RESEARCH ARTICLE

Evaluating the effects of landscape structure on the recovery of an invasive vertebrate after population control

Pablo García-Díaz ⬤ · **Dean P. Anderson** · **Miguel Lurgi** ⬤

Abstract

Context Effective landscape control of invasive species is context-dependent due to the interplay between the landscape structure, local population dynamics, and metapopulation processes. We use a modelling approach incorporating these three elements to explore the drivers of recovery of populations of invasive species after control.

Objectives We aim to improve our understanding of the factors influencing the landscape-level control of invasive species.

Methods We focus on the case study of invasive brushtail possum (*Trichosurus vulpecula*) control in New Zealand. We assess how 13 covariates describing the landscape, patch, and population features influence the time of population recovery to a management density threshold of two possums/ha. We demonstrate the effects of those covariates on population recovery under three scenarios of population growth: logistic growth, strong Allee effects, and weak Allee effects.

Results Recovery times were rapid regardless of the simulated population dynamics (average recovery time < 2 years), although populations experiencing Allee effects took longer to recover than those growing logistically. Our results indicate that habitat availability and patch area play a key role in reducing times to recovery after control, and this relationship is consistent across the three simulated scenarios.

Conclusions The control of invasive possum populations in patchy landscapes would benefit from a patch-level management approach (considering each patch as an independent management unit), whereas simple landscapes would be better controlled by taking a landscape-level view (the landscape as the management unit). Future research should test the predictions of our models with empirical data to refine control operations.

Keywords Allee effects · Brushtail possum · Habitat availability · Landscape and patch metrics · New Zealand

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Introduction

Invasive alien species, the subset of alien species that spread and successfully establish populations throughout a recipient landscape, are a major contributor to the current biodiversity crisis (Bellard et al. 2016). Despite the promise shown by novel techniques such as gene-editing (Piaggio et al. 2017) for eradicating invasive species, long-term control for maintaining population densities below a certain threshold remains the main strategy to manage the impacts of invasive species over large landscapes (With 2002; Lurgi et al. 2016; Braysher 2017). Control is justified by empirical density-impact curves, which describe the relationship between the invasive species density and the damage caused (Yokomizo et al. 2009; Ricciardi et al. 2013; Norbury et al. 2015). Population suppression, based on density-impact curves to define target thresholds, is currently considered the best practice in invasive species management at landscape levels whenever eradication is deemed unfeasible (Bomford and O'Brien 1995; Braysher 2017; Kopf et al. 2017).

The control of invasive species across whole landscapes is highly desirable to mitigate their impacts, but it can be plagued with severe operational and strategic complexities and trade-offs (Kopf et al. 2017). Effective landscape control of invasive species is complicated by a myriad of factors, including landscape structure, potential metapopulation dynamics, landholder collaboration, Allee effects, and the ecology of the target species itself (Hanski and Gaggiotti 2004; Taylor and Hastings 2005; Baker 2017; Glen et al. 2017; Wilkins et al. 2018). In turn, this means that effective control strategies are highly context-dependent, and may require a reasonable level of knowledge about both the target invasive species and the landscape to be able to achieve goals and obtain benefits. Furthermore, control must be conducted in perpetuity to maintain benefits, lest the invasive population will recover and produce impacts again. Consequently, it is crucial to identify the minimum period between control operations required to meet the management objectives and make long-term landscape-level control feasible. Controlling the invasive species too frequently will waste valuable resources, whereas infrequent control operations will not achieve the management objectives.

Under the circumstances surrounding the management of invasive species, characterised by severe uncertainties, a realistic quantitative model grounded on ecological theory can help identify major knowledge gaps and features of the landscape and population dynamics that are essential for designing effective and targeted control strategies (Lurgi et al. 2016; Anderson et al. 2017; Dietze 2017; Dietze et al. 2018). Alternately, when framed in an adaptive management context, lessons from such realistic models can provide a solid basis to commence operations even in the absence of detailed data on the landscape and populations within the area to be managed (Conroy and Peterson 2013; Salafsky et al. 2016; Holden and Ellner 2016; Dietze et al. 2018). Here, we developed a quantitative simulation model to investigate how population and metapopulation dynamics of an invasive species respond to population reduction in large landscapes.

