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RESEARCH ARTICLE

Landscape patterns drive provision of nature's contributions to people by mobile species

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Abstract

1. Predicting how nature's contributions to people (NCP) vary spatially remains a challenge. For NCP provided by mobile species, it is unclear how predictions need to account for the influence of multiple habitat types that act as sources, sinks and potential distractors of the NCP-providing species. Existing approaches that do not account for these effects may inaccurately predict outcomes in real landscapes.
2. To move beyond these limitations, we transfer quantitative inference approaches from movement ecology to explore how spatial habitat patterns determine the negative NCP of the invasive common brushtail possum *Trichosurus vulpecula* in New Zealand. We used a Bayesian model to investigate how the size of, and distance from, grassland and indigenous and exotic forest patches together contribute to relative possum density (measured by capture probability across a trapping network) in a heterogeneous 11,000-ha landscape.
3. We found that indigenous and exotic forest area were the most important factors in determining possum density. Although capture probability declined with increasing grassland area, the addition of grassland did not improve the relative model fit above one with indigenous forest as the only habitat.
4. We expected differences in predicted possum density at habitat boundaries, for example, due to preferential foraging at edges. We found that indigenous and exotic forests contributed to capture probability interactively, such that capture probability at the between-habitat edge was lower than expected, given the habitat area. We also found that models allowing for non-linear habitat effects of exotic forests or grasslands, but not indigenous forests, were significantly better at predicting possum density than simpler models.
5. *Synthesis and applications.* Our novel approach for spatial prediction can be applied to any of nature's contributions to people (NCP), and extended to identify trade-offs and synergies among multiple NCP. For example, the negative NCP of possum density trades off with multiple known positive NCP from indigenous forests, including culturally significant non-material NCP, and material NCP

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produced by exotic forests. We recommend that landscape management plans to maximise these positive NCP in future scenarios also consider how the risk of possum density may dampen net NCP provision. To minimise this negative NCP, our results support trap deployment in both indigenous and exotic forest.

KEYWORDS

Bayesian, capture probability, distance-decay, ecosystem services, invasive species, NCP, spatial prediction, *Trichosurus vulpecula*

1 | INTRODUCTION

Landscapes sustain biodiversity and provide many of nature's contributions to people (NCP; Bruley et al., 2021; Díaz et al., 2018). Within landscapes, land uses differ in the NCP that they provide (Frei et al., 2018; Gómez-Creutzberg et al., 2021). However, positive NCP, such as pollination and biological pest control, are delivered by mobile animal species, which may move from one habitat to provide NCP in another (Kremen et al., 2007). Similarly, negative NCP such as pathogens or weeds can spill over among habitats (Blitzer et al., 2012; Moxley et al., 2017).

Prior research on such spillover has implicitly assumed that organisational flow (and associated NCP) decays unidirectionally with distance from a source habitat, with regressions of distance from habitats against a particular contribution being used to quantify the effect of one habitat on another (Ricketts et al., 2008; Woodcock et al., 2016). Such distance-decay relationships could theoretically be used for landscape prediction of NCP (Kass et al., 2023), essentially generating a 'halo' around donor habitats. However, in many cases spatial variation of NCP is non-linear (Mitchell et al., 2015), and landscapes comprise multiple interconnected habitat patches that individually contribute to and/or receive NCP delivered by mobile species (Kremen et al., 2007). Surrounding landscape characteristics also alter animal movement; for example, the distraction effects of adjacent habitats influence the movement of insect pollinators (Lander et al., 2011) and mammals (Kramer-Schadt et al., 2011). In this context, the influence of habitats on NCP depends not on linear distance from a habitat, but on two-dimensional habitat configuration and bidirectional movement among multiple patches (Mitchell et al., 2015). Although abundant research in landscape ecology has shown that landscape composition affects NCP (Le Provost et al., 2023; Mitchell et al., 2015; Ricketts et al., 2008), the challenge remains to make predictions at different points in real landscapes by accounting for the concurrent influence of multiple habitats that act as sources, sinks and potential distractors of mobile species.

Fortunately, in addressing this challenge we can look to well-established approaches utilised in other ecological research areas to estimate overlapping contributions from multiple habitat sources. For example, seminal work in forest population ecology uses inverse modelling to predict spatial patterns of seedling recruitment in forest stands where individual trees have overlapping and varied seed shadows (Clark et al., 1999; Ribbens et al., 1994). We demonstrate a

novel application of these methods for spatial analysis of NCP that addresses the effects of multiple habitat types and patches.

