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### **Paper:**

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1 **Title:** Eradicating abundant invasive prey could cause unexpected and varied biodiversity  
2 outcomes: the importance of multi-species interactions

3

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26 **Abstract**

- 27 1. Abundant and widely-distributed invasive prey can negatively affect co-occurring  
28 native species by competing for food and/or shelter, removing vegetation cover and  
29 reducing habitat complexity (changing predation risk), and by sustaining elevated  
30 abundances of invasive mesopredators. However, information regarding the  
31 community and trophic consequences of controlling invasive prey, and their temporal  
32 dynamics, remain poorly understood.
- 33 2. We used multi-species ecological network models to simulate the consequences of  
34 changing European rabbit *Oryctolagus cuniculus* abundance in an arid mammalian  
35 community. We quantified how changes in the dominant prey (rabbits) affected  
36 multiple trophic levels, examining changes in predator-prey interactions through time  
37 and how they affected native prey persistence.
- 38 3. Our results suggest that removal of rabbits can benefit native biodiversity  
39 immediately at removal rates between 30 and 40%. However, beyond these levels,  
40 densities of small native mammals will decline in the short term. The processes  
41 underpinning these declines are: (i) increased competition for resources (vegetation)  
42 with kangaroos *Macropus spp.*, whose numbers increase due to their release from  
43 competition with rabbits; and (ii) increased predation (prey switching) by feral cats  
44 *Felis catus*. Both of these effects are mediated by dingoes *Canis dingo*, a native apex  
45 predator.
- 46 4. Importantly, native mammal abundance recovers after a time delay, which is  
47 prolonged when high rates of rabbit control are applied. This is likely due to a  
48 reduction in hyper-predation by invasive feral cats and red foxes *Vulpes vulpes*  
49 following rabbit removal.

50 5. Continued eradication of rabbits in arid Australia will benefit native species due to a  
51 decrease in apparent competition for resources and by alleviating hyper-predation  
52 from invasive mesopredators. Furthermore, ecosystem-level conservation benefits of  
53 reducing invasive prey abundance are as important as direct control of invasive  
54 mesopredators.

55

56 ***Synthesis and applications.*** Multi-species ecological network models provide wildlife  
57 managers with tools to better understand and predict the complex effects of species removal  
58 and control on both intact and modified ecosystems. Our results show that management of the  
59 Australian arid zone can benefit from controlling invasive prey as well as invasive predators.  
60 However, invasive species control can cause unexpected outcomes on native biodiversity.  
61 This extends to other systems where dominant prey may play fundamental roles in ecosystem  
62 structure and function.

63

64 **Keywords:** biological invasions; ecological networks; community dynamics; hyper-  
65 predation; prey switching; species removal; apex predator; trophic cascade

66

67 **Introduction**

68 Biological invasions constitute one of the greatest threats to biodiversity, detrimentally  
69 affecting native species, ecological communities and ecosystem processes (Bellard, Cassey &  
70 Blackburn 2016). Invaders can adversely affect native populations directly through  
71 competition, predation, hybridization and disease, and indirectly by disrupting habitat  
72 suitability (Doherty *et al.* 2016). Therefore, reducing the ecological impacts of invasive  
73 species is a primary goal of conservation management (Jones *et al.* 2016).

74 Biotic interactions between invaders and native species are of particular importance  
75 for conservation outcomes, yet rarely is the ecological complexity of managing invasive  
76 species sufficiently considered (Courchamp, Chapuis & Pascal 2003). Consequently, the  
77 outcomes of pest management on native species remains poorly understood (Bull &  
78 Courchamp 2009), despite potentially far reaching effects for ecological communities  
79 (Ballari, Kuebbing & Nuñez 2016).

80 There is increasing recognition that multi-species, community-level approaches are  
81 needed to manage invasive species (Bode, Baker & Plein 2015; Baker, Gordon & Bode  
82 2016). This is because the reduction or eradication of populations of invasive species can  
83 often lead to unexpected flow-on consequences for community structure and ecosystem  
84 processes, if species interactions aren't understood and accounted for by managers (Ballari,  
85 Kuebbing & Nuñez 2016). Perturbing ecosystems through invasive species control can lead  
86 to a variety of outcomes, and might result in temporary and/or long-term changes to  
87 ecosystem states. Local populations of native species can recover rapidly if the invasive  
88 species causing the largest threat to population persistence is correctly identified and  
89 controlled sufficiently. However, if control efforts are insufficient to effectively depress the  
90 abundance of the invasive species then populations of native species and degraded  
91 ecosystems may not recover or they may revert to their former (eroded) states quickly.

92 During such phases of non-equilibrium dynamics, it is plausible that further damage may  
93 compound impacts on native biodiversity and ecosystems (Courchamp, Chapuis & Pascal  
94 2003; Ballari, Kuebbing & Nuñez 2016). Effective control (severe population reduction or  
95 eradication) of invasive species can also restructure food webs leading to the loss (or near  
96 loss) of endemic species through prey switching (Norbury 2001; Gibson 2006) and  
97 unforeseen negative effects of hyper-predation (an additional predation pressure that arises  
98 when the abundance of a predator is enhanced by the presence of another species of prey) on  
99 the abundance of native biodiversity (Courchamp, Langlais & Sugihara 2000).