We focussed on the management of invasive brushtail possums (*Trichosurus vulpecula*; possum hereafter) populations in New Zealand as a case study. We addressed how the time of possum recovery to a specified density threshold following control was influenced by the compounded effects of landscape and patch features, population growth and dispersal rates, and Allee effects (Fig. 1 and Table 1). Possums were brought from Australia and deliberately released from the 1830s until the 1920s to establish a fur trade industry in New Zealand, and by the end of the 20th century they had spread and colonised most of the country (Montague 2000; Cowan 2001; Long 2003). Invasive possums cause substantial negative ecological impacts on the native fauna and flora of New Zealand, via depredation and intensive browsing, and are the main wild reservoir of bovine tuberculosis, which severely affects livestock health (Office of the Parliamentary Commissioner for the Environment 1994; Montague 2000; Cowan 2001; Nugent et al. 2001, 2015; Norbury et al. 2015; Byrom et al. 2016). Consequently, invasive possum populations are the subject of extensive management campaigns to reduce their densities to near zero, with the over-arching aim of minimising their impacts on native species and hamper their role as bovine tuberculosis vectors (Montague 2000; Russell et al. 2015; Anderson et al. 2015; Livingstone et al. 2015; Byrom et al. 2016; Gormley et al. 2016; Forsyth et al. 2018). Not surprisingly, the possum ecology in the country is
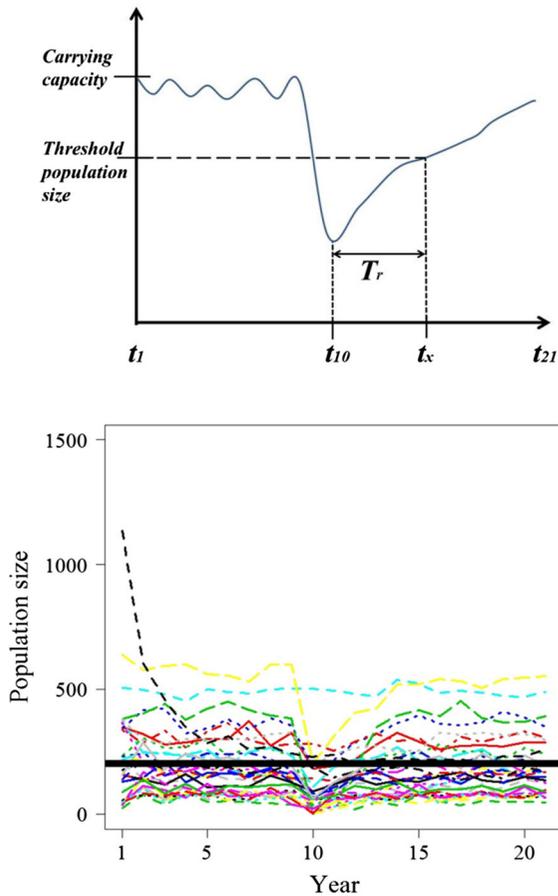
Fig. 1 Simulated brushtail possum local population dynamics. Top panel: conceptual diagram of the temporal dynamics of a single patch population as simulated here. The population size fluctuates around the carrying capacity until population control on year t_{10}. Afterwards, the population in the patch takes Tr years to reach a target threshold population size, below which management aims to maintain the population in the patch. Note that this graph represents only one patch, but we simulated multiple patches in each model run. Bottom panel: example of a single numerical simulation of the logistic population growth model with no Allee effects. The lines show one single model run of the population dynamics of different patches in the same landscape and the horizontal solid black line represents the two possums/ha target threshold density. Population control was induced on year 10

well studied, which afforded us the opportunity to develop realistic quantitative models of their population dynamics at landscape levels (Hickling and Pekelharing 1989; Montague 2000; Cowan 2001; Ramsey and Efford 2010; Rouco et al. 2013; Livingstone et al. 2015).

We identified the factors that affect the time to recovery to a density threshold of two inds/ha under a

