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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

Introduction

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^2), 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 Chequenot & 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 ~80 km^2 =

222   8000 ha (see Appendix S2 for further details). Thus, the spatial scale of this model was ~80

223   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, …, 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

390   al. 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

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 o

647 Table S1 for species-specific parameter values.

Model	Variables
Primary productivity $$\Delta V = -55.12 - 0.0153V - 0.00056V^2 + 2.5Y$$	V = Pasture biomass, Y
Numerical response of herbivores $$r_{N,t} = -a_N + c_N[1 - \exp(-d_N V_{t-1})] - P_{t-1}$$	N = species, a_N = maxi which a_N is ameliorated biomass at previous tim $L_{F,t}$ and $M_{D,N,t}$) on speci
Functional response of herbivores $$B_{t,N} = \left(w_N^{3/4}\right)v_N[1 - \exp(-V_t/f_N)](X_{t-1})(365/4)$$	w_N = herbivore species consumption rate of her = foraging efficiency, X
Numerical response of foxes and cats $$r_{N,t} = -a_N + c_N[1 - \exp(-d_N V_{t-1})] - P_{t-1}$$	N = species, a_N = maxi predation, c_N = rate at v efficiency, V_{t-1} = dingo killed by dingoes (meso
Functional response of foxes to rabbits $$g_{F,t} = (k/w)R_{t-1}^2/(R_{t-1}^2 + H_{III}^2)$$	k = maximum consump abundance, H_{III} = half s
Functional response of foxes or cats to small native prey and of cats to rabbits $$l_{F,t} = (k/w)S_{t-1}/(S_{t-1} + H_{II})$$	k = maximum consump average weight, S = sm

saturation term for Typ

Total predation rate per rabbit by fox or cat

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

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

Total predation per small mammal by fox or cat

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

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

Numerical response of dingoes

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

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

Functional response of dingoes to rabbits or kangaroos

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

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

Total predation per animal by dingo

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

$m_{D,N,t}$ = predation rate (
= herbivore or mesopre

648

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 25th and 75th 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 25th and 75th 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 25th and 75th 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.**

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