100 Although models of complex food web structures, describing interactions between  
101 species in ecosystems, have been used for over four decades to advance ecological theory and  
102 better understand complex community structures and dynamics (e.g. May 1973; Pimm 1984),  
103 they are now being used to guide conservation management (McDonald-Madden *et al.* 2016)  
104 and test alternative pest management actions (Bode, Baker & Plein 2015). Ecological  
105 network models are being used with increasing frequency in conservation and invasion  
106 biology for the reason that they provide suitable frameworks to test for unexpected and  
107 potentially undesirable consequences of eradicating species or groups of species from natural  
108 systems. This is because they incorporate the potential indirect effects that species might have  
109 on one another i.e., the effect of a species on another being mediated by a third (other)  
110 species. Indirect effects in networks of ecological interactions, via top-down and bottom-up  
111 mechanisms, are powerful regulators of community dynamics (Menge 1995).

112 Mainland Australia and its mammal communities provide ideal and tractable systems  
113 for examining the potential consequences of perturbing ecological networks, consisting of  
114 both invasive and native predators and prey. Across much of Australia's arid biome (~70% of  
115 Australia or 7.5 million km<sup>2</sup>), key species in the ecological network include invasive  
116 mesopredators (feral cats, *Felis catus*, and red foxes, *Vulpes vulpes*) and invasive small

117 mammals (European rabbits, *Oryctolagus cuniculus*), native large herbivores (kangaroos,  
118 *Macropus* and *Osphranter* spp.), a native apex predator (dingoes, *Canis dingo*) and typically  
119 more restricted and threatened small native mammals (e.g. bilbies, *Macrotis lagotis*)  
120 (Wallach *et al.* 2016). In this ecosystem, rabbits are a ‘dominant prey’ and integral to the  
121 functioning of the ecological network. Rabbits (i) compete directly with small sized native  
122 mammals and native herbivores for food and/or shelter; (ii) remove vegetation, reduce habitat  
123 complexity and change predation risk for native prey species; and (iii) sustain and potentially  
124 increase invasive mesopredator abundance (Johnson 2006).

125         Species interactions have been considered to some extent in mathematical models  
126 applied to aspects of this Australian ecosystem. These studies have shown the importance of  
127 considering ecological interactions when identifying “whole ecosystem” type responses to  
128 species management. For example, Pech & Hood (1998) disentangled the likely effects of a  
129 downward pressure on rabbit abundance (caused by rabbit hemorrhagic disease, an important  
130 biocontrol for European rabbits in their invasive range (Fordham *et al.* 2012)) on a  
131 mesopredator and a generic small native mammal. Choquenot & Forsyth (2013) used a  
132 similar approach to establish the likely effects of controlling dingoes on kangaroo  
133 populations, showing the potential for cascading effects of controlling an apex predator. More  
134 recently, an extension of this model allowed Prowse *et al.* (2015) to better understand the  
135 economic benefits of maintaining populations of dingoes for the cattle industry. Here, we  
136 extend these empirically-based approaches, increasing the complexity (and likely ecological  
137 reality) of the ecological network, to provide an improved understanding of the community-  
138 wide consequences of managing rabbits in arid Australia. Although community-based models  
139 have previously been used to understand the effects of removing species from ecosystems  
140 similar to the one studied here, these studies have mainly focused on removing top predators,  
141 modelling the consequences of removing top-down effects on ecosystem processes (e.g.,

142 Colman *et al.* 2014; Dexter *et al.* 2013).

143 Previous studies suggest that successful rabbit control could have wide reaching effects  
144 on native biodiversity in Australia (Pedler *et al.* 2016), in addition to economic benefits  
145 (Cooke, Jones & Wong 2010). However, to date, research has not considered the outcomes of  
146 rabbit management at the ecosystem level. Based on previous work and expert knowledge,  
147 we establish the possible flow-on effects of rabbit removal on the abundances of other key  
148 species in a model Australian arid ecosystem (Fig. 1). We then develop and use an explicit  
149 multi-species ecological network model to test these hypotheses. More specifically we: (i)  
150 describe and quantify how changes in rabbit abundances are likely to affect multiple trophic  
151 levels (mesopredator, apex predator, native prey, and large herbivore abundance); and (ii)  
152 examine the temporal dimension (dynamic nature) of changes in predator-prey interactions  
153 (including potential prey switching and hyper-predation) and how these might affect the  
154 persistence of native prey.

155 Our results and simulation-based tool provide wildlife and pest managers with a better  
156 understanding of how ecological communities might respond to targeted rabbit management.  
157 The approach can be extended to other systems in order to examine predator-prey interactions  
158 and make *a priori* predictions about the ecological consequences of management  
159 interventions, including pest control and species reintroductions.

160

## 161 **Materials and Methods**

162 We developed a model based on discrete-time difference equations and simulated the  
163 dynamics of trophic interactions in an arid ecosystem in Australia, consisting of 6 different  
164 species plus a basal (vegetation) resource (Fig. 2). The species modelled in this simplified,  
165 but ecologically realistic, food web were: European rabbits (*Oryctolagus cuniculus*); bilby  
166 (*Macrotis lagotis*; a native critical weight range ‘small’ mammal); kangaroos (*Macropus* and

167 *Osphranter* spp.); European fox (*Vulpes vulpes*); feral cat (*Felis catus*); and dingo (*Canis*  
168 *dingo*). We used this dynamic food web model to establish whether decreasing the abundance  
169 of rabbits is likely to reduce mesopredator populations and predation to levels that would  
170 support recovery of native mammals.

