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

3

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14

15 **Abstract**

16 ***Context***

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

21 ***Objectives***

22 We aim to improve our understanding of the factors influencing the landscape control of invasive species.

23 ***Methods***

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

29 ***Results***

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

34 *Conclusions*

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

39

40 **Keywords:** Allee effects; brushtail possum; habitat availability; landscape and patch metrics; New Zealand

41

42 Introduction

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

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

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

74 We focussed on the management of invasive brushtail possums (*Trichosurus vulpecula*; possum
75 hereafter) populations in New Zealand as a case study. We addressed how the time of possum recovery to a
76 specified density threshold following control was influenced by the compounded effects of landscape and patch
77 features, population growth and dispersal rates, and Allee effects (Fig. 1 and Table 1). Possums were brought
78 from Australia and deliberately released from the 1830s until the 1920s to establish a fur trade industry in New
79 Zealand, and by the end of the 20th century they had spread and colonised most of the country (Montague 2000;

80 Cowan 2001; Long 2003). Invasive possums cause substantial negative ecological impacts on the native fauna
81 and flora of New Zealand, via depredation and intensive browsing, and are the main wild reservoir of bovine
82 tuberculosis, which severely affects livestock health (Office of the Parliamentary Commissioner for the
83 Environment 1994; Montague 2000; Cowan 2001; Nugent et al. 2001, 2015; Norbury et al. 2015; Byrom et al.
84 2016). Consequently, invasive possum populations are the subject of extensive management campaigns to reduce
85 their densities to near zero, with the over-arching aim of minimising their impacts on native species and hamper
86 their role as bovine tuberculosis vectors (Montague 2000; Russell et al. 2015; Anderson et al. 2015; Livingstone
87 et al. 2015; Byrom et al. 2016; Gormley et al. 2016; Forsyth et al. 2018). Not surprisingly, the possum ecology in
88 the country is well studied, which afforded us to opportunity develop realistic quantitative models of their
89 population dynamics at landscape levels (Hickling and Pekelharing 1989; Montague 2000; Cowan 2001; Ramsey
90 and Efford 2010; Rouco et al. 2013; Livingstone et al. 2015).

91

92 We identified the factors that affect the time to recover to a density threshold of two inds/ha under a
93 variety of circumstances. Two possums per hectare is a density below which possum populations produce
94 negligible impacts on native plant species in New Zealand (Nugent et al. 2001; Norbury et al. 2015). Invasive
95 possum populations in New Zealand experience density-dependent responses to changes in abundances, pointing
96 to the potential impact of Allee effects on the population dynamics of the species (Clout and Efford 1984; Cowan
97 et al. 1997; Ramsey and Efford 2010). Allee effects are an important driver of biological invasions, and can both
98 help populations overcome control efforts or be exploited by managers to improve the efficacy of management
99 actions (Taylor and Hastings 2005; Berec et al. 2007; Courchamp et al. 2008; Hui and Richardson 2017; Wilkins
100 et al. 2018). Given the importance of Allee effects, we examined the time to recover under three population
101 dynamics scenarios: logistic model (without Allee effects), weak Allee effects, and strong Allee effects.
102 Populations subject to strong Allee effects are characterised by a population size threshold below which the
103 population growth rate is negative (Boukal and Berec 2002; Courchamp et al. 2008). Alternately, positive
104 population growth rates characterise weak Allee effects (Courchamp et al. 2008). In the context of invasive
105 possum populations, weak Allee effects may thus lead to either rapid recovery after control, or to local population
106 extinction if populations are driven to sizes below a given Allee threshold under which extinction is virtually
107 unavoidable (Taylor and Hastings 2005; Berec et al. 2007; Hui and Richardson 2017). Our results can be adapted
108 to plan robust landscape control strategies either by focussing management efforts on the factors more likely to
109 increase the times to recovery or by drafting research strategies to better understand those factors before
110 implementing any control operation. Although we have focused on investigating the landscape control of invasive
111 possum populations as a case example, our research methods and key conclusions offer insights into the ecological
112 responses of populations to a severe disturbance (i.e., population reduction). Finally, our findings provide testable
113 quantitative relationships to explore empirically in future research.

