

Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: The importance of multispecies interactions

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Abstract

1. Abundant and widely distributed invasive prey can negatively affect co-occurring native species by competing for food and/or shelter, removing vegetation cover and reducing habitat complexity (changing predation risk), and by sustaining elevated abundances of invasive mesopredators. However, information regarding the community and trophic consequences of controlling invasive prey and their temporal dynamics remain poorly understood.
2. We used multispecies ecological network models to simulate the consequences of changing European rabbit *Oryctolagus cuniculus* abundance in an arid mammalian community. We quantified how changes in the dominant prey (rabbits) affected multiple trophic levels, examining changes in predator-prey interactions through time and how they affected native prey persistence.
3. Our results suggest that removal of rabbits can benefit native biodiversity immediately at removal rates between 30% and 40%. However, beyond these levels, densities of small native mammals will decline in the short term. The processes underpinning these declines are: (a) increased competition for resources (vegetation) with kangaroos *Macropus* spp., whose numbers increase due to their release from competition with rabbits and (b) increased predation (prey switching) by feral cats *Felis catus*. Both effects are mediated by dingoes *Canis dingo*, a native apex predator.
4. Importantly, native mammal abundance recovers after a time delay, which is prolonged when high rates of rabbit control are applied. This is likely due to a reduction in hyperpredation by invasive feral cats and red foxes *Vulpes vulpes* following rabbit removal.
5. Continued eradication of rabbits in arid Australia will benefit native species due to a decrease in apparent competition for resources and by alleviating hyperpredation from invasive mesopredators. Furthermore, ecosystem-level conservation benefits of reducing invasive prey abundance are as important as direct control of invasive mesopredators.
6. *Synthesis and applications.* Multispecies ecological network models provide wildlife managers with tools to better understand and predict the complex effects of species removal and control on both intact and modified ecosystems. Our results

show that management of the Australian arid zone can benefit from controlling invasive prey as well as invasive predators. However, invasive species control can cause unexpected outcomes on native biodiversity. This extends to other systems where dominant prey may play fundamental roles in ecosystem structure and function.

KEYWORDS

apex predator, biological invasions, community dynamics, ecological networks, hyperpredation, prey switching, species removal, trophic cascade

1 | INTRODUCTION

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

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

There is increasing recognition that multispecies, community-level approaches are needed to manage invasive species (Baker, Gordon, & Bode, 2016; Bode, Baker, & Plein, 2015). This is because the reduction or eradication of populations of invasive species can often lead to unexpected flow-on consequences for community structure and ecosystem processes if species interactions are not understood and accounted for by managers (Ballari et al., 2016). Perturbing ecosystems through invasive species control can lead to a variety of outcomes and might result in temporary and/or long-term changes to ecosystem states. Local populations of native species can recover rapidly if the invasive species causing the largest threat to population persistence is correctly identified and controlled sufficiently. However, if control efforts are insufficient to effectively depress the abundance of the invasive species, then populations of native species and degraded ecosystems may not recover or they may revert to their former (eroded) states quickly. During such phases of nonequilibrium dynamics, it is plausible that further damage may compound impacts on native biodiversity and ecosystems (Ballari et al., 2016; Courchamp et al., 2003). Effective control (severe population reduction or eradication) of invasive species can also restructure food webs leading to the loss (or near loss)

of endemic species through prey switching (Gibson, 2006; Norbury, 2001) and unforeseen negative effects of hyperpredation (an additional predation pressure that arises when the abundance of a predator is enhanced by the presence of another species of prey) on the abundance of native biodiversity (Courchamp, Langlais, & Sugihara, 2000).

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

Mainland Australia and its mammal communities provide ideal and tractable systems for examining the potential consequences of perturbing ecological networks, consisting of both invasive and native predators and prey. Across much of Australia's arid biome (c. 70% of Australia or 7.5 million km²), key species in the ecological network include invasive mesopredators (feral cats *Felis catus*, and red foxes *Vulpes vulpes*) and invasive small mammals (European rabbits *Oryctolagus cuniculus*), native large herbivores (kangaroos *Macropus* and *Osphranter* spp.), a native apex predator (dingoes *Canis dingo*) and typically more restricted and threatened small native mammals (e.g., bilbies *Macrotis lagotis*) (Wallach et al., 2017). In this ecosystem, rabbits are a "dominant prey" and integral to the functioning of the ecological network. Rabbits (a) compete directly with small-sized native mammals and native herbivores for food and/or shelter; (b) remove vegetation, reduce habitat complexity and change predation risk for native prey species; and (c) sustain and potentially increase invasive mesopredator abundance (Johnson, 2006).