171         We did not try and capture every species in the ecological network in the model  
172 because doing so would make the model computationally unwieldy, providing results that  
173 would be difficult to duplicate and interpret (Drossel & McKane 2002). Instead, using  
174 published research and expert knowledge, we endeavoured to capture the primary species  
175 interactions and ecological consequences that are likely to be affected by rabbit management.  
176 We were unable to account for potential prey switching by cats and foxes from rabbits to  
177 reptiles and invertebrates, due to a lack of empirical data. Likewise, the diet of dingoes is  
178 known to be broad, varying in different ecosystems, sometimes including mammalian prey in  
179 the critical weight range of 35 to 5500 g. However, on average, dingoes typically consume  
180 orders of magnitudes fewer critical weight range mammals than do invasive mesopredators  
181 (e.g., Davis *et al.* 2015). Thus, to simulate the main interactions and community structure in  
182 the arid Australian ecosystem, the potential (but negligible) trophic interaction between the  
183 dingo and small native mammal prey was not incorporated into the model, preventing any  
184 potential prey-switching to small native mammals by dingoes. In favour of simplicity (e.g.,  
185 Robley *et al.* 2004), and a lack of empirical data suggesting otherwise, we assumed that the  
186 three herbivore species in the network are competing for the same resource without resource  
187 partitioning. Furthermore, we assumed that mesopredators rely solely on rabbits and small  
188 mammals for food, however, there might be other prey items that could maintain their  
189 abundances.

190

191 ***Food web structure***

192 The structure of the food web (Fig. 2) established the paths for biomass flux among species,  
193 except for the dingo-cat and dingo-fox interactions, which did not involve biomass transfer.  
194 These two interactions were treated as ammensalisms, whereby the mesopredator (fox/cat) is  
195 negatively affected by the dingo, but the dingo does not receive a direct benefit (Abrams  
196 1987). Ammensalism in the model, therefore, represents intraguild competition between  
197 mesopredators, a community motif rarely considered in food web studies (Amarasekare  
198 2008). By simulating a mixture of antagonistic and ammensal interactions, our model  
199 addresses an important and novel aspect of research on food webs - the incorporation of  
200 multiple interaction types in dynamical ecological networks studies (Mougi 2016).

201

## 202 ***Model simulations***

203 Our food web model extended the discrete-time difference equations of Pech & Hood (1998),  
204 Robley et al. (2004), Pople et al. (2010), and Choquenot & Forsyth (2013) to consider a larger  
205 number of species and interactions (Table 1 and Appendix S1). Model validation was done  
206 by comparing the outcomes of the population dynamics of the species in the community with  
207 the results published for the different parts of the model in isolation (Pech & Hood 1998;  
208 Choquenot & Forsyth 2013). Since information on the population dynamics of cats was not  
209 available (Robley et al. 2004), their dynamics were considered to be similar to that of the fox.  
210 To simulate the community-wide effects of rabbit removal, rabbit abundance was reduced  
211 across a range of removal fractions (i.e., the fraction of the population of rabbits that was  
212 removed from the community), which spanned from 0.1 to 0.9 at an interval of 0.1. We did  
213 not simulate complete rabbit removal as it is a very unlikely scenario in the study system.  
214 Initial abundances for all species were sampled using Latin hypercube sampling,  
215 implemented using the *lhs* package in R (R Development Core Team 2013). This approach  
216 generates a stratified random subset of parameter input values for simulation, by assigning a

217 plausible range for each variable and sampling all portions of its distribution (Norton 2015).  
218 We generated 5,000 independent initial abundance configurations, which we used as  
219 independent initial states for model simulations. Ranges for initial abundances used in the  
220 hypercube sampling were based on minimum and maximum abundances observed in the wild  
221 for a spatial extent equivalent to the home range of a pack of dingoes, which is  $\sim 80 \text{ km}^2 =$   
222  $8000 \text{ ha}$  (see Appendix S2 for further details). Thus, the spatial scale of this model was  $\sim 80$   
223  $\text{km}^2$ .

224 Simulations were run for 250 years (1000 time steps). Initial transient dynamics were  
225 allowed to occur for a period of 150 years (600 time steps), closely resembling the amount of  
226 time rabbits have been in Australia prior to the deliberate introduction of myxoma virus in the  
227 1950's as a biocontrol measure, which negatively perturbed rabbit numbers (Cooke *et al.*  
228 2013). During the following 50 years (200 time steps) a perturbation was applied to the  
229 system by consistently removing (i.e. during each time step) a fraction of the rabbit  
230 population according to the different levels of removal/perturbation specified above ( $[0.1,$   
231  $0.2, 0.3, \dots, 0.9]$ ). For the last 50 years (last 200 time steps) of each simulation we ceased  
232 rabbit control, and populations were allowed to recover from the perturbation. This simulates  
233 a press perturbation that lasts for a relatively long time, after which the system is allowed to  
234 recover (Schmitz 1997), allowing the ecosystem-level benefits of rabbit management to be  
235 directly explored. This experimental design was replicated 5,000 times (each time using one  
236 of the 5,000 initial states of abundance) for the 9 different values of rabbit control, yielding a  
237 total of 45,000 simulations. Initial conditions for abundance (sampled from the latin  
238 hypercube) were the same across the 9 values of rabbit control but varied across the 5,000  
239 replicates for each treatment. The food web model was developed in R (R Development Core  
240 Team 2013) programming language (see Appendix S3). Model parameter values, including  
241 their sources, are provided in Table S1.