114

115 **Material and methods**

116 *Landscape generation*

117 We generated artificial landscapes as a 10x10km square comprised of suitable and unsuitable habitat,
 118 which were or were not occupied by possum populations, respectively. The proportion of suitable habitat in the
 119 landscape was drawn from a uniform distribution, $\sim U(0.1, 0.6)$, to represent a relatively ample range of values
 120 while still allowing for a fraction of unsuitable habitat. The minimum value of 40% of unsuitable habitat was set
 121 to correspond to the average fraction of farmland cover in New Zealand
 122 ([http://archive.stats.govt.nz/browse_for_stats/environment/environmental-reporting-series/environmental-](http://archive.stats.govt.nz/browse_for_stats/environment/environmental-reporting-series/environmental-indicators/Home/Land/land-use.aspx)
 123 [indicators/Home/Land/land-use.aspx](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).
 124 Once the proportion of suitable landscape was defined, we divided it into habitat patches, characteristic of
 125 spatially-structured metapopulations (Hanski 1998; Hanski and Ovaskainen 2003; Hanski and Gaggiotti 2004),
 126 using a rejection algorithm (see Online Resource 1). After defining the number of patches and their corresponding
 127 areas (km²), we positioned all of them in the geographical space by sampling without replacement x and y -centroid
 128 coordinates from the landscape.

129 Network theory provides a natural framework for conceptualising and manipulating landscapes (Rozenfeld
 130 et al. 2008; Chadès et al. 2011; Lurgi et al. 2016). We converted our landscapes into networks of interconnected
 131 patches (nodes in the terminology of network theory) by considering connected (linked) patches whose centroids
 132 are at a Euclidean distance less than the annual dispersal distance between patches of the brushtail possum (see
 133 *Patch and landscape population dynamics* section below). This is a reasonable assumption given that landscape
 134 connectivity should be assessed based on the movement capacities of the species (Taylor et al. 2006; Glen et al.
 135 2017).

136

137 *Patch and landscape population dynamics*

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

140

$$141 \quad N_{i,t+1} = R_{i,t+1} - E_{i,t+1} + \sum I_{i,j,t+1} \quad (1)$$

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

147

$$148 \quad \mu_{i,t+1} = N_{i,t} + (rN_{i,t}) \left(\frac{K_i - N_{i,t}}{K_i} \right) \quad (2)$$

149

150 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
 151 size in time 1 for simplicity), and $r \sim U(0.1, 1)$ is the range of potential possum per capita growth rates (Hickling
 152 and Pekelharing 1989; Hone et al. 2010). We incorporated local demographic and environmental stochastic effects
 153 by drawing patch population sizes, $R_{i,t+1}$, from a Poisson distribution:

154

$$155 \quad R_{i,t+1} \sim \text{Poisson}(\mu_{i,t+1}) \quad (3)$$

156

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

162

$$163 \quad E_{i,t+1} \sim \text{Binom}(R_{i,t+1}, pd_i) \quad (4)$$

164

165 where pd_i was the individual probability of dispersal of individuals in patch, i drawn from $\text{Beta}(2, 5)$. These values
 166 of the Beta distribution parameters for the probability of annual individual dispersal were set to peak around 0.2,
 167 yielding values representative of dispersal in possum populations (Ramsey and Efford 2010; Etherington et al.
 168 2014). Second, the dispersal of emigrants from patch i to other local populations was modelled using a dispersal
 169 kernel:

170

$$171 \quad dk_{i,j} = \exp^{-cD_{i,j}} \quad (5)$$

$$172 \quad c \sim U(0.1, 1) \quad (6)$$

173

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

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

182

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

184

185 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
 186 kernel values from patch j to all patches $i \neq j$. This modelling approach for $I_{i,j,t+1}$ assumes that all dispersing
 187 possums survive and settle elsewhere, consistent with the low mortality and high settlement rates of dispersing
 188 possums in New Zealand landscapes (Clout and Efford 1984; Cowan et al. 1997). We accommodated Allee effects
 189 in our modelling framework by substituting equation (2) with the following (Boukal and Berec 2002):

190

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

$$A_i = 0.2K_i \quad (9)$$

193

194 where A_i was the patch-specific Allee threshold and all other parameters were defined as in (2). The Allee
 195 threshold was set to be at 20% of the patch carrying capacity, and we simulated weak and strong Allee effects by
 196 making A_i either negative or positive, respectively (Boukal and Berec 2002). The 20% threshold value for the
 197 Allee effect to kick in reflects the finding of potentially density-dependent possum responses to population
 198 suppression below 20% of their initial densities (Clout and Efford 1984; Cowan et al. 1997; Ramsey and Efford
 199 2010).