variety of circumstances. Two possums per hectare is a density below which possum populations produce negligible impacts on native plant species in New Zealand (Nugent et al. 2001; Norbury et al. 2015). Invasive possum populations in New Zealand experience density-dependent responses to changes in abundances, pointing to the potential impact of Allee effects on the population dynamics of the species (Clout and Efford 1984; Cowan et al. 1997; Ramsey and Efford 2010). Allee effects are an important driver of biological invasions, and can both help populations overcome control efforts or be exploited by managers to improve the efficacy of management actions (Taylor and Hastings 2005; Berec et al. 2007; Courchamp et al. 2008; Hui and Richardson 2017; Wilkins et al. 2018). Given the importance of Allee effects, we examined the time to recovery under three population dynamics scenarios: logistic model (without Allee effects), weak Allee effects, and strong Allee effects. Populations subject to strong Allee effects are characterised by a population size threshold below which the population growth rate is negative (Boukal and Berec 2002; Courchamp et al. 2008). On the other hand, positive population growth rates characterise weak Allee effects (Courchamp et al. 2008). In the context of possum management, weak Allee effects may lead to rapid recovery after control, whereas strong Allee effects can be harnessed to drive populations to extinction by suppressing them below a given Allee treshold (Taylor and Hastings 2005; Berec et al. 2007; Hui and Richardson 2017). Our results can be adapted to plan robust landscape control strategies either by focussing management efforts on the factors more likely to increase the times to recovery or by drafting research strategies to better understand those factors before implementing any control operation. Although we have focused on investigating the landscape control of invasive possum populations as a case example, our research methods and key conclusions offer insights into the ecological responses of populations to a severe disturbance (i.e., population reduction). Finally, our findings provide testable quantitative relationships to explore empirically in future research.

Table 1 Definitions and summary statistics of the 13 covariates used to model the simulated time to recovery of brushtail possums populations to the two ind/ha recovery threshold

Covariate	Covariate definition	Logistic growth Mean ± standard deviation 95% credible intervals	Weak Allee Mean ± standard deviation 95% credible intervals	Strong Allee Mean ± standard deviation 95% credible intervals
Landscape scale				
Number of patches	Input: total number of suitable patches in the landscape	24.61 ± 8.32 (9, 40)	25.29 ± 9.09 (8, 41)	23.73 ± 7.55 (10, 38)
Connectance7	Input: proportion of the landscape that is suitable habitat	0.84 ± 0.20 (0.20, 0.98)	0.84 ± 0.18 (0.25, 0.98)	0.81 ± 0.23 (0.10, 0.98)
Proportion habitat	Measured: fraction of realised links (out of all possible ones) between patches in the metapopulation.	0.34 ± 0.14 (0.12, 0.59)	0.35 ± 0.14 (0.11, 0.59)	0.36 ± 0.14 (0.11, 0.59)
Patch-level				
Area	Input: area of the patch (km^2)	1.59 ± 2.02 (0.03, 7.15)	1.64 ± 2.16 (0.04, 7.43)	1.69 ± 1.99 (0.04, 7.70)
Distance nearest	Measured: distance to the nearest patch (km)	1.19 ± 0.74 (0.20, 3.00)	1.17 ± 0.74 (0.19, 2.87)	1.19 ± 0.75 (0.19, 2.98)
Patch connectivity	Measured: number of links with other patches	19.86 ± 8.95 (2, 37)	20.44 ± 9.40 (4, 39)	18.37 ± 8.44 (1, 35)
K	Input: patch carrying capacity	801.32 ± 1021.90 (16, 3600)	820.44 ± 1085.28 (17, 3741)	846.01 ± 1003.12 (18, 3853)
Normalised betweenness	Measured: the number of existing paths in the network (a path connects two patches) that cross through a given patch	0.13 ± 0.38 (0.00, 0.81)	0.12 ± 0.33 (0.01, 0.71)	0.16 ± 0.51 (0.00, 1)
r	Input: per capita annual growth rate due to births and deaths	0.55 ± 0.26 (0.13, 0.98)	0.56 ± 0.27 (0.12, 0.98)	0.57 ± 0.26 (0.13, 0.98)
Control efficacy	Input: proportion of animals removed during control	0.50 ± 0.29 (0.03, 0.98)	0.50 ± 0.29 (0.03, 0.97)	0.49 ± 0.29 (0.02, 0.98)
Species-level				
Dispersal probability	Input: annual probability of dispersal	0.29 ± 0.16 (0.04, 0.65)	0.29 ± 0.16 (0.05, 0.64)	0.29 ± 0.16 (0.04, 0.65)
Density	Input: individuals/km^2	503.03 ± 20.66 (463, 542)	501.23 ± 23.34 (462, 549)	500.42 ± 21.81 (456, 540)
c	Input: dispersal kernel shape parameter	0.58 ± 0.27 (0.13, 0.99)	0.57 ± 0.25 (0.14, 0.98)	0.25 ± 0.25 (0.12, 0.99)

Summary statistics were obtained after 200 runs of the three different population dynamics scenarios