242 To look at the long-term effects of rabbit removal on our modelled Australian arid  
243 ecological community we: (i) calculated the median abundance of each species during the last  
244 10 years of rabbit control; and (ii) the average abundances of species post-rabbit control using  
245 a 5-year sliding window. We did not use a 10-year sliding window because it would exclude  
246 the first and last ten years of post-control data. We quantified the realised strength of each  
247 interaction in the food web during each of the three periods (50 years prior to control, during  
248 control, after control) in order to determine the mechanisms underpinning the responses of  
249 the community to rabbit removal. Interaction strengths were quantified for model iterations  
250 by calculating their median values across each time period. We used these estimates as a  
251 measure of the effect of each species on each of its resource items in the food web.  
252 Interaction strength can be quantified in two ways in our model: (i) as the per capita predation  
253 rate of a predator on its prey, and (ii) as the total amount of biomass going from one species  
254 (node in the network) to another. The first measure provides information on the strength of  
255 the effect of an individual predator on its prey population, while the second measure provides  
256 an estimate of the quantity of resource intake by the whole predator population. Thus, the  
257 model outputs quantify interaction strengths between animal species as the total per capita  
258 predation rate (Table 1); and between herbivores and pasture as the functional response of  
259 herbivores (Table 1) i.e., the total amount of pasture biomass for a given herbivore species.  
260

### 261 *Statistical analyses*

262 We used polynomial regression to determine changes in median abundances of the species in  
263 the food web to rabbit control. To quantify the changes in the interaction strengths between  
264 species in response to rabbit control, we divided the rabbit control treatments into three  
265 categories: (i) 10-40%, (ii) >40-70%, and (iii) >70% of rabbit removal. We then analysed  
266 differences in the ranges of interaction strengths across these three levels of rabbit control.

267 We used a global sensitivity analysis to identify which parameters had the strongest  
268 influence on the median abundance of small native mammals (Wells *et al.* 2016). We  
269 established plausible ranges for each parameter in Table S1 (+/- 10% of the estimated value)  
270 and used Latin hypercube sampling in R (*lhs* package) to generate 10,000 evenly distributed  
271 samples across the parameter space. Because little is known about the interaction strengths  
272 between the apex predator and the mesopredators, we used wider uncertainty bounds (+/-  
273 50% of the estimated value) for the relevant parameters concerning these interactions in the  
274 sensitivity analysis (i.e.,  $k_{D,F}$  and  $k_{D,C}$  in Table S1). We recorded the median abundance of the  
275 small native mammal species over a 20-year period (without rabbit control), following a  
276 burn-in period. We used boosted regression trees to estimate the relative importance of key  
277 parameters on the median abundance of the small native mammal species (learning rate =  
278 0.0001, tree complexity = 5, bag fraction = 0.5, and k-fold cross-validation procedure), using  
279 the *gbm.step* function from the *dismo* package in R.

280

## 281 **Results**

282 The removal of rabbits was most beneficial for bilby, and by extension other small mammals,  
283 during the rabbit control period when the fraction of rabbits removed from the population was  
284 between 30 and 40% (Fig. 3). Much larger fractions of rabbit control (i.e., >70% of  
285 eradication), caused the abundances of small mammals to be lower in comparison with those  
286 of low to intermediate levels of rabbit control. Conversely, mesopredator abundance declined  
287 in response to all fractions of rabbit population reduction (Fig. 3).

288 The two main interacting processes behind the decrease in small mammal abundance  
289 were: (i) increased apparent competition for resources (vegetation) with kangaroos (as  
290 evident by a marked increase in kangaroo abundance across fractions of rabbit control; Fig.  
291 S1), and (ii) increased per capita predation by cats (Fig. 4). The response was particularly

292 strong for increased apparent competition, however, increased predation by cats (i.e. top-  
293 down control) had an important influence when rabbit removal was  $\geq 40\%$  (Fig. 4b).  
294 Predation by foxes on small native mammals was not affected by rabbit removal (Fig. 4c).  
295 The different functional responses of fox and cats on rabbits are likely behind these  
296 differential changes in predation on small native mammals by mesopredators.

297         The removal of rabbits was beneficial for dingoes. A steep increase in dingo median  
298 abundance was observed for rabbit removal fractions between 10% and 50%, after which it  
299 began to plateau (Fig. 5). Dingo abundance was primarily driven by the availability of its  
300 main prey, kangaroos. The fraction of kangaroos eaten per day (top right panel in Fig. 5)  
301 increased with small-intermediate fractions of rabbit removal. An increase in kangaroo  
302 intake was accompanied by less frequent large rabbit intake rates (bottom right panel in Fig.  
303 5). Increases in dingo abundance were, in turn, followed by decreases in mesopredator  
304 abundances (which are killed by dingoes). Fig. 3 shows that fox and cat abundances  
305 decreased as the fraction of rabbits removed increased.

306         When rabbit removal ceased, the abundance of small native mammals went through  
307 three distinct temporal phases of change: abundance initially declined, then increased  
308 steeply, then resumed its decline (Fig. 6). The magnitude of these changes differed across  
309 fractions of rabbit control, with larger fractions of rabbit removal (0.7 and 0.9), being the  
310 most beneficial for small mammal abundance in the medium to long term if rabbit control  
311 were to end suddenly. Interestingly, 40 years after rabbit removal ended, small mammal  
312 numbers dropped below abundance levels when rabbit removal ceased, suggesting that the  
313 renewed availability of staple prey (rabbits) for mesopredators (Fig. S2) has the potential to  
314 have a long-standing negative impact on small mammal populations (Fig. 6). Top-down and  
315 bottom-up effects were both important in regulating small mammal abundance post rabbit  
316 removal. Vegetation biomass removed by kangaroos was highest for high fractions of rabbit

317 removal (Fig. 6, top-right panel), suggesting that resource competition between kangaroos  
318 and small mammals intensifies with increased numbers of rabbits removed (since both use  
319 vegetation as their primary resource). Conversely, predation by cats on small mammals  
320 remained the same for small to large fractions of rabbit removal (Fig. 6, bottom-right panel).