200

201 *Numerical simulations*

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

210

$$K_i = N_{i,t} = Dp AP_i \quad (10)$$

$$Dp \sim \text{Poisson}(\lambda = 500) \quad (11)$$

213

214 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
215 landscape. The value for Dp was independently drawn for each simulation from a Poisson distribution with a
216 mean of $500 \text{ inds}/\text{km}^2$ (Montague 2000; Ruscoe et al. 2011; Rouco et al. 2013).

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

223

224 *Statistical analysis*

225 We analysed the output of our simulations by modelling the time to recovery on each patch (response
226 variable) as a function of 13 covariates (explanatory covariates) that were either input to or derived from our
227 simulations (see Table 1 for details). These 13 covariates balance a good representation of the local and landscape
228 dynamics with the possibility of being measured in empirical situations, making tests of our model predictions
229 more feasible. Overall, we obtained 4229, 4240, and 4177 parameter combinations for the logistic model, weak
230 Allee, and strong Allee scenarios, respectively. Note that the number of combinations exceeds the number of
231 simulations, and varies across the three scenarios, because we produced one landscape per simulation, within each
232 of which the number of patches is variable and larger than one. There was one parameter combination per patch
233 and replicated simulation. We employed Bayesian regularised time-to-event regressions to model times to
234 recovery as a function of the 13 landscape, patch, species, and population-level covariates. Statistical
235 regularisation, including Bayesian regularisation, produces robust statistical models even in cases when there are
236 many covariates, and there is likely cross-correlation between the covariates (Gelman et al. 2013; Hooten and
237 Hobbs 2015). In our models, times to recovery (Tr) were assumed to be random vectors drawn from an exponential
238 distribution with the rate parameter (ω) being modelled as a function of the 13 covariates using a log link. The
239 regularised regressions were defined as follows:

240

$$241 \quad \log(\omega_i) = \beta_0 + \sum_{z=1}^{13} \beta_z X_{i,z} \quad (12)$$

242

$$243 \quad Tr_i \sim \text{Exp}(\omega_i) \quad (13)$$

244

245 where β_0 and β_z are the intercept and slopes of the regression, and $X_{i,z}$, $z = 1, \dots, 13$, are the 13 covariates. Note
246 that in this type of regression there is an inverse relationship between the rate parameter (ω) and the time to
247 recovery. Typically, this leads to a negative (positive) parameter estimate, e.g., a negative (positive) slope,

248 resulting in a positive (negative) relationship between the parameter and the time to recovery. The exponential
249 distributions were censored at 10 years after control to account for the fact that some patch populations did not
250 recover after the simulated period finished. All the covariates were standardised (centred by their mean and scaled
251 by the standard deviation) for the analyses. We used relatively uninformative Normal priors for the intercept,
252 $\sim N(0, \sigma = 3.16)$. We used Normal priors on the slopes of all the covariates to construct the regularised model,
253 $\sim N(0, \sigma)$, $\sigma \sim \text{Exp}(0.5)$. The Exponential prior on the standard deviation shrinks the posterior estimates of the slopes
254 towards zero when they contribute little to explaining the variability in the time to recovery, resulting in a
255 regularised model (O'Hara and Sillanpää 2009; Gelman et al. 2013; Hooten and Hobbs 2015). Therefore, only
256 those covariates with an important influence on time to recovery will have an effect size substantially different
257 from zero, whereas the other covariates will have a minimal contribution to the final structure of the time-to-event
258 regressions.

259 We fit the Bayesian regularised models using the NIMBLE package for the R statistical environment (R
260 Development Core Team 2015; de Valpine et al. 2017). We ran the Bayesian models using three chains with
261 20,000 iterations each, and no thinning. After visually checking for mixing and convergence of the chains, we
262 discarded the first 2,000 iterations of each chain as burn-in time. Our procedures produced 54,000 draws of the
263 marginal posterior distribution of each parameter in the time-to-event regressions. We fit the Bayesian models
264 independently to the data from the three population growth scenarios. We evaluated the goodness of fit of the
265 models by calculating Bayesian p -values based on the difference in the Freeman-Tukey test values between the
266 fitted model and data simulated under the assumption that the model was correct (Gelman et al. 2013; Kéry and
267 Royle 2016). Extreme Bayesian p -values (e.g., < 0.05 or > 0.95) tend to indicate a poorly fitting model, whereas
268 the closer Bayesian p -values are to 0.5 the better is the fit of the model (Gelman et al. 2013). The annotated
269 NIMBLE code for fitting the time-to-event regressions is available in Online Resource 1.