All the covariates were standardised before conducting the statistical analyses. Input indicates a covariate whose values were set at the beginning of the simulations, whereas measured refers to covariates whose values were calculated from the results obtained in the simulations. Refer to methods for further details

Materials and methods

Landscape generation

We generated artificial landscapes as a 10×10 km square comprised of suitable and unsuitable habitat, which were or were not occupied by possum populations, respectively. The proportion of suitable habitat in the landscape was drawn from a uniform distribution, $\sim U(0.1, 0.6)$, to represent a relatively ample range of values while still allowing for a fraction of unsuitable habitat. The minimum value of 40% of unsuitable habitat was set to correspond to the average fraction of farmland cover in New Zealand (http://archive.stats.govt.nz/browse_for_stats/environment/environmental-reporting-series/environmental-indicators/Home/Land/land-use.aspx), which is usually considered as poor possum habitat (Montague 2000). Once the proportion of suitable landscape was defined, we divided it into habitat patches, characteristic of spatially-structured metapopulations (Hanski 1998; Hanski and Ovaskainen 2003; Hanski and Gaggiotti 2004), using a rejection algorithm (see Online Resource 1). After defining the number of patches and their corresponding areas (km^2), we positioned all of them in the geographical space by sampling without replacement x and y-centroid coordinates from the landscape.

Network theory provides a natural framework for conceptualising and manipulating landscapes (Rozenfeld et al. 2008; Chadès et al. 2011; Lurgi et al. 2016). We converted our landscapes into networks of interconnected patches (nodes in the terminology of network theory) by considering connected (linked) patches whose centroids are at a Euclidean distance less than the annual dispersal distance between patches of the brushtail possum (see "Patch and landscape population dynamics" section below). This is a reasonable assumption given that landscape connectivity should be assessed based on the movement capacities of the species (Taylor et al. 2006; Glen et al. 2017).

Patch and landscape population dynamics

We modelled the population size at each local patch, incorporating both local and metapopulation dynamics, at the end of any given year, $N_{i,\,t+1}$, as:

$$N_{i,\,t+1} = R_{i,t+1} - E_{i,t+1} + \Sigma I_{i,j,t+1}, \tag{1}$$

where $R_{i,t+1}$ is the patch population size resulting from local population dynamics incorporating stochastic effects (see below), $E_{i,t+1}$ is the total annual number of individuals emigrating from the patch, and $\Sigma I_{i,j,t+1}$ is the total annual number of individuals immigrating into the local patch from all other patches in the landscape. The population dynamics at each local patch were modelled using a logistic equation incorporating annual birth and death processes:

$$\mu_{i,t+1} = N_{i,t} + (\mathrm{r}N_{i,t})\left(\frac{K_i - N_{i,t}}{K_i}\right), \tag{2}$$

where $N_{i,t}$ is the population size in patch i at time t, K_i its carrying capacity (here equated to the patch population size in time 1 for simplicity), and $r \sim U(0.1, 1)$ is the range of potential possum per capita growth rates (Hickling and Pekelharing 1989; Hone et al. 2010). We incorporated local demographic and environmental stochastic effects by drawing patch population sizes, $R_{i,t+1}$, from a Poisson distribution:

$$R_{i,t+1} \sim Poisson(\mu_{i,t+1}). \tag{3}$$

Local population growth and metapopulation dynamics were modelled as asynchronous processes. This is representative of species for which reproduction and dispersal occur as relatively discrete events separated in time, as it is the case for possums (Clout and Efford 1984; Montague 2000). Dispersal between local populations occurred after local population growth and was modelled as a two-step process. First, the total annual number of individuals emigrating from patch i, $E_{i,t+1}$, was drawn from a binomial distribution:

$$E_{i,t+1} \sim Binom(R_{i,t+1}, pd_i), \tag{4}$$

where pd_i was the individual probability of dispersal of individuals in patch, i drawn from $Beta(2, 5)$. These values of the Beta distribution parameters for the probability of annual individual dispersal were set to peak around 0.2, yielding values representative of dispersal in possum populations (Ramsey and Efford 2010; Etherington et al. 2014). Second, the dispersal of emigrants from patch i to other local populations was modelled using a dispersal kernel:

$$dk_{i,j} = \exp^{-cD_{i,j}}, \tag{5}$$

$$c \sim U(0.1, 1), \tag{6}$$

where $dk_{i,j}$ defined the dispersal kernel between the origin patch i and the destination patch j as an exponential distance-decay function (Nathan et al. 2012), $D_{i,j}$ was the Euclidean distance between the centroids of the patches i and j, and c was the shape parameter of the dispersal kernel. Values for c were drawn from a uniform distribution bounded by the inverse of the dispersal distance (i.e., 1/km). This means that 1 and 10 kilometres were the simulated minimum and maximum dispersal distances of individuals, respectively (Ramsey and Efford 2010; Etherington et al. 2014).