321 Our simulation results (assessed through the median abundance of small native  
322 mammals) were most sensitive to the estimate of growth rate for small (generic) native  
323 mammals, followed by growth rate estimates for foxes and rabbits (Fig. S3).

324

## 325 **Discussion**

326 Invasive species threaten biodiversity worldwide. Understanding the ecological role of  
327 invasive species in the communities in which they become established is important for  
328 identifying their potential threats to biodiversity, and the community-level effects that are  
329 likely to occur following their active management (e.g., Bergstrom *et al.* 2009). We show  
330 possible flow-on effects of actively reducing the abundance of a common and highly  
331 invasive species (the European rabbit, *Oryctolagus cuniculus*) on a simulated ecological  
332 network, representative of arid Australia. Our findings reveal that rabbit management can  
333 immediately benefit native biodiversity at removal rates of up to 40% of the total rabbit  
334 population. At removal rates greater than 40%, the positive effects of rabbit management are  
335 delayed, but more pronounced. However, if the active management of rabbits were to stop  
336 abruptly, the positive effect of small to intermediate fractions of rabbit removal (~40%)  
337 would be short-lived, and small mammal populations would benefit more if rabbit control  
338 were applied at higher levels. Our findings highlight the importance of considering  
339 community dynamics and short and long-term pest management goals in wildlife  
340 interventions.

341           The initial decrease in small native mammal abundance in response to large levels of  
342 rabbit removal (> 40% removal) was due to two main factors: (i) increased competition for  
343 resources with kangaroos, and (ii) hyper-predation by mesopredators (foxes and cats) of the  
344 (now more) vulnerable prey. When rabbit abundance was heavily reduced, kangaroos  
345 increased their intake of primary resources (a phenomenon observed in the wild; Cooke,  
346 unpublished data), causing increased competition for vegetation-based resources with small  
347 mammals. At the same time mesopredators remained abundant (at least for a while), and  
348 having less prey available, they were forced to switch diets to small native mammals. This  
349 potential synergism of bottom-up and top-down pressures has the potential to negatively  
350 affect small native mammal abundance when rabbit removal levels are high. After rabbit  
351 control ended (post-control period), effects of this perturbation were still noticeable through  
352 the food web. This was shown by the recovery of small mammal populations that were  
353 depressed by high levels of rabbit removal, and a continued increase in dingo abundance.  
354 These two responses are linked. An increase in the abundance of the apex predator facilitates  
355 increased control of mesopredators (fox and cats), which is ultimately beneficial for small  
356 native mammals (Ritchie & Johnson 2009).

357           These conclusions are somewhat sensitive to the estimates of population growth rate  
358 for small mammals, foxes, and rabbits. While population growth rates for foxes and rabbits in  
359 arid Australia are well established (Hone 1999), estimates for small mammals are less certain,  
360 an issue potentially compounded by having grouped small mammals into a single species.  
361 Our results were only marginally sensitive to assumptions regarding interaction strengths.  
362 This is fortunate because these were the parameters in our model with the greatest level of  
363 uncertainty. Importantly, our findings are in direct agreement with previous on-ground  
364 studies reporting the bounce-back of native small mammals following severe rabbit  
365 population crashes in response to the release of a new biocontrol agent (Pedler *et al.* 2016).

366 Furthermore, the role of the dingo as a top predator, which facilitates the maintenance of  
367 biodiversity in Australian ecosystems, has been shown empirically (Letnic, Ritchie, &  
368 Dickman 2012); and increased predation by cats on alternative prey has been documented as  
369 a consequence of rabbit control (Norbury 2001; Murphy *et al.* 2004).

370 Our results highlight the power of using simulation-based ecological-network models  
371 to assess the potential effects of controlling invasive species on the wider ecological  
372 community. In the context of arid Australia, this is salient because large efforts continue to be  
373 directed towards the eradication of rabbits and other invasive species (Cooke *et al.* 2013); and  
374 new bio-control agents (i.e. more virulent strains of rabbit haemorrhagic disease) are  
375 scheduled for release in the immediate future (Wishart & Cox 2016). We show that frequent  
376 (but not necessarily sustained) large reductions in rabbit abundance are likely to have the  
377 most positive benefit for small native mammals. This is because of the predator-prey  
378 interaction between rabbits and invasive mesopredators (in the presence of dingoes) and  
379 subsequent flow on effects for native mammals.