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

top-down effects on ecosystem processes (e.g., Colman, Gordon, Crowther, & Letnic, 2014; Dexter, Hudson, James, MacGregor, & Lindenmayer, 2013).

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

Our results and simulation-based tool provide wildlife and pest managers with a better understanding of how ecological communities might respond to targeted rabbit management. The approach can be extended to other systems in order to examine predator-prey

Phases of rabbit control	Ecosystem state						
Pre-control							
	S	S	VA	VA	VA	S	A
Immediate post-control							
	+	--	--	-	-	+	+
Post-control (sustained control)							
	++	++	-	-	-	++	+
Post-control (unsustained control)							
	-	-	+	+	+	-	*

FIGURE 1 Ways in which the effects of rabbit removal could cascade through an Australian arid ecosystem. Based on previous studies (Holden & Mutze, 2002; Pedler et al., 2016; and Read & Bowen, 2001), we hypothesise possible flow-on effects of rabbit removal on the abundances of other key species in the Australian arid ecosystem. We show potential ecosystem states corresponding to different phases of rabbit control: (i) precontrol; (ii) immediate postcontrol; (iii) postcontrol with sustained control; and (iv) postcontrol when control is not sustained. Symbols +, -, and * refer to relative abundance of species populations and their change in response to rabbit numbers. In the precontrol ecosystem, state classifications of relative abundances are given: S = scarce, A = abundant, VA = very abundant. In the postcontrol scenarios: - = moderate decline, -- = steep decline, + = moderate increase, ++ = steep increase, * = stable)

interactions and make a priori predictions about the ecological consequences of management interventions, including pest control and species reintroductions.

2 | MATERIALS AND METHODS

We developed a model based on discrete time difference equations and simulated the dynamics of trophic interactions in an arid ecosystem in Australia, consisting of six different species plus a basal (vegetation) resource (Figure 2). The species modelled in this simplified, but ecologically realistic, food web were European rabbits *O. cuniculus*; bilby *M. lagotis*—a native critical weight range “small” mammal; kangaroos *Macropus* and *Osphranter* spp.; European fox *V. vulpes*; feral cat *F. catus*; and dingo *C. dingo*. We used this dynamic food web model to establish whether decreasing the abundance of rabbits is likely to reduce mesopredator populations and predation to levels that would support recovery of native mammals.

We did not try and capture every species in the ecological network in the model because doing so would make the model computationally unwieldy, providing results that would be difficult to duplicate and interpret (Drossel & McKane, 2002). Instead, using published research and expert knowledge, we endeavoured to capture the primary species interactions and ecological consequences that are likely to be affected by rabbit management. We were unable to account for potential prey switching by cats and foxes from rabbits to reptiles and invertebrates, due to a lack of empirical data. Likewise, the diet of dingoes is known to be broad, varying in different ecosystems, sometimes including mammalian prey in the critical weight range of 35–5,500 g. However, on average, dingoes typically consume orders of magnitudes fewer critical weight range mammals

than do invasive mesopredators (e.g., Davis et al., 2015). Thus, to simulate the main interactions and community structure in the arid Australian ecosystem, the potential (but negligible) trophic interaction between the dingo and small native mammal prey was not incorporated into the model, preventing any potential prey switching to small native mammals by dingoes. In favour of simplicity (e.g., Robley, Reddiex, Arthur, Pech, & Forsyth, 2004), and a lack of empirical data suggesting otherwise, we assumed that the three herbivore species in the network are competing for the same resource without resource partitioning. Furthermore, we assumed that mesopredators rely solely on rabbits and small mammals for food; however, there might be other prey items that could maintain their abundances.

