317 higher when digging mammals were present (Table 4, Termites; Fig. 4a-c). ~~Aridity~~ The location
318 ~~of sanctuaries~~ did not affect resource abandonment by termites (Table 4, Termites). The number
319 of termites remaining on resources declined with time since disturbance at Yookamurra and
320 Scotia Sanctuaries (Fig. 4a-b) (effect size contrast: 15 mins > 3 hrs > 24 hrs ($p < 0.05$). The
321 number of termites remaining after disturbance at Arid Recovery fluctuated between the 3 hr and
322 24 hr observation times (Fig. 4c).

323 Ants were observed carrying termites away from disturbed resources and we used ant attendance
324 at resources as a surrogate for ant predation on termites. Time since disturbance, engineer status
325 and ~~aridity-sanctuary~~ interacted to affect ant attendance at resources. Control and reintroduction
326 sites differed after 3 hrs and 24 hrs, but only at Scotia and Yookamurra sanctuaries. At 24 hrs,
327 the effect size (difference between control and reintroduction) decreased ~~with increasing~~
328 ~~aridity~~ from Yookamurra sanctuary to Arid Recovery, which was the most arid sanctuary (Figs.
329 4d-f). *Iridomyrmex purpureus* was the most frequently observed ant species preying on termites.

330

331



332

333 Fig. 4. Mean \pm SE resource abandonment by termites (a-c) and termite predation by ants (d-f)
 334 following soil disturbance. Graphs are presented in order of the aridity at each sanctuary, from
 335 least arid (a & d, Yookamurra), to most arid (c & f, Arid Recovery).

336

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338

339 **4. Discussion**

340 Previous studies have shown that digging mammals alter invertebrate community assemblages
341 through ecosystem engineering (Davidson and Lightfoot, 2007; Read et al., 2008). Their effects
342 are associated with changes to habitat structure and/or complexity, such that assemblages that
343 take advantage of engineered habitats (for example, burrows), are distinct from surrounding
344 habitats that have not been engineered (e.g. Bravo et al., 2009). Invertebrate ~~and invertebrate~~
345 assemblages may be further altered through predation by reintroduced digging mammals and
346 resulting trophic cascades (Silvey et al., 2015). This is the first study to ~~We~~ show that
347 interactions with digging mammals reintroduced digging mammals ~~also~~ negatively affect
348 ecosystem functions performed by invertebrates termite activity, an impact that has not been
349 previously examined in the context of reintroducing regionally-extinct species. Termite activity
350 was approximately 25% lower and resource abandonment about 50% higher than controls when
351 digging mammals were reintroduced. We also observed a decrease in the effect magnitude of
352 termite responses from Yookamurra sanctuary to Arid Recovery. These may be attributed to
353 greater aridity levels and resource availability at Arid Recovery versus the other sanctuaries,
354 which we will discuss.

355 Digging mammals such as the greater bilby and burrowing bettong move a significant volume of
356 soil each year (Eldridge and James, 2009). Termites were expected to alter their resource
357 consumption to avoid soil disturbances (Brown et al., 1999), resulting in a ~~decreased~~ decreases
358 rate of termite activity that could ultimately influence decomposition, one of their primary
359 ecological functions. -Data from Experiment I supported this prediction: shallow resources that
360 were exposed to the most intense levels of soil disturbance (those at shallow depths) were
361 consumed less by termites when engineers digging mammals were present. In contrast, resource
362 consumption was independent of resource disturbance intensity (resource depth) disturbance

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363 when [engineers digging mammals](#) were absent. This shift in resource consumption suggests that
364 termites were either actively avoiding, or were less successful at consuming resources ~~where soil~~
365 ~~disturbance was greater~~ [when digging mammals were present](#). Termite populations decline
366 following habitat disturbances that disrupt their food supplies, for example, shortly following
367 fires, or when habitats shift towards lower plant diversity (e.g. in plantations) (Dosso et al.,
368 2013). It is therefore possible that this change in function resulted from a change in population
369 density of termites. However, preliminary data suggest that this is not the case (Coggan & Gibb
370 in prep), so changes in resource consumption may be the result of changes in termite behaviour,
371 considered in Experiment 2.