380 Unexpected detrimental effects of removing invasive species have been observed  
381 empirically in other ecosystems (Ballari, Kuebbing & Nuñez 2016), and the importance of  
382 applying community-wide approaches for managing invasive species has been recognised  
383 (e.g., Bull & Courchamp 2009). For example, a meta-analysis of the effects of lagomorph  
384 introductions across the globe found that their removal from their exotic range should only be  
385 done after considering the whole suite of potential ecosystem responses (Barbar, Hiraldo &  
386 Lambertucci 2016). Doing so requires a wider use of community-based approaches in  
387 invasion biology and management. Our study is one of the first approaches to provide a more  
388 comprehensive, community-wide, understanding of the potential effects of eradicating  
389 invasive species (but see Bode, Baker & Plein 2015; McDonald-Madden *et al.* 2016; Bode *et al.*  
390 2017). It complements previous studies considering community-wide effects of removing

391 species in similar Australian ecosystems (e.g., Dexter *et al.* 2013; Colman *et al.* 2014) by  
392 providing a dynamical modelling approach.

393

### 394 ***Management implications and applications***

395 Rabbits in arid Australia are managed using a ‘press and pulse’ type framework (Bender,  
396 Case & Gilpin 1984), where rabbits are controlled using viral biocontrol agents (*press*) and  
397 episodes of warren ripping and baiting (*pulse*) (Wells *et al.* 2016). Our finding that a  
398 sustained rate of rabbit removal of 40 % provides the greatest benefit to small mammals has  
399 strong implications for the on-ground management of rabbits in their invasive range, because  
400 this *press* mortality rate corresponds closely to disease-induced mortality rates following the  
401 long-term establishment of rabbit haemorrhagic disease and myxomatosis in disease  
402 burdened rabbit populations (Fordham *et al.* 2012); the primary biocontrol agents used to  
403 manage rabbits in arid Australia. Therefore, if the goal of rabbit management in arid Australia  
404 is to provide benefits to small mammal populations (e.g., by facilitating increased population  
405 abundances) then it seems clear that the present management strategy, involving a sustained  
406 press at intermediate levels of mortality, and/or time-limited removals of higher fractions of  
407 the rabbit populations, is appropriate.

408 More broadly, our network-based approach can easily be applied to other systems  
409 where there is sufficient information on the strength of interactions between species  
410 (functional responses), and population-level responses of species to resources (total  
411 responses). For example, our modelling framework could be used to assess the community-  
412 level effects of widespread badger (*Meles meles*) culling to stop the spread of tuberculosis  
413 (Donnelly *et al.* 2006). Badgers are arguably keystone species through their role as ecosystem  
414 engineers, building burrow networks used by other animals. Badger culling would thus  
415 prevent other species, such as, ironically, the European rabbit in its native range, from

416 successfully colonising and maintaining stable populations. The same role is fulfilled by  
417 digging marsupials in Australia, where the potential community-wide consequence of their  
418 loss (Fleming *et al.* 2014) could also be analysed using a network approach like the one  
419 presented here (e.g. Wallach *et al.* 2016).

420         Furthermore, our modelling approach and framework is suited to examining and  
421 predicting the ecological effects of reintroductions (including rewilding), where there is great  
422 uncertainty in ecological outcomes (Nogués-Bravo *et al.* 2016). Instead of simulating species  
423 removal, our simulation-based model could be adapted and used to assess the community-  
424 wide effects of reintroducing top predators (e.g. lynx, dingoes, or wolves) or smaller-bodied,  
425 yet also functionally important species (e.g. western quolls, beavers), into areas of their  
426 historic range where they are no longer found. Food web approaches have been successfully  
427 used to reveal the consequences of ‘invasions’ into complex ecological networks (e.g.,  
428 Galiana *et al.* 2014; Lurgi *et al.* 2014), showing that unexpected outcomes might follow from  
429 the introduction of new nodes/species in the network. Similar surprises are likely to occur  
430 when reintroducing species through rewilding (e.g., Nogués-Bravo *et al.* 2016). Therefore,  
431 our approach could be used to increase understanding and awareness of what the potential  
432 ecological consequences of reintroduction biology and rewilding might be.

433         Among all aspects of invasion biology, biotic interactions between invaders and  
434 native species are of particular importance. Yet the effects of invasive species at the  
435 community level are typically overlooked (Mellin *et al.* 2016), primarily because of a lack of  
436 data on species interactions and growth rates needed to parameterise and run complex  
437 ecological models like our arid-zone rabbit management model. Consequently, far-reaching  
438 and potentially deleterious effects of controlling invasive species continue to be overlooked  
439 in management decisions. Fortunately, the field of ecological modelling is advancing rapidly  
440 in response to increasing computational capabilities, and there is now a push globally for the

441 collection of data that will allow for these state-of-the-art models to be parameterised more  
442 frequently (see for example Urban *et al.* 2016).

443 In addition to exploring opportunities to implement our modelling approach to similar  
444 management questions in other ecological systems, future extensions to this work should  
445 include using our model to further explore the importance (for small mammals) of time-  
446 limited removals of high fractions of the rabbit population, implemented on top of a sustained  
447 lower-level mortality rate (i.e., from biocontrol). Moreover, future research should also focus  
448 on increasing the size of the food web, to include additional species known to be present in  
449 the Australian arid ecosystem; establishing field experiments to better determine the  
450 functional form of the competitive relationship between kangaroos and rabbits, which may  
451 not be linear (Cooke and Mutze, unpublished data); and investigating the responses of this  
452 system to rabbit control in a spatial context, whereby a collection of local model communities  
453 like the one used here are linked together in a regional metacommunity. The latter is  
454 important because, the effective management of rabbit populations has been recently shown  
455 to be highly dependent on the spatial arrangement of local populations (Lurgi *et al.* 2016).