2.1 | Food web structure

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

2.2 | Model simulations

Our food web model extended the discrete-time difference equations of Pech and Hood (1998), Robley et al. (2004), Pople et al. (2010), and Choquenot and Forsyth (2013) to consider a larger number of species and interactions (Table 1 and Appendix S1). Model validation was done by comparing the outcomes of the population dynamics of the species in the community with the results published for the different parts of the model in isolation (Choquenot & Forsyth, 2013; Pech & Hood, 1998). Since information on the population dynamics of cats was not available (Robley et al., 2004), their dynamics were considered to be similar to that of the fox. To simulate the community-wide effects of rabbit removal, rabbit abundance was reduced across a range of removal fractions (i.e., the fraction of the population of rabbits that was removed from the community), which spanned from 0.1 to 0.9 at an interval of 0.1. We did not simulate complete rabbit removal as it is a very unlikely scenario in the study system. Initial abundances for all species were sampled using Latin hypercube sampling, implemented using the *lhs* package in R (R Development Core Team 2013). This approach generates a stratified random subset of parameter input values for simulation, by assigning a plausible range for each variable and sampling all portions of its distribution (Norton, 2015). We generated 5,000 independent initial abundance configurations, which we used as independent initial

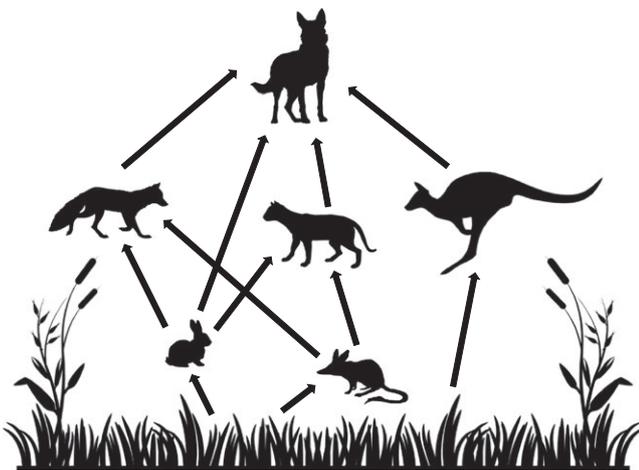


FIGURE 2 Simplified version of the Australian arid ecosystem food web. Animal silhouettes represent species in the food web and arrows between them ecological interactions. These can be either trophic (as in the case of consumer–resource relationships) or amensalistic (as those between the dingo and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

TABLE 1 Key formulas for the structure of the food web model. See Appendix S1 for a detailed explanation of model equations and variables and 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 = rainfall over previous quarter
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 = maximum instantaneous rate of decline, c_N = rate at which a_N is ameliorated, d_N = demographic efficiency, V_{t-1} = pasture biomass at previous time step, P_{t-1} = total predation per quarter ($G_{F,t}$, $L_{F,t}$ and $M_{D,N,t}$) on species N during the previous time step
Functional response of herbivores $B_{t,N} = \left(\frac{w_N^{3/4}}{v_N}\right) v_N [1 - \exp(-V_t/f_N)] (X_{t-1}) (365/4)$	w_N = herbivore species N average weight, v_N = maximum consumption rate of herbivore N , V_t = pasture biomass at quarter t , f_N = foraging efficiency, X = herbivore species abundance
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 = maximum instantaneous rate of decline without predation, c_N = rate at which a_N is ameliorated, d_N = demographic efficiency, V_{t-1} = dingo prey biomass (mesopredators), P_{t-1} = fraction killed by dingoes (mesopredators)
Functional response of foxes to rabbits $g_{F,t} = (k/w) R_{t-1}^2 / (R_{t-1}^2 + H_{III}^2)$	k = maximum consumption rate, w = rabbit average weight, R = rabbit abundance, H_{III} = half saturation term for Type III functional response
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 consumption rate, w = small native prey or rabbit average weight, S = small native prey or rabbit abundance, H_{II} = half saturation term for Type II functional response
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 (functional response), R = rabbit abundance, F = 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 (functional response) on small native prey, $g_{F,t}$ = predation rate (functional response) on rabbits, k = maximum consumption rate, F = fox or cat abundance, S = small native prey abundance
Numerical response of dingoes $r_{D,t} = \begin{cases} -a_D + m_{D,N,t} \times d_D, & -a_D + m_{D,N,t} \times d_D < 0 \\ (-a_D + m_{D,N,t} \times d_D) \left(1 - \frac{D_{t-1}}{K_D}\right), & -a_D + m_{D,N,t} \times d_D \geq 0 \end{cases}$	a_D = maximum instantaneous rate of decline, $m_{D,N,t}$ = total predation rate of dingo on all prey items in current time step, d_D = demographic efficiency, D_{t-1} = dingo abundance in previous time step, K_D = 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 rate of prey N , X = prey species abundance, $f_{D,N}$ = foraging efficiency on prey N
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 (functional response), D = dingo abundance, X = herbivore or mesopredator abundance

states for model simulations. Ranges for initial abundances used in the hypercube sampling were based on minimum and maximum abundances observed in the wild for a spatial extent equivalent to the home range of a pack of dingoes, which is c. 80 km² = 8,000 ha (see Appendix S2 for further details). Thus, the spatial scale of this model was c. 80 km².