270

271 **Results**

272 Our simulations indicate that Allee effects have an important effect on times to population recovery
273 compared to logistically growing populations. Populations following a logistic growth were likely to recover
274 within the 10-year period after control (11.0% of simulated populations did not recover; 474 of 4226 simulated
275 populations). The strength of Allee effects decreased the likelihood of recovery substantially. Under the weak
276 Allee effect scenario, only 18.9% (802 of 4240) populations were not able to recover, while under strong Allee
277 effects this number increased to 34.6% (1447 of 4177) populations. In the cases where populations reached the
278 threshold density, the recovery was fast after control, with mean recovery times of less than two years in the three
279 scenarios. Nonetheless, whenever there were weak Allee effects, those populations that recovered within the 10-
280 year period took marginally longer to reach the density threshold (weak Allee effects, mean \pm standard deviation:
281 1.81 ± 1.90 years, 95% Credible Intervals: [1, 9]) than populations growing according to a logistic model ($1.68 \pm$
282 1.62 , 95% CIs: [1, 7]) or experiencing strong Allee effects (1.59 ± 1.64 ; 95% CIs: [1, 7]).

283 Our Bayesian regularised regressions fitted the simulated data adequately, as indicated by non-extreme
284 Bayesian p -values in the three scenarios (logistic model: 0.39; weak Allee effects: 0.65; strong Allee effects:

285 0.54). The regressions revealed that the times to recovery were mainly determined by the same set of covariates
286 regardless of the scenario (Fig. 2, see also posterior estimates of all the regression parameters in Table A1 in
287 Online Resource 2). In the three scenarios, populations inhabiting large patches with a small per capita growth
288 rate in landscapes with low habitat availability tended to take longer to recover than patches with average
289 characteristics (negative relationship between the latter two covariates and the time to recovery; Fig. 2). On the
290 other hand, populations in patches with a small probability of dispersal, near other patches, and subject to less
291 control pressure recovered faster than patches with average characteristics (positive relationships; Fig. 2).

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

298

299 **Discussion**

300 Our simulation modelling revealed that invasive possum populations recovered relatively fast after
301 moderate population control across the landscape (95% CIs ranging from 1 to 9 years after control across
302 scenarios). However, populations experiencing Allee effects were less likely to recover, and those recovering took
303 longer to achieve previous abundance levels than in the logistic growth model scenario. This key result highlights
304 the need for a serious commitment to providing sufficient resources over the long term to control populations
305 timely and regularly to obtain benefits from possum control before the populations reach the density threshold.
306 Otherwise, irregular population control, or control after the time of recovery, will likely produce suboptimal
307 outcomes in possum management.

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

322 leading to faster population recovery. In summary, our results show that the control of invasive possums in simple
323 landscapes will benefit from taking a landscape-level perspective (e.g., maximising control efforts across the
324 whole landscape), whereas control operations in complex landscapes will be better off by taking a more nuanced
325 patch-level view (e.g., tackling each habitat patch as an independent management unit).

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

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

350 The landscape management of invasive species is becoming more common worldwide, and it is expected
351 to continue growing in the nearby future thanks to ambitious initiatives with either a global, such as the IUCN's
352 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)
353 (Russell et al. 2015). In this work, we have demonstrated how a quantitative ecological model leads to important
354 insights into the management of invasive species: complex and simple landscapes should be approached
355 differently, with invasive species management in the latter type likely benefiting from allocating control efforts
356 to habitat patches according to their size and connectivity (Chadès et al. 2011). Additionally, our modelling
357 exercise provides lessons that can be used as a basis for future research and to reduce uncertainties in the landscape
358 management of invasive species, acting as a way of prioritising the characteristics of the landscape and populations
359 that deserve additional research consideration during the planning and early implementation of population control
360

361 (Conroy and Peterson 2013; Dietze 2017; Dietze et al. 2018). More broadly, the corroboration of most of our
362 conclusions with the principles of population and metapopulation theory demonstrates the potential of ecological
363 theory to inform invasive species management, echoing previous calls for a better integration of invasion ecology
364 and management with other ecological disciplines (Driscoll and Lindenmayer 2012; Vaz et al. 2017).

365

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