456 Although our model provides a more advanced understanding of the far-reaching  
457 implications of rabbit management in arid Australia, we recognise that the model system  
458 focuses on one possible ecological scenario, with other, perhaps more complex species  
459 interactions, being possible. Importantly, our assumption that the three herbivore species do  
460 not exhibit resource partitioning is unlikely to change our conclusions, since the absence of  
461 the primary prey (rabbits) for mesopredators will still prompt the decline of small mammal  
462 populations. Our treatment of small native mammals as a single species highlights the need to  
463 be view management recommendations emerging from our model cautiously, particularly if  
464 they are being implemented at the species level for native small mammals. Future work that

465 extends our approach to explore more complex ecological communities and different  
466 environmental scenarios is strongly encouraged.

467

#### 468 **Conclusions**

469 The full set of responses a community can display after perturbations in the abundance of a  
470 species can only be understood when considering all possible interactions within the  
471 community. Our model-based framework provides wildlife and pest managers with a better  
472 understanding of the potential effects of species removal and control on intact and modified  
473 ecosystems. We highlight the need to focus management efforts on invasive prey as well as  
474 on invasive predators, and this extends to other systems where ‘dominant’ prey may play  
475 fundamental roles in community structure and ecosystem function.

476

#### 477 **Authors’ contributions**

478 The design of this project was the result of discussions involving all authors. M.L. generated  
479 the modelling framework, ran the simulations and analysed the results. All authors  
480 contributed to the writing of the manuscript. All authors gave final approval for publication.

481

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486 conflicts of interest.

487

#### 488 **Data accessibility**

489 Source code of the model developed for simulations available via the Dryad Digital  
490 Repository <https://doi.org/10.5061/dryad.p1t111n> (Lurgi, Ritchie & Fordham 2018).

491

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645 **Tables**

646 Table 1. Key formulas for the structure of the food web model. See Appendix S1 for a detailed explanation of

647 Table S1 for species-specific parameter values.

Model	Variables
<p><b>Primary productivity</b></p> $\Delta V = -55.12 - 0.0153V - 0.00056V^2 + 2.5Y$	$V$ = Pasture biomass, $Y$
<p><b>Numerical response of herbivores</b></p> $r_{N,t} = -a_N + c_N[1 - \exp(-d_N V_{t-1})] - P_{t-1}$	$N$ = species, $a_N$ = maximum mortality rate, $c_N$ = maximum consumption rate, $d_N$ = mortality rate of herbivores, $V_{t-1}$ = pasture biomass at previous time step, $P_{t-1}$ = predation rate (mesoherbivores) on species $N$ ( $L_{F,t}$ and $M_{D,N,t}$ ) on species $N$
<p><b>Functional response of herbivores</b></p> $B_{t,N} = (w_N^{3/4})v_N[1 - \exp(-V_t/f_N)](X_{t-1})(365/4)$	$w_N$ = herbivore species weight, $v_N$ = maximum consumption rate of herbivores, $f_N$ = foraging efficiency, $X_{t-1}$ = abundance of species $N$ at previous time step
<p><b>Numerical response of foxes and cats</b></p> $r_{N,t} = -a_N + c_N[1 - \exp(-d_N V_{t-1})] - P_{t-1}$	$N$ = species, $a_N$ = maximum mortality rate, $c_N$ = rate at which foxes and cats consume herbivores, $d_N$ = mortality rate of foxes and cats, $V_{t-1}$ = dingo abundance, $P_{t-1}$ = predation rate (mesoherbivores) on species $N$ ( $L_{F,t}$ and $M_{D,N,t}$ ) on species $N$
<p><b>Functional response of foxes to rabbits</b></p> $g_{F,t} = (k/w)R_{t-1}^2/(R_{t-1}^2 + H_{III}^2)$	$k$ = maximum consumption rate of foxes, $w$ = average weight of foxes, $R_{t-1}$ = rabbit abundance, $H_{III}$ = half saturation abundance
<p><b>Functional response of foxes or cats to small native prey and of cats to rabbits</b></p> $l_{F,t} = (k/w)S_{t-1}/(S_{t-1} + H_{II})$	$k$ = maximum consumption rate of foxes or cats, $w$ = average weight of foxes or cats, $S_{t-1}$ = small native prey or rabbit abundance, $H_{II}$ = half saturation abundance

**Total predation rate per rabbit by fox or cat**

$$G_{F,t} = (365/4)(g_{F,t}F_{t-1})/R_{t-1}$$

**Total predation per small mammal by fox or cat**

$$L_{F,t} = (365/4)(l_{F,t}(1 - g_{F,t}/k) F_{t-1})/S_{t-1}$$

**Numerical response of dingoes**

$$r_{D,t} = \begin{cases} -a_D + m_{D,N,t} \times d_D, & -a_D + m_{D,N,t} \times d_D < 0 \\ (-a_D + m_{D,N,t} \times d_D) \left(1 - \frac{D_{t-1}}{K_D}\right), & -a_D + m_{D,N,t} \times d_D \geq 0 \end{cases}$$

**Functional response of dingoes to rabbits or kangaroos**

$$m_{D,N,t} = k_{D,N}[1 - \exp(-X_{t-1}/f_{D,N})]$$

**Total predation per animal by dingo**

$$M_{D,N,t} = (365/4)(m_{D,N,t}D_{t-1})/X_{t-1}$$

saturation term for Type

$g_{F,t}$  = predation rate (function of fox or cat abundance

$l_{F,t}$  = predation rate (function of predation rate (function of consumption rate,  $F$  = abundance

$a_D$  = maximum instantaneous rate of dingo on all prey efficiency,  $D_{t-1}$  = dingo carrying capacity