Simulations were run for 250 years (1,000 time steps). Initial transient dynamics were allowed to occur for 150 years (600 time steps), closely resembling the amount of time rabbits have been in Australia prior to the deliberate introduction of myxoma virus in the 1950s as a biocontrol measure, which negatively perturbed rabbit numbers (Cooke, Chudleigh, Simpson, & Saunders, 2013). During the following 50 years (200 time steps), a perturbation was applied to the system by consistently removing (i.e., during each time step) a fraction of the rabbit population according to the different levels of removal/perturbation specified above ([0.1, 0.2, 0.3, ..., 0.9]). For the last 50 years (last 200 time steps) of each simulation, we ceased rabbit control, and populations were allowed to recover from the perturbation. This simulates a press perturbation that lasts for a relatively long time, after which the system is allowed to recover (Schmitz, 1997), allowing the ecosystem-level benefits of rabbit

management to be directly explored. This experimental design was replicated 5,000 times (each time using one of the 5,000 initial states of abundance) for the nine different values of rabbit control, yielding a total of 45,000 simulations. Initial conditions for abundance (sampled from the latin hypercube) were the same across the nine values of rabbit control but varied across the 5,000 replicates for each treatment. The food web model was developed in R (R Development Core Team, 2013) programming language (see Appendix S3). Model parameter values, including their sources, are provided in Table S1.

To look at the long-term effects of rabbit removal on our modelled Australian arid ecological community, we: (a) calculated the median abundance of each species during the last 10 years of rabbit control and (b) the average abundances of species post-rabbit control using a 5-year sliding window. We did not use a 10-year sliding window because it would exclude the first and last 10 years of post-control data. We quantified the realised strength of each interaction in the food web during each of the three periods (50 years prior to control, during control, after control) in order to determine the mechanisms underpinning the responses of the community to rabbit removal. Interaction strengths were quantified for model iterations by calculating their median values across each time period. We used

these estimates as a measure of the effect of each species on each of its resource items in the food web. Interaction strength can be quantified in two ways in our model: (a) as the per capita predation rate of a predator on its prey and (b) as the total amount of biomass going from one species (node in the network) to another. The first measure provides information on the strength of the effect of an individual predator on its prey population, while the second measure provides an estimate of the quantity of resource intake by the whole predator population. Thus, the model outputs quantify interaction strengths between animal species as the total per capita predation rate (Table 1); and between herbivores and pasture as the functional response of herbivores (Table 1), that is, the total amount of pasture biomass for a given herbivore species.

2.3 | Statistical analyses

We used polynomial regression to determine changes in median abundances of the species in the food web to rabbit control. To quantify the changes in the interaction strengths between species in response to rabbit control, we divided the rabbit control treatments into three categories: (a) 10%–40%, (b) >40%–70%, and (c) >70% of rabbit removal. We then analysed differences in the ranges of interaction strengths across these three levels of rabbit control.

We used a global sensitivity analysis to identify which parameters had the strongest influence on the median abundance of small native mammals (Wells et al., 2016). We established plausible ranges for each parameter in Table S1 ($\pm 10\%$ of the estimated value) and used Latin hypercube sampling in R (*lhs* package) to generate 10,000 evenly distributed samples across the parameter space. As little is known about the interaction strengths between the apex predator and the mesopredators, we used wider uncertainty bounds ($\pm 50\%$ of the estimated value) for the relevant parameters concerning these interactions in the sensitivity analysis (i.e., $k_{D,F}$ and $k_{D,C}$ in Table S1).

We recorded the median abundance of the small native mammal species over a 20-year period (without rabbit control), following a burn-in period. We used boosted regression trees to estimate the relative importance of key parameters on the median abundance of the small native mammal species (learning rate = 0.0001, tree complexity = 5, bag fraction = 0.5, and k-fold cross-validation procedure), using the *gbm.step* function from the *dismo* package in R.

3 | RESULTS

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

The two main interacting processes behind the decrease in small mammal abundance were (a) increased apparent competition for resources (vegetation) with kangaroos (as evident by a marked increase in kangaroo abundance across fractions of rabbit control; Figure S1) and (b) increased per capita predation by cats (Figure 4). The response was particularly strong for increased apparent competition; however, increased predation by cats (i.e., top-down control) had an important influence when rabbit removal was $\geq 40\%$ (Figure 4b). Predation by foxes on small native mammals was not affected by rabbit removal (Figure 4c). The different functional responses of fox and cats on rabbits are likely behind these differential changes in predation on small native mammals by mesopredators.