The total annual number of individuals immigrating to patch i from patch j ($I_{i,j,t+1}$), was the result of a multinomial draw to ensure that all dispersing individuals from patch j arrive in another patch in the landscape:

$$I_{t+1} \sim Multinom\big(E_{j,t+1}, \, dk_j\big), \tag{7}$$

where I_{t+1} was a vector of the number of new immigrants into patches $i \neq j$, and dk_j was a vector of the dispersal kernel values from patch j to all patches $i \neq j$. This modelling approach for $I_{i,j,t+1}$ assumes that all dispersing possums survive and settle elsewhere, consistent with the low mortality and high settlement rates of dispersing possums in New Zealand landscapes (Clout and Efford 1984; Cowan et al. 1997). We accommodated Allee effects in our modelling framework by substituting Eq. (2) with the following (Boukal and Berec 2002):

$$\mu_{i,t+1} = N_{i,t} + \big(r_i N_{i,t}\big)\left(1 - \frac{N_{i,t}}{K_i}\right)\left(\frac{N_{i,t}}{K_i} - \frac{A_i}{K_i}\right), \tag{8}$$

$$A_i = 0.2 K_i, \tag{9}$$

where A_i was the patch-specific Allee threshold and all other parameters were defined as in (2). The Allee threshold was set to be at 20% of the patch carrying capacity, and we simulated weak and strong Allee effects by making A_i either negative or positive, respectively (Boukal and Berec 2002). The 20% threshold value for the Allee effect to kick in reflects the finding of potentially density-dependent possum responses to population suppression below 20% of their initial densities (Clout and Efford 1984; Cowan et al. 1997; Ramsey and Efford 2010).

Numerical simulations

We ran 200 simulations of each three scenarios: logistic model (without Allee effects), weak Allee effects, and strong Allee effects. Simulations for each of these three scenarios were conducted independently. During each simulation (Fig. 1), we initialised our model, as described above, and ran it for a total of 21 years. Our simulations spanned 21 years because we induced population control on year 10 in all habitat patches and, therefore, we simulated 10 years of population dynamics before control (a sufficient burn-in time for the population size to reach the steady state; Fig. 1), and 10 years after control to evaluate whether populations recover within a decade of control. At the beginning of the simulations, each patch i was assigned a carrying capacity, K_i, and initial population size, $N_{i,\,t1}$, equal to the carrying capacity and given by:

$$K_i = N_{i,t1} = Dp\,AP_i, \tag{10}$$

$$Dp \sim Poisson(\lambda = 500), \tag{11}$$

where AP_i is the area of the patch (km^2), and Dp is the average density (ind/km^2) of the species in the landscape. The value for Dp was independently drawn for each simulation from a Poisson distribution with a mean of 500 inds/km^2 (Montague 2000; Ruscoe et al. 2011; Rouco et al. 2013).

Population control was induced as a pulse perturbation in each patch on year 10 of the simulations by drawing the fraction of the population remaining in the patch after control from a Beta distribution, $\sim Beta(1,1)$. This parameterisation of the Beta distribution implies that, across all the patches, the average percentage of the initial population remaining after control was 50%, with values spanning the wide range between 3 and 98% (see Table 1). Population control was induced before growth and dispersal on year 10. All the simulations were conducted in R (R Development Core Team 2015), and the annotated code is available in Online Resource 1.