In this study, we focus on the extent to which the area and spatial configuration of habitats within landscapes determine the negative NCP of an invasive species (the common brushtail possum *Trichosurus vulpecula*; hereafter 'possum') in Aotearoa New Zealand. Possums threaten indigenous bird species via egg and chick predation and competition, and via defoliation leading to population decline of forest tree species and canopy dieback (Clout, 2006). This significant presence in indigenous forests could spill over into the surrounding landscape, providing a negative NCP which may be traded off against positive NCP known to be associated with forests (Gómez-Creutzberg et al., 2021; Ricketts et al., 2008). Possums are also a wildlife/maintenance host for bovine tuberculosis and thereby present an ongoing disease spillback risk to livestock (Clout, 2006; Paterson et al., 1995).

Possum home ranges include multiple habitat types and span many hectares, depending on resource availability, population density and breeding seasonality (Paterson et al., 1995; Rouco et al., 2017). Possums occupy and forage in urban gardens (Adams et al., 2014), grassland and scrub (Rouco et al., 2017) and agricultural land, negatively affecting crop yield and stocking rates in the latter (Dodd et al., 2006). These unforested habitats may meet foraging requirements but are likely insufficient as a sole habitat because possums require tree hollows or burrows for daytime dens (Clout, 2006). Conversely, exotic forest plantations can provide possums with dens but limited foraging resources (Warburton, 1978). Possums may therefore face trade-offs in habitat patch selection as they move through landscapes to meet their needs for shelter and nutrition. To strengthen the predictions that drive possum management, it is crucial that these spatial trade-offs are well understood. These spatial trade-offs occur for a range of other NCP, such as habitat types varying in nesting and floral resources and therefore in their ability to support insect-mediated pollination (Kremen et al., 2007) and avian-mediated seed dispersal (Şekercioğlu, 2006).

The aim of this study is to explore how the risk of relative possum density (measured as capture probability in existing trapping networks) varies spatiotemporally with the area and proximity of habitats. By doing this, we illustrate how point-based measures of NCP can be used to generate predictive models that account for the size and distance of different habitat patches. Specifically, we ask the following questions: (1) Which habitats are the greatest sources of possums, and how does this contribution decrease with area of each

habitat type at a given distance? (2) Is the combined effect of multiple habitats on capture probability additive, or is a given habitat's effect influenced by neighbouring habitats? (3) How does the spatial configuration of the surrounding landscape influence capture probability, summing the effects of multiple habitats? From these questions, we form these hypotheses. H_1 : indigenous forest is the most important habitat in predicting capture probability (providing both food and shelter), followed by exotic forest (providing mainly shelter), then grassland (providing mainly food; Question 1). H_{2a} : capture probability linearly increases from low to medium areas of indigenous forest (due to gains in food and shelter), then increases at a decreasing rate from medium to high forested areas once food and shelter requirements are met (Question 1). H_{2b} : capture probability linearly increases from low to medium areas of exotic forest or grassland (due to preferential foraging at edges), then decreases from medium to large areas of habitat due to loss of habitat for food or shelter respectively (Question 1). H_{3a} : capture probability in areas of contiguous indigenous forest will initially increase with the addition of grassland habitat nearby (due to additional food resources and preferential foraging at edges; Youngentob et al., 2012), but then decrease linearly due to loss of habitat for shelter as the landscape becomes increasingly grassland dominated (Question 2). H_{3b} : capture probability in areas of indigenous forest will initially remain unchanged with additional exotic forest habitat in the landscape (due to substitution of habitat for shelter), but then decrease linearly with increasing exotic forest cover, due to lack of food resources available in exotic forest (Question 2). H_{3c} : capture probability in areas of exotic forest will increase with additional grassland habitat nearby (due to additional food resources and preferential foraging at forest-grassland edges), but then decrease linearly as exotic forest is further replaced by grassland, due to loss of habitat for shelter (Question 2). H_4 : capture probability will decrease non-linearly as distance from indigenous forest edge increases into any other habitat (Question 3). H_5 : capture probability will be higher in larger forest patches, holding all else constant (Question 3). These hypotheses are summarised in Figure 1.