The removal of rabbits was beneficial for dingoes. A steep increase in dingo median abundance was observed for rabbit removal

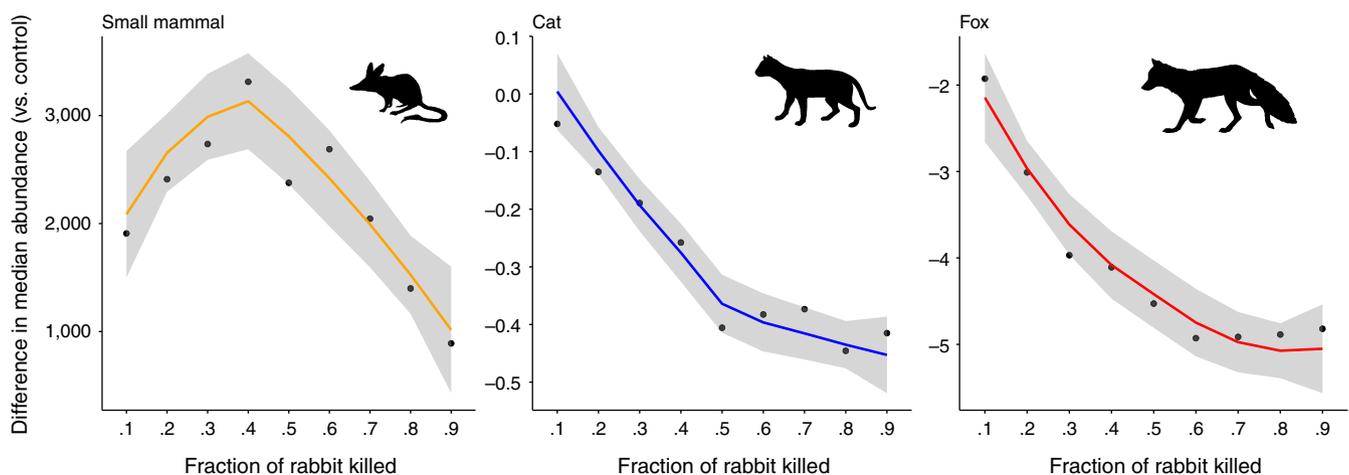


FIGURE 3 Effects of rabbit removal on small native mammal and mesopredators. Change in median abundance (calculated for the last 10 years of the rabbit control period) from the no rabbit control baseline plotted against the fraction of rabbit removal for three species in the food web: small mammal, cat, and fox. Values below 0 represent smaller abundances compared to a no rabbit control scenario. Points represent the mean abundance values across the 5,000 replicates. Lines show a local polynomial regression fit to the whole dataset (i.e., 5,000 replicates per fraction of rabbit removal). Shaded areas represent 90% confidence intervals on the simulated data