Statistical analysis

We analysed the output of our simulations by modelling the time to recovery on each patch (response variable) as a function of 13 covariates (explanatory covariates) that were either input to or derived from our simulations (see Table 1 for details). These 13

covariates balance a good representation of the local and landscape dynamics with the possibility of being measured in empirical situations, making tests of our model predictions more feasible. Overall, we obtained 4229, 4240, and 4177 parameter combinations for the logistic model, weak Allee, and strong Allee scenarios, respectively. Note that the number of combinations exceeds the number of simulations, and varies across the three scenarios, because we produced one landscape per simulation, within each of which the number of patches is variable and larger than one. There was one parameter combination per patch and replicated simulation. We employed Bayesian regularised time-to-event regressions to model times to recovery as a function of the 13 landscape, patch, species, and population-level covariates. Statistical regularisation, including Bayesian regularisation, produces robust statistical models even in cases when there are many covariates, and there is likely cross-correlation between the covariates (Gelman et al. 2013; Hooten and Hobbs 2015). In our models, times to recovery (Tr) were assumed to be random vectors drawn from an exponential distribution with the rate parameter (ω) being modelled as a function of the 13 covariates using a log link. The regularised regressions were defined as follows:

$$\log(\omega_i) = \beta_0 + \sum_{z=1}^{13} \beta_z X_{i,z}, \tag{12}$$

$$Tr_i \sim Exp(\omega_i), \tag{13}$$

where β_0 and β_z are the intercept and slopes of the regression, and $X_{i,z}$, $z = 1,\ldots, 13$, are the 13 covariates. Note that in this type of regression there is an inverse relationship between the rate parameter (ω) and the time to recovery. Typically, this leads to a negative (positive) parameter estimate, e.g., a negative (positive) slope, resulting in a positive (negative) relationship between the parameter and the time to recovery. The exponential distributions were censored at 10 years after control to account for the fact that some patch populations did not recover after the simulated period finished. All the covariates were standardised (centred by their mean and scaled by the standard deviation) for the analyses. We used relatively uninformative Normal priors for the intercept, $\sim N(0, \sigma = 3.16)$. We used Normal priors on the slopes of all the covariates to construct the regularised model, $\sim$ $N(0, \sigma)$, $\sigma \sim Exp(0.5)$. The Exponential prior on the standard deviation shrinks the posterior estimates of the slopes towards zero when they contribute little to explaining the variability in the time to recovery, resulting in a regularised model (O'Hara and Sillanpää 2009; Gelman et al. 2013; Hooten and Hobbs 2015). Therefore, only those covariates with an important influence on time to recovery will have an effect size substantially different from zero, whereas the other covariates will have a minimal contribution to the final structure of the time-to-event regressions.

We fitted the Bayesian regularised models using the NIMBLE package for the R statistical environment (R Development Core Team 2015; de Valpine et al. 2017). We ran the Bayesian models using three chains with 20,000 iterations each, and no thinning. After visually checking for mixing and convergence of the chains, we discarded the first 2000 iterations of each chain as burn-in time. Our procedures produced 54,000 draws of the marginal posterior distribution of each parameter in the time-to-event regressions. We fit the Bayesian models independently to the data from the three population growth scenarios. We evaluated the goodness of fit of the models by calculating Bayesian p-values based on the difference in the Freeman–Tukey test values between the fitted model and data simulated under the assumption that the model was correct (Gelman et al. 2013; Kéry and Royle 2016). Extreme Bayesian p-values (e.g., < 0.05 or > 0.95) tend to indicate a poorly fitting model, whereas the closer Bayesian p-values are to 0.5 the better is the fit of the model (Gelman et al. 2013). The annotated NIMBLE code for fitting the time-to-event regressions is available in Online Resource 1.

Results

Our simulations indicate that Allee effects have an important effect on times to population recovery compared to logistically growing populations. Populations following a logistic growth were likely to recover within the 10-year period after control (11.0% of simulated populations did not recover; 474 of 4226 simulated populations). The strength of Allee effects decreased the likelihood of recovery substantially. Under the weak Allee effect scenario, only 18.9% (802 of 4240) populations were not able to recover, while under strong Allee effects this number increased to