$k_{D,N}$  = maximum intake  $f_{D,N}$  = foraging efficiency

$m_{D,N,t}$  = predation rate (function of herbivore or mesopredator abundance

649 **Figures captions**

650

651 **Fig. 1. Ways in which the effects of rabbit removal could cascade through an Australian**

652 **arid ecosystem.** Based on previous studies (Read & Bowen 2001; Holden & Mutze 2002;

653 and Pedler *et al.* 2016) we hypothesise possible flow-on effects of rabbit removal on the

654 abundances of other key species in the Australian arid ecosystem. We show potential

655 ecosystem states corresponding to different phases of rabbit control: (i) pre-control, (ii)

656 immediate post-control, (iii) post-control with sustained control, and (iv) post-control when

657 control is not sustained. Symbols +, -, and \* refer to relative abundance of species

658 populations and their change in response to rabbit numbers. In the pre-control ecosystem state

659 classifications of relative abundances are given: S = scarce, A = abundant, VA = very

660 abundant. In the post control scenarios: - = moderate decline, -- = steep decline, + = moderate

661 increase, ++ = steep increase, \* = stable).

662 **Fig. 2: Simplified version of the Australian arid ecosystem food web.** Animal silhouettes  
663 represent species in the food web and arrows between them ecological interactions. These can  
664 be either trophic (as in the case of consumer-resource relationships) or amensalistic (as those  
665 between the dingo and both mesopredators, cat and fox). Each arrow corresponds to an  
666 interaction in the dynamical model (see methods).

667 **Fig. 3. Effects of rabbit removal on small native mammal and mesopredators.** Change in  
668 median abundance (calculated for the last 10 years of the rabbit control period) from the no  
669 rabbit control baseline plotted against the fraction of rabbit removal for three species in the  
670 food web: small mammal, cat and fox. Values below 0 represent smaller abundances  
671 compared to a no rabbit control scenario. Points represent the mean abundance values across  
672 the 5000 replicates. Lines show a local polynomial regression fit to the whole data set (i.e.,  
673 5000 replicates per fraction of rabbit removal). Shaded areas represent 90% confidence  
674 intervals on the simulated data.

675 **Fig. 4. Potential mechanisms driving changes in the abundances of a small native**  
676 **mammal.** Plots show resource use (vegetation biomass intake) by the kangaroo population  
677 **(a)** and the per capita predation rate by cats **(b)** and foxes **(c)** on small mammals (biomass of  
678 small mammals eaten) for different fractions of rabbit removal across 5,000 replicated  
679 simulations for each removal fraction. Solid line inside boxes shows the median. Bottom and  
680 top of boxes are the 25<sup>th</sup> and 75<sup>th</sup> percentiles (i.e., lower and upper quartiles), respectively.  
681 Whiskers above and below boxes show maximum (or +1.5 times the interquartile range,  
682 whatever is smaller), and minimum (or -1.5 times the interquartile range, whatever is larger)  
683 values, respectively. Vegetation biomass intake is measured in kg and per capita predation  
684 rate is the fraction of biomass of prey consumed by an individual predator.

685 **Fig. 5. Effect of rabbit removal on dingo abundance.** Left panel shows the difference in  
686 dingo median abundance (vs. no rabbit control) as a function of rabbit control. Points  
687 represent the mean across 5000 replicates. Lines show the fit of a polynomial regression  
688 model to the data (i.e., 5000 replicates per fraction of rabbit removal). Shaded area depicts  
689 the 90% confidence interval on the simulated data. Box plots in the right panels show  
690 changes in the dietary intake (i.e., the median of the number of individuals of prey eaten by  
691 the predator population) of kangaroo and rabbits by dingoes in response to different levels of  
692 rabbit removal. Solid line inside boxes shows the median. Bottom and top of boxes are the  
693 25<sup>th</sup> and 75<sup>th</sup> percentiles (i.e., lower and upper quartiles), respectively.

694 **Fig. 6. Effect of rabbit removal on small native mammal after rabbit removal period.**  
695 Left panel shows change in small mammal abundance over time, when compared with the  
696 no rabbit removal baseline, following the termination of rabbit control at levels of 10 to 90%  
697 removal. Numbers below 0 represent abundance levels smaller than in the absence of rabbit  
698 control. Lines show a local polynomial regression fit to the whole data set (i.e., 5000  
699 replicates per fraction of rabbit removal). Shaded area depicts the 90% confidence interval of  
700 the fit. Box plots in the right panels show changes in the removal of vegetation biomass by  
701 kangaroo (top) and changes in the per capita predation rate of small native mammal by cat  
702 (bottom), through different levels of rabbit removal. Solid line inside boxes shows the  
703 median. Bottom and top of boxes are the 25<sup>th</sup> and 75<sup>th</sup> percentiles (i.e., lower and upper  
704 quartiles), respectively.

705 **Supporting Information**

706 Additional Supporting Information may be found in the online version of this article:

707

708 **Appendix S1. Food web model specification.**

709 **Table S1. Model parameters and values.**

710 **Appendix S2. Estimation of initial abundance ranges for the species in the model.**

711 **Appendix S3. Source code for the model in R.**

712 **Fig. S1. Effects of rabbit control on kangaroo abundance.**

713 **Fig. S2. Recovery of rabbit populations after the removal period for different levels of**  
714 **rabbit control.**

715 **Fig. S3. Model sensitivity to parameter values.**

716