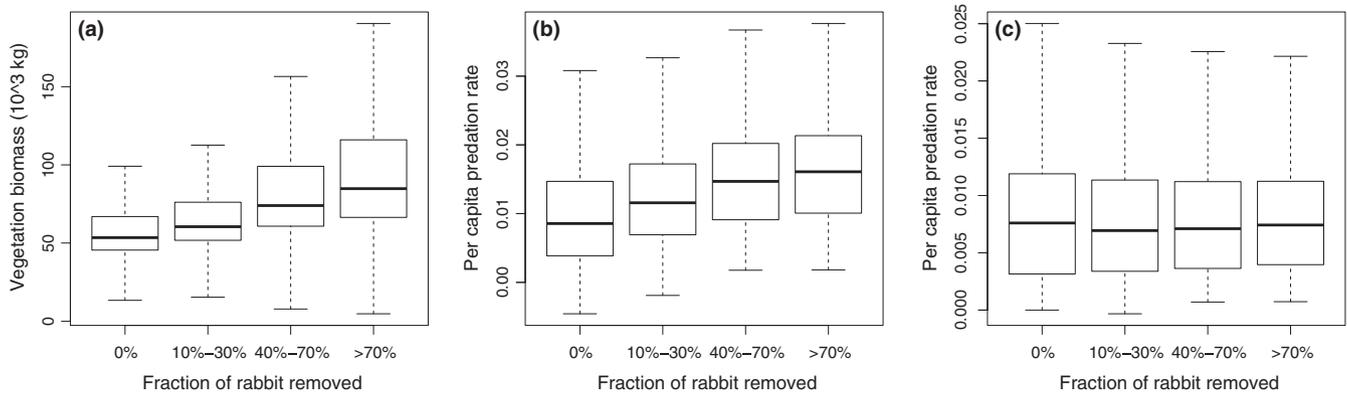


FIGURE 4 Potential mechanisms driving changes in the abundances of a small native mammal. Plots show resource use (vegetation biomass intake) by the kangaroo population (a) and the per capita predation rate by cats (b) and foxes (c) on small mammals (biomass of small mammals eaten) for different fractions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

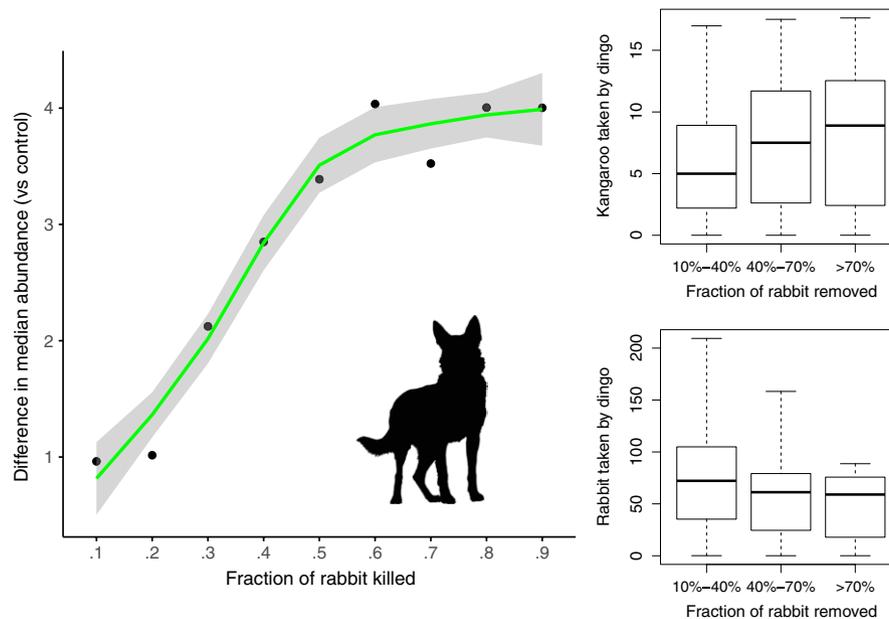


FIGURE 5 Effect of rabbit removal on dingo abundance. Left panel shows the difference in dingo median abundance (vs. no rabbit control) as a function of rabbit control. Points represent the mean across 5,000 replicates. Lines show the fit of a polynomial regression model to the data (i.e., 5,000 replicates per fraction of rabbit removal). Shaded area depicts the 90% confidence interval on the simulated data. Box plots in the right panels show changes in the dietary intake (i.e., the median of the number of individuals of prey eaten by the predator population) of kangaroo and rabbits by dingoes in response to different levels of rabbit removal. Solid line inside boxes shows the median. Bottom and top of boxes are the 25th and 75th percentiles (i.e., lower and upper quartiles), respectively

fractions between 10% and 50%, after which it began to plateau (Figure 5). Dingo abundance was primarily driven by the availability of its main prey, kangaroos. The fraction of kangaroos eaten per day (top right panel in Figure 5) increased with small intermediate fractions of rabbit removal. An increase in kangaroo intake was accompanied by less frequent large rabbit intake rates (bottom right panel in Figure 5). Increases in dingo abundance were, in turn, followed by decreases in mesopredator abundances (which are killed by dingoes).

Figure 3 shows that fox and cat abundances decreased as the fraction of rabbits removed increased.