372 We showed a clear ~~(aridity dependent)~~ diminution in termite activity in the upper layers of soil
373 in the presence of digging mammals, [although this was greater at Yookamurra and Scotia](#)
374 [sanctuaries](#). While previous studies have focussed on the biodiversity impacts of the loss of
375 ecosystem engineers (Romero et al., 2015), few studies have examined the ecological cascades
376 or functional changes resulting from changes in behaviour or population densities of species with
377 which ecosystem engineers such as digging mammals interact. ~~-Termites are the dominant~~
378 ~~detritivores in arid Australia (Morton et al. 2011), and the change in activity resulting in lower~~
379 ~~levels of resource consumption in the presence of digging mammals may translate into decreased~~
380 ~~decomposition (in the manner that functioning decreases along disturbance intensity gradients,~~
381 ~~i.e. McDonnell et al., 1997).~~ Any such changes in termite-driven decomposition may
382 significantly alter soil nutrient cycling, with potential cascades through to habitat productivity.

383 Our study suggests that reintroduction of [digging mammals that function as](#) ecosystem engineers
384 might lead to decreases in decomposition rates, at least in the upper soil layer where foraging
385 disturbance is most intense. Although it is possible that termite-driven decomposition has
386 increased following the loss of digging mammals from the Australian arid zone, the outcome of

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387 reintroductions for nutrient cycling are likely to be complex, with further studies required to
388 better elucidate the full complexity of interactions.

389 Reintroductions of digging mammals were associated with ~~increased-greater~~ resource
390 abandonment by termites, suggesting a behavioural response to disturbance might be the
391 mechanism determining reduced resource consumption. Several species of [native](#) mammals
392 ([digging and non-digging](#)) reintroduced to our study sites prey on invertebrates, which may result
393 in cascading effects on invertebrate assemblages. For example, Silvey et al. (2015) documented
394 mesopredator release in arachnid assemblages, where mammal predation reduced the abundance
395 of the dominant scorpion species, triggering a trophic cascade in scorpion and ground-dwelling
396 spider communities (Silvey et al., 2015). Previous studies have also reported that some species
397 display behavioural responses to predators that minimise predation risk, but [which also](#) reduce
398 foraging success (i.e. the 'landscape of fear', Lima and Dill, 1990), although ~~extreme~~-hunger will
399 ~~reverse-alter~~ the priorities of risk in order to avoid certain death by starvation over uncertain
400 death by potential predators (Lima, 1998). Differences in resource abandonment ~~rates~~ between
401 control and reintroduction sites ~~for similarly disturbed resources~~ suggest that termites may
402 experience a landscape of fear effect in the presence of digging mammals. Laboratory
403 experiments show that resource abandonment by termites depends on the level of danger that
404 termites perceive (Gautam and Henderson, 2012). Increased ~~rates of resource~~ abandonment in
405 reintroductions might therefore be a result of perceived threats of predation by [reintroduced](#)
406 [native mammals \(including digging species\)](#) ~~digging mammals~~ or other organisms affected by
407 the reintroductions.

408 Disturbed resources were attended by ants within minutes of ~~exposure when engineers were~~
409 ~~present~~[exposure, and their attendance was greater at disturbed resources when digging mammals](#)
410 [were present](#). Although effects of digging mammals on ant assemblages have not been reported,

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411 habitat disturbance alters invertebrate assemblages, favouring aggressive ant genera such as
412 *Iridomyrmex* (Gibb and Hochuli, 2003). Ant attendance at resources was greater in
413 reintroduction than control sites, suggesting ant predation rates on termites may be higher when
414 termites are exposed to disturbance when digging mammals are present. Declines in numbers of
415 termites at resources in the presence of digging mammals may therefore have resulted from both
416 the direct process of predation by ants or digging mammals, and the indirect process of predation
417 or disturbance avoidance.

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418 Changes in termite activity in the presence of digging mammals tended to be greatest at
419 Yookamurra sanctuary, moderate at Scotia sanctuary, and not different from controls at Arid
420 Recovery. We suggest that the differences in effect magnitude were associated with habitat
421 (resource) availability, which differed at each sanctuary, for example, where vegetation resources
422 covered more area at Yookamurra and Scotia than at Arid Recovery, which had more bare
423 ground. The historical use of sanctuary land to run non-native livestock (cattle and/or sheep)
424 before they were re-purposed for conservation is one factor that could strongly affect habitat
425 availability. The presence of livestock in arid lands has lasting impacts on habitat structure.
426 These include changes in the proportions of bare ground and low vegetation to taller plant types
427 (e.g. shrubs), and the long-term impact on habitat cover can be observed when livestock is
428 absent as those taller plant classes return (e.g. Eldridge et al., 2011). Persistent soil disturbance in
429 addition to different mammal densities (where digging is an engineering function) also limits
430 opportunities for plants to establish (e.g. Gurney et al., 2015; McAfee et al., 2015). Both of these
431 factors are likely to contribute to the habitat cover observed at each sanctuary, in addition to
432 aridity, which was lower at Yookamurra and Scotia than at Arid Recovery. The influence of
433 rainfall (aridity) over productivity is one of the defining aspects of arid habitats (Fischer and
434 Turner, 1978; Hadley and Szarek, 1981; Rodríguez-Castañeda, 2013), with less vegetation