2 | MATERIALS AND METHODS

2.1 | Study site and data

Our study site is the Māhia Peninsula in Hawke's Bay, New Zealand (39°9'S; 177°53'E) (Figure 2), a predominantly pastoral landscape containing forest interspersed with grassland and scrub. To explore how the probability of possum capture varied across this landscape, we sourced trapping data from <http://trap.nz/> on 10 August 2023. Our data follow a network of ground set Victor number 1 leg-hold traps (Oneida Victor Inc Ltd, Cleveland, United States) that were monitored from 20 September 2019 to 28 July 2023 as part of a larger, long-term possum eradication programme that included extensive bait station work. Neither fieldwork permission nor ethical approval was required for this work, as the purpose of trapping was pest management rather than research. For the majority of the

study region, 'Pest off' Brodifacoum bait (Animal Control Products Ltd, Whanganui, New Zealand) was used to reduce the population to low numbers. However, in the Māhia Peninsula Scenic Reserve, an indigenous forest administered by the Department of Conservation, Brodifacoum application is not permitted and the eradication programme was unable to gain an exemption for its use. Therefore, 'Double Tap' Diphacinone/Cholecalciferol bait (Connovation Ltd, Manukau, New Zealand) was used in place of Brodifacoum to reduce possum numbers, however, it was significantly less effective at possum removal. This meant that trapping efforts were concentrated in and around the Reserve.

After a data cleaning process (see Appendix S1), our final dataset included 16,015 observations across 3036 unique traps. These observations included captures (2859) and non-captures (sprung empty: 2384; still set: 10,772). Of those individuals captured, 70% were the target species (possum: 1999), and the remainder were non-target species (rat: 788; other: 72), which were not analysed here. Bait type was recorded for each trap observation (55.5% visual lure; 42.9% flour blaze; 1.6% other). Finally, the number of active trapping nights varied across the 46-month study period; the median trap was active for 8 nights (mean: 55; max: 909) and was checked 4 times during that period (mean: 5.3; max: 46). Processed trapping data are available at <https://doi.org/10.6084/m9.figshare.c.7392709>.

We sourced habitat data from the Land Cover Database v5.0 for Mainland New Zealand, available at <https://lris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-version-50-mainland-new-zealand>. We grouped habitat types into four broad categories: exotic forest, indigenous forest, grassland and scrub (see Appendix S2). Unvegetated land cover and water bodies were not considered in our analyses as these act as barriers to, rather than sources of, possums (Adams et al., 2014; Cook et al., 2021).

2.2 | Statistical modelling

Conceptually, our modelling approach predicted possum capture probability ($y_{i,m,t}$ below) at a trap i in grid cell m (details of gridding below) on a given night t in the 48-month study period by taking into account the surrounding landscape, previous captures occurring nearby, and other trapping features. Our main component of interest was the landscape, that is, the contribution to capture probability of each habitat type and the interactions among them. Our other model components controlled for: the habitat type in cell m in which the trap i was deployed, the effect of possums being removed from the neighbourhood by other traps, bait type and date of night t , all of which improved model fit when independently tested (models 1–5 in Table 1).

We modelled the possum capture data ($y_{i,m,t}$) as a Bernoulli process:

$$y_{i,m,t} \sim \text{Bernoulli}(\theta_{i,m,t}), \quad (1)$$

$$\theta_{i,m,t} = 1 - \left(1 - \theta_{i,m,t}^*\right)^{A_{i,t}}, \quad (2)$$

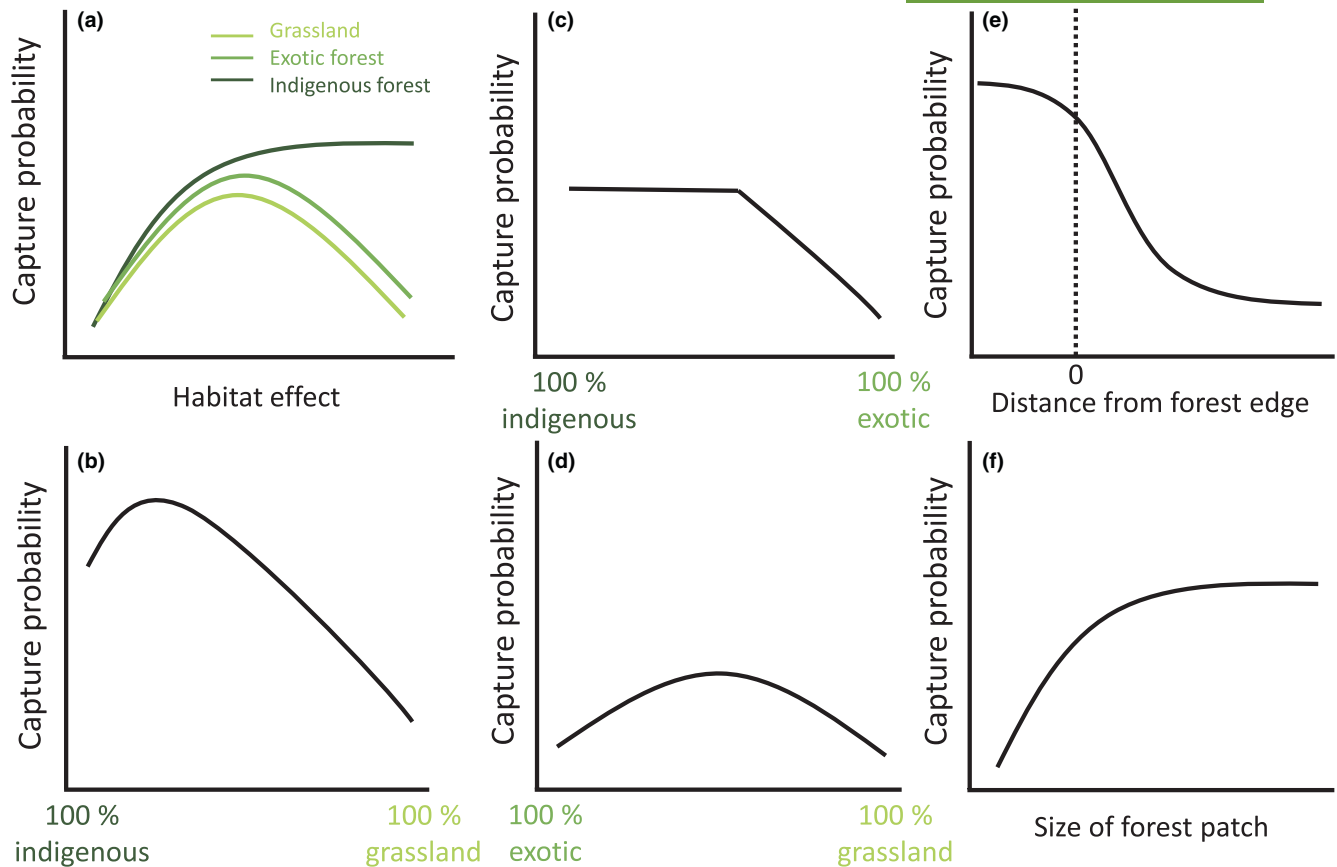


FIGURE 1 The hypotheses tested as a conceptual summary. Panel (a) represents H_1 and H_{2a-b} , where habitat effects in order of importance to capture probability are indigenous forest, exotic forest then grassland (H_1), and where the role of habitat effects is non-linear, such that increasing from low to medium areas of indigenous forest, exotic forest or grassland would increase capture probability, but decrease from medium to high areas of exotic forest or grassland habitat (H_{2b}), and saturate otherwise (H_{2a}). These hypotheses were tested in Figure 3. Panels (b)–(d) show the effects of indigenous forest–grassland, indigenous forest–exotic forest and exotic forest–grassland trade-offs respectively (hypotheses H_{3a-c}). We expect that capture probability in areas of contiguous indigenous forest would initially increase with additional grassland habitat (due to additional food resources and preferential foraging at edges), but then decrease linearly due to loss of habitat for shelter (H_{3a} , tested in Figure S3). When indigenous forested areas gained additional exotic forest habitat, we expected that capture probability would initially remain unchanged (due to substitution of habitat for shelter), but then decrease linearly due to lack of food resources (H_{3b}). We predicted trading off exotic forest for grassland would initially increase capture probability (due to additional food resources and preferential foraging at edges), but then decrease linearly due to loss of habitat for shelter (H_{3c}). Panel (e) represents H_4 , that capture probability would decrease non-linearly with distance from an indigenous forest-to-grassland edge (explored in Figure 4). Panel (f) represents H_5 , where capture probability would increase as indigenous forest patch size increases, but this effect would saturate at large patch sizes (explored in Figure S5).

where $\theta_{i,m,t}^*$ is the predicted capture probability given covariates, and $\theta_{i,m,t}$ is the capture probability adjusted for the availability status of trap i on night t ($A_{i,t}$). We set $A_{i,t} = 1$ (fully available on night t) if the trap captured a possum or if the trap was still set when checked. We set $A_{i,t} = 0.5$ if the trap sprung empty or captured a non-target species (Beauvais & Buskirk, 1999), representing an assumption that either event reduced the trap's availability on average to half the night.