34.6% (1447 of 4177) populations. In the cases where populations reached the threshold density, the recovery was fast after control, with mean recovery times of less than 2 years in the three scenarios. Nonetheless, whenever there were weak Allee effects, those populations that recovered within the 10-year period took marginally longer to reach the density threshold (weak Allee effects, mean ± standard deviation: 1.81 ± 1.90 years, 95% Credible Intervals: [1, 9]) than populations growing according to a logistic model (1.68 ± 1.62, 95% CIs [1, 7]) or experiencing strong Allee effects (1.59 ± 1.64; 95% CIs [1, 7]).
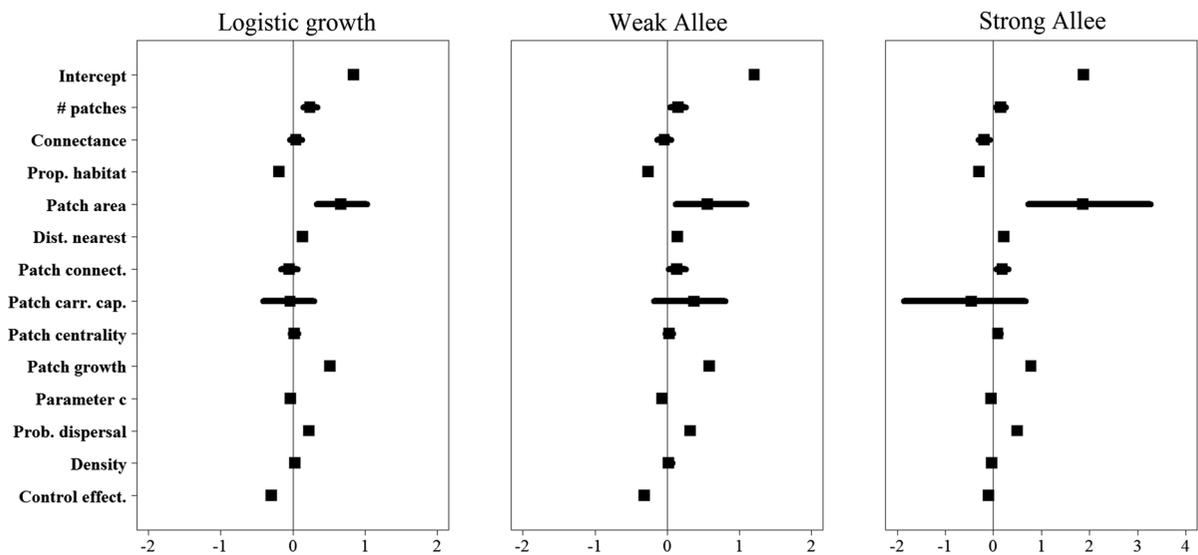
Our Bayesian regularised regressions fitted the simulated data adequately, as indicated by non-extreme Bayesian p-values in the three scenarios (logistic model: 0.39; weak Allee effects: 0.65; strong Allee effects: 0.54). The regressions revealed that the times to recovery were mainly determined by the same set of covariates regardless of the scenario (Fig. 2, see also posterior estimates of all the regression parameters in Table A1 in Online Resource 2). In the three scenarios, populations inhabiting large patches with a small per capita growth rate in landscapes with low habitat availability tended to take longer to recover than patches with average characteristics (negative relationship between the latter two covariates and the

time to recovery; Fig. 2). On the other hand, populations in patches with a small probability of dispersal, near other patches, and subject to less control pressure recovered faster than patches with average characteristics (positive relationships; Fig. 2).

Despite the similarities in our results across scenarios, strong Allee effects influence times to recovery differently compared to the other two simulated population dynamics. Whenever there were strong Allee effects, our Bayesian regularised regressions revealed the positive effects of two covariates that did not show important effects in the other two scenarios: landscape connectance and patch carrying capacity (Fig. 2). These relationships indicate that patches in more connected landscapes and with a small carrying capacity recovered slowly compared to other habitat patches in situations where there were strong Allee effects.

Discussion

Our simulation modelling revealed that invasive possum populations recovered relatively fast after moderate population control across the landscape (95% CIs ranging from 1 to 9 years after control

Fig. 2 Effects of landscape and population-level features on time to recovery after control. Mean and 95% Credible Intervals of the posterior distributions of the 13 covariates used in the Bayesian regularised exponential regression to model times to recovery of simulated possum populations under three population dynamics models. Note that in the exponential log regression, negative (positive) estimates indicate a positive (negative) relationship with the time to recovery. Refer to Table 1 for further details and definitions of the covariates

across scenarios). However, populations experiencing Allee effects were less likely to recover, and those recovering took longer to achieve previous abundance levels than in the logistic growth model scenario. This key result highlights the need for a serious commitment to providing sufficient resources over the long term to control populations timely and regularly to obtain benefits from possum control before the populations reach the density threshold. Otherwise, irregular population control, or control after the time of recovery, will likely produce suboptimal outcomes in possum management.