When rabbit removal ceased, the abundance of small native mammals went through three distinct temporal phases of change: abundance initially declined, then increased steeply, then resumed its decline (Figure 6). The magnitude of these changes differed across fractions of rabbit control, with larger fractions of rabbit removal (0.7 and 0.9), being the most beneficial for small mammal

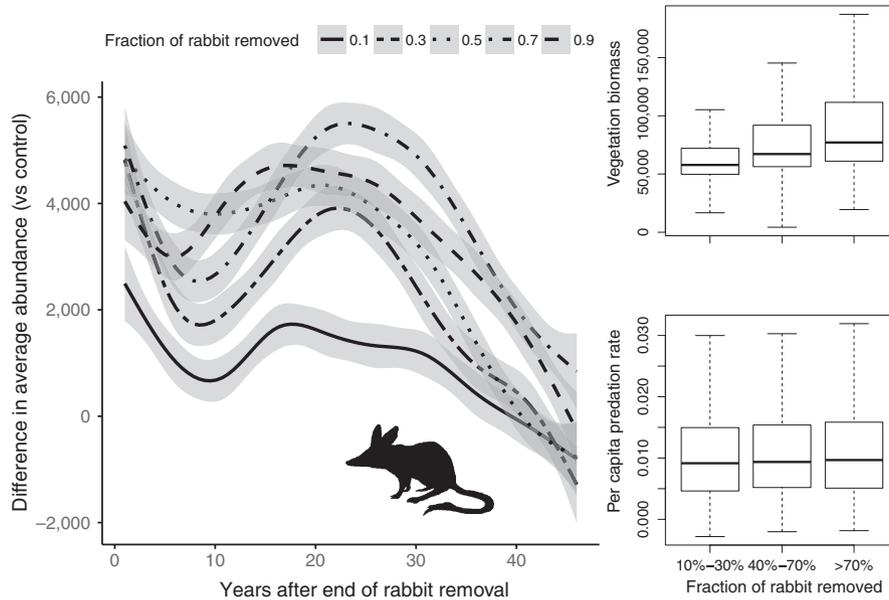


FIGURE 6 Effect of rabbit removal on small native mammal after rabbit removal period. Left panel shows change in small mammal abundance over time, when compared with the no rabbit removal baseline, following the termination of rabbit control at levels of 10%–90% removal. Numbers below 0 represent abundance levels smaller than in the absence of rabbit control. Lines show a local polynomial regression fit to the whole dataset (i.e., 5,000 replicates per fraction of rabbit removal). Shaded area depicts the 90% confidence interval of the fit. Box plots in the right panels show changes in the removal of vegetation biomass by kangaroo (top) and changes in the per capita predation rate of small native mammal by cat (bottom), through different levels of rabbit removal. Solid line inside boxes shows the median. Bottom and top of boxes are the 25th and 75th percentiles (i.e., lower and upper quartiles), respectively

abundance in the medium to long term if rabbit control were to end suddenly. Interestingly, 40 years after rabbit removal ended, small mammal numbers dropped below abundance levels when rabbit removal ceased, suggesting that the renewed availability of staple prey (rabbits) for mesopredators (Figure S2) has the potential to have a long-standing negative impact on small mammal populations (Figure 6). Top-down and bottom-up effects were both important in regulating small mammal abundance post rabbit removal. Vegetation biomass removed by kangaroos was highest for high fractions of rabbit removal (Figure 6, top right panel), suggesting that resource competition between kangaroos and small mammals intensifies with increased numbers of rabbits removed (since both use vegetation as their primary resource). Conversely, predation by cats on small mammals remained the same for small to large fractions of rabbit removal (Figure 6, bottom right panel).

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

4 | DISCUSSION

Invasive species threaten biodiversity worldwide. Understanding the ecological role of invasive species in the communities in which they become established is important for identifying their potential threats to biodiversity, and the community-level effects that are likely to occur following their active management (e.g., Bergstrom

et al., 2009). We show possible flow-on effects of actively reducing the abundance of a common and highly invasive species (the European rabbit *O. cuniculus*) on a simulated ecological network, representative of arid Australia. Our findings reveal that rabbit management can immediately benefit native biodiversity at removal rates of up to 40% of the total rabbit population. At removal rates greater than 40%, the positive effects of rabbit management are delayed, but more pronounced. However, if the active management of rabbits were to stop abruptly, the positive effect of small to intermediate fractions of rabbit removal (~40%) would be short-lived, and small mammal populations would benefit more if rabbit control were applied at higher levels. Our findings highlight the importance of considering community dynamics and short- and long-term pest management goals in wildlife interventions.