Across our set of models (Table 1) we predicted $\theta_{i,m,t}^*$ using a basic model structure with the following set of predictors:

$$\text{logit}\left(\theta_{i,m,t}^*\right) = \beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},j} + \varepsilon_m \quad (3)$$

where $\text{Rem}_{i,t}$ is the cumulative effect of possums removed by any trap in the neighbourhood of trap i on any night prior to t (see Equation 5), $\text{TrapHab}_{i,m}$ is a binary variable that equals 1 if the cell m within which trap i fell was indigenous forest, $\text{BaitLure}_{i,t}$ is a binary variable that equals 1 if trap i was baited with lure (rather than flour blaze or other bait) at time t , $\text{Date}_{i,t}$ is the day since the start of data collection t on which trap i was checked, $\text{HabEff}_{\text{indfor},j}$ is the cumulative spatial habitat effect of indigenous forests (see Equation 4), and ε_m is the random intercept of cell m in which trap i fell to account for spatial non-independence in the study design. Other covariates that were added to this basic structure in later models are detailed below.

The contribution of indigenous forests to capture probability ($\text{HabEff}_{\text{indfor},j}$) accounted for both the area of, and proximity to, that forest. To calculate $\text{HabEff}_{\text{indfor},j}$ for each trap, we first gridded the