The effective control of invasive species, including possums, is commonly deemed challenging due to the idiosyncrasies of each landscape (Anderson et al. 2017; Baker 2017; Kopf et al. 2017; Glen et al. 2017), but our findings suggest that this is not always the case. Across the three types of population dynamics, our simulations indicate that the times to population recovery tended to be shaped by the same factors. At a landscape level, our results show that simple landscapes, characterised by a high availability of habitat, hosting high population densities and with a small distance between patches of suitable habitat, will require frequent control efforts to maintain possums below the desired density threshold. The other side of this coin implies that complex patchy landscapes, those characterised by the presence of suitable habitat patches scattered across the landscape, will be more amenable to long-term possum control and may require less frequent interventions. At a patch level, our simulations show that populations in smaller patches were less resilient to control than those in larger patches. In the case of the existence of strong Allee effects, two additional covariates need to be considered: landscape connectance and patch carrying capacity (Fig. 2). High connectance resulted in slower population recovery times, whereas patches with smaller carrying capacities required less time to recover. These effects emerged from low dispersal rates implying that possums remained in their patch until it reached its carrying capacity and, therefore, leading to faster population recovery. In summary, our results show that the control of invasive possums in simple landscapes will benefit from taking a landscape-level perspective (e.g., maximising control efforts across the whole landscape), whereas control operations in complex landscapes will be better off by taking a more nuanced patch-level view (e.g., tackling each habitat patch as an independent management unit).

Our research has direct implications for the ongoing landscape control of invasive possums in New Zealand (Montague 2000; Anderson et al. 2015; Livingstone et al. 2015; Gormley et al. 2016). The current management strategy consists in conducting control campaigns covering the whole landscape, which are repeated every 5 years for a decade or 15 years depending on the possum density and the likelihood of bovine tuberculosis persistence (Nugent et al. 2015; Gormley et al. 2016). Our results suggest that this general strategy could be fine-tuned to the peculiarities of each landscape. Simple landscapes with an abundance of possum habitat may need to be controlled more frequently than the current 5-year interval to prevent rebounding possum numbers. This finding is in agreement with the recent observation that populations of invasive possum in New Zealand that have been subject to control show up to a 75% reduction in abundance within 7 years after control, when compared with non-controlled populations (Forsyth et al. 2018). Alternately, the control of complex landscapes could incorporate fewer operations in small and relatively isolated patches. These general recommendations can be easily embedded within existing cost–benefit frameworks used to guide possum control operations in New Zealand (Gormley et al. 2016, 2017).

Our findings broadly concur with the expectations drawn from metapopulation theory and population ecology (Hanski 1998; Courchamp et al. 2008). In particular, our findings agree with previous research showing that landscapes with a high habitat availability, frequently characterised by relatively large patches and small inter-patch distances (producing a high connectivity), tend to host stable and growing populations across a range of species (Hanski 1998; With 2002; Glen et al. 2013; Baker 2017; Fahrig 2017). In our simulations for the possum, populations tended to recover rapidly, showing higher resilience, in landscapes with those features promoting population and metapopulation stability. The potential to exploit naturally occurring Allee effects to manage invasive species has been recognised previously (Taylor and Hastings 2005; Courchamp et al. 2008; Wilkins et al. 2018), and our results provide additional evidence indicating that strong Allee effects undermine the ability of populations to recover after control.

The consistent finding of the role of Allee effects in invasions warrants further research into potential ways to effectively exploit them in management applications.

The landscape management of invasive species is becoming more common worldwide, and it is expected to continue growing in the nearby future thanks to ambitious initiatives with either a global, such as the IUCN's Honolulu Challenge on Invasive Alien Species (https://www.iucn.org/theme/species/our-work/invasive-species/honolulu-challenge-invasive-alien-species), or a regional scope (e.g., Predator Free New Zealand 2050) (Russell et al. 2015). In this work, we have demonstrated how a quantitative ecological model leads to important insights into the management of invasive species: complex and simple landscapes should be approached differently, with invasive species management in the latter type likely benefiting from allocating control efforts to habitat patches according to their size and connectivity (Chadès et al. 2011). Additionally, our modelling exercise provides lessons that can be used as a basis for future research and to reduce uncertainties in the landscape management of invasive species, acting as a way of prioritising the characteristics of the landscape and populations that deserve additional research consideration during the planning and early implementation of population control (Conroy and Peterson 2013; Dietze 2017; Dietze et al. 2018). More broadly, the corroboration of most of our conclusions with the principles of population and metapopulation theory demonstrates the potential of ecological theory to inform invasive species management, echoing previous calls for a better integration of invasion ecology and management with other ecological disciplines (Driscoll and Lindenmayer 2012; Vaz et al. 2017).

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