The initial decrease in small native mammal abundance in response to large levels of rabbit removal (>40% removal) was due to two main factors: (a) increased competition for resources with kangaroos and (b) hyperpredation by mesopredators (foxes and cats) of the (now more) vulnerable prey. When rabbit abundance was heavily reduced, kangaroos increased their intake of primary resources (a phenomenon observed in the wild; Cooke, unpublished data), causing increased competition for vegetation-based resources with small mammals. At the same time, mesopredators remained abundant (at least for a while), and having less prey available, they were forced to switch diets to small native mammals. This potential synergism of bottom-up and top-down pressures has the potential to negatively affect small native mammal abundance when rabbit removal levels are high. After rabbit control ended (postcontrol period), effects of

this perturbation were still noticeable through the food web. This was shown by the recovery of small mammal populations that were depressed by high levels of rabbit removal and a continued increase in dingo abundance. These two responses are linked. An increase in the abundance of the apex predator facilitates increased control of mesopredators (fox and cats), which is ultimately beneficial for small native mammals (Ritchie & Johnson, 2009).

These conclusions are somewhat sensitive to the estimates of population growth rate for small mammals, foxes, and rabbits. While population growth rates for foxes and rabbits in arid Australia are well established (Hone, 1999), estimates for small mammals are less certain, an issue potentially compounded by having grouped small mammals into a single species. Our results were only marginally sensitive to assumptions regarding interaction strengths. This is fortunate because these were the parameters in our model with the greatest level of uncertainty. Importantly, our findings are in direct agreement with previous on-ground studies reporting the bounce back of native small mammals following severe rabbit population crashes in response to the release of a new biocontrol agent (Pedler et al., 2016). Furthermore, the role of the dingo as a top predator, which facilitates the maintenance of biodiversity in Australian ecosystems, has been shown empirically (Letnic, Ritchie, & Dickman, 2012); and increased predation by cats on alternative prey has been documented as a consequence of rabbit control (Murphy, Keedwell, Brown, & Westbrooke, 2004; Norbury, 2001).

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

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

Australian ecosystems (e.g., Colman et al., 2014; Dexter et al., 2013) by providing a dynamical modelling approach.

4.1 | Management implications and applications

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

More broadly, our network-based approach can easily be applied to other systems where there is sufficient information on the strength of interactions between species (functional responses), and population-level responses of species to resources (total responses). For example, our modelling framework could be used to assess the community-level effects of widespread badger *Meles meles* culling to stop the spread of tuberculosis (Donnelly et al., 2006). Badgers are arguably keystone species through their role as ecosystem engineers, building burrow networks used by other animals. Badger culling would thus prevent other species, such as, ironically, the European rabbit in its native range, from successfully colonising and maintaining stable populations. The same role is fulfilled by digging marsupials in Australia, where the potential community-wide consequence of their loss (Fleming et al., 2014) could also be analysed using a network approach like the one presented here (e.g., Wallach et al., 2017).

Furthermore, our modelling approach and framework are suited to examining and predicting the ecological effects of reintroductions (including rewilding), where there is great uncertainty in ecological outcomes (Nogués-Bravo, Simberloff, Rahbek, & Sanders, 2016). Instead of simulating species removal, our simulation-based model could be adapted and used to assess the community-wide effects of reintroducing top predators (e.g., lynx, dingoes, or wolves) or smaller bodied, yet also functionally important species (e.g., western quolls, beavers), into areas of their historic range where they are no longer found. Food web approaches have been successfully used to reveal the consequences of “invasions” into complex ecological networks (e.g., Galiana, Lurgi, Montoya, & López, 2014; Lurgi, Galiana, López, Joppa, & Montoya, 2014), showing that unexpected outcomes might follow from the introduction of new nodes/species in the network. Similar surprises are likely to occur when reintroducing species

through rewilding (e.g., Nogués-Bravo et al., 2016). Therefore, our approach could be used to increase understanding and awareness of what the potential ecological consequences of reintroduction biology and rewilding might be.

Among all aspects of invasion biology, biotic interactions between invaders and native species are of particular importance. Yet, the effects of invasive species at the community level are typically overlooked (Mellin et al., 2016), primarily because of a lack of data on species interactions and growth rates needed to parameterise and run complex ecological models like our arid-zone rabbit management model. Consequently, far-reaching and potentially deleterious effects of controlling invasive species continue to be overlooked in management decisions. Fortunately, the field of ecological modelling is advancing rapidly in response to increasing computational capabilities, and there is now a push globally for the collection of data that will allow for these state-of-the-art models to be parameterised more frequently (see for example Urban et al., 2016).

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

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

5 | CONCLUSIONS

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

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AUTHORS' CONTRIBUTIONS

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

DATA ACCESSIBILITY

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

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SUPPORTING INFORMATION

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