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435 [expected in more arid habitats \(Oksanen et al., 1981\). Results from the first experiment indicated](#)
436 [that avoiding disturbance was important for termites in less-arid sanctuaries, where resources](#)
437 [such as wood and leaf litter were more available. The cost of leaving a resource would be higher](#)
438 [in more arid environments where fewer alternative resources were available. Resource scarcity,](#)
439 [such as the low wood availability observed at Arid Recovery, might thus encourage higher](#)
440 [fidelity to resources by termites. Different responses to resource-use based on the relative value](#)
441 [of scarce resources have previously been observed in termites, for example, *Reticulitermes*](#)
442 [flavipes consumed resources more slowly when resources were scarce \(Lenz et al., 2009\).](#)
443 [Productivity might also affect ant predation: more productive environments might support larger](#)
444 [densities of ants, such that the chance of discovery of termite prey would be higher. Further](#)
445 [investigation is required to test this hypothesis.](#)

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446 5. Conclusions

447 [We observed clear effects of digging mammal reintroductions on termite activity, which were](#)
448 [significantly reduced when those mammals were present. An additional pattern suggested that](#)
449 [termite responses were influenced by resource availability, which could be affected by factors](#)
450 [such as aridity and land-use history.](#) Our explicit test of termite responses to soil disturbance by
451 mammals adds to our growing empirical understanding of interactions between digging
452 mammals and ground-dwelling invertebrates. Our results suggest that Australian arid ecosystems
453 may have been substantially different prior to the ecological extinction of digging mammalian
454 engineers. They also highlight the complexity of species interactions, with mammal disturbance
455 also altering termite interactions with invertebrate predators (ants). Termites are important food
456 resources for other species, key detritivores in the decomposition process, and ecosystem
457 engineers that affect soil processes and vegetation patterns, especially in arid environments
458 [\(Evans et al., 2011; Gibb, 2012b; Mora et al., 2005\). The lessening of termite activity when](#)

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459 [digging mammals were present is an interesting point to consider, as it could indicate a shift in](#)
460 [the location of resource decomposition into deeper, less-disturbed soil. The relevance of](#)
461 [sanctuary-specific background factors including aridity land-use history \(among others\) still](#)
462 [require empirical exploration beyond what we uncovered using only three sites. The trends that](#)
463 [we observed agree with the context-dependency of engineering impacts \(McAfee et al., 2015\),](#)
464 [but run counterpoint to theories that engineering ought to benefit interacting organisms with](#)
465 [increasing environmental adversity \(Crain and Bertness, 2006\).](#) –This novel finding suggests that
466 it may be more difficult to generalise about the effects of digging mammals on ecosystems than
467 anticipated, and that higher carrying capacities of less arid environments may also be linked with
468 greater ecosystem sensitivity. This study adds to the small, but growing, volume of research
469 showing that the decline of digging mammals has had broad-reaching effects on invertebrates
470 (e.g. Davidson and Lightfoot, 2007; Silvey et al., 2015), and makes substantial advances in our
471 understanding of impacts on invertebrate-driven decomposition, a critical ecosystem function.

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473 **6. Acknowledgements**

474 We thank D. Eldridge, M. Van de Wetering, S. Avitabile, J. Grubb, S. Watson and anonymous
475 reviewers for their valuable assistance in preparing this manuscript. We are grateful to the
476 volunteers who assisted with fieldwork and also to the ANZ Holsworth Wildlife Research
477 Endowment, Australian Wildlife Conservancy, Arid Recovery and the Australia and Pacific
478 Science Foundation for their financial and logistical support. NVC was supported by an
479 Australian Postgraduate Award, HG was supported by a Future Fellowship (FT130100821).

480 **6.1. Conflict of interest disclaimer**

481 We confirm no conflicts of interest on behalf of the authors associated with this manuscript.

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