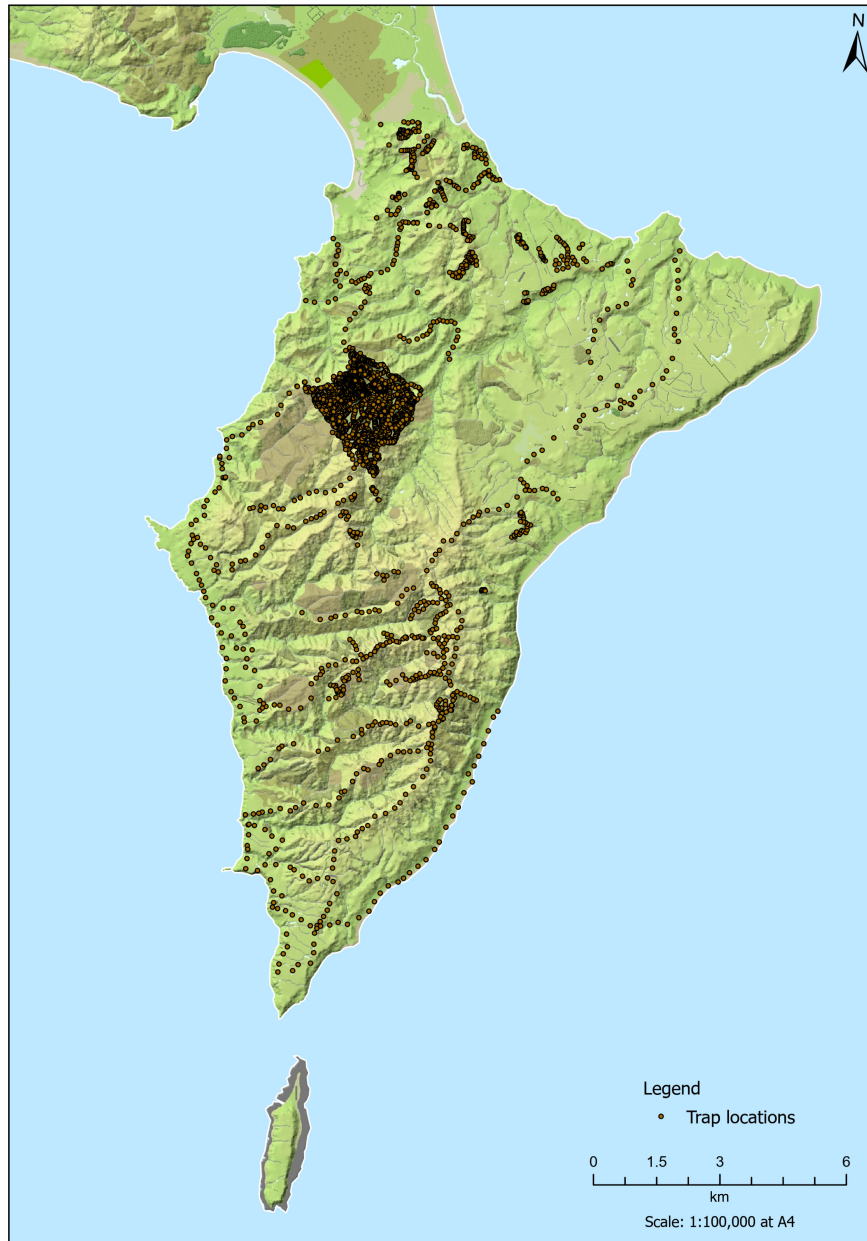


FIGURE 2 Map of trap locations across the Māhia Peninsula.

11,045 ha landscape and assigned to each 100-m cell the majority habitat within. We positioned traps in this landscape based on their GPS coordinates.

Next, we estimated a spatial decay parameter for $\text{HabEff}_{\text{indfor},i}$ and $\text{Rem}_{i,t}$, where decay effects, if present, would be constrained by the home range size within which a possum experienced habitat effects. Home range size estimates vary; ranging from 0.26 to 79.7 ha across New Zealand (Richardson et al., 2017), including 8.2 ha estimated at our study site (Sweetapple & Latham, 2020). Here, we constructed a circular buffer with a 400-m radius around each trap, which equates to an area of ≈ 50.3 ha. We deliberately exceeded the estimated size from Sweetapple & Latham, 2020, as we used a half-normal distance-decay function to allow for a cell's effect to diminish with increasing distance from a trap (Equation 4). We also explored the impact of defining the buffer at different scales; this only influenced $\text{HabEff}_{\text{indfor},i}$, which increased

with decreasing scale and reached an asymptote after 500 m (Figure S1). For each trap, we measured the distance to all cell centroids that fell within its buffer (median: 49). We excluded the cell in which the trap was located, as this was accounted for separately in the control variable $\text{TrapHab}_{i,m}$ (Equation 3). We modelled the potential effect of each cell of each habitat type within this buffer, weighted by their distance from a trap. We calculated this habitat effect as follows:

$$\text{HabEff}_{\text{indfor},i} = \begin{cases} 0, & \text{if } N_i = 0 \\ \sum_{j=1}^{N_i} \exp\left(-\frac{d_{\text{indfor},ij}^2}{2\gamma^2}\right), & \text{if } N_i \geq 1, \end{cases} \quad (4)$$

where $d_{h,ij}^2$ is the Euclidean distance from trap i to the centroid of cell j of habitat 'indfor', and γ is a distance-decay parameter that reduced the effect of cell j with increasing distance to trap i . Alternative

TABLE 1 Full list of models tested, with their model fit relative to the best-fitting model (difference in Leave-one-out information criterion; ΔLOOIC), measure of convergence (proportion of parameters for which $\hat{R} < 1.05$), and parameters included in predicting capture probability, $\text{logit}(\theta_{i,m,t}^*)$.

Model	Hypothesis	ΔLOOIC	$\text{Pr}(\hat{R} < 1.05)$	Parameters predicting capture probability
1	Controls	696.6	1.00	β_0
2	Controls	684.1	0.99	$\beta_0 + \beta_1 \text{Rem}_{i,t}$
3	Controls	654.0	1.00	$\beta_0 + \beta_1 \text{TrapHab}_{i,m}$
4	Controls	691.1	1.00	$\beta_0 + \beta_1 \text{BaitLure}_{i,t}$
5	Controls	192.4	0.99	$\beta_0 + \beta_1 \text{Date}_{i,t}$
6	Controls	638.7	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m}$
7	Controls	676.5	0.99	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{BaitLure}_{i,t}$
8	Controls	191.5	0.99	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{Date}_{i,t}$
9	Controls	647.5	1.00	$\beta_0 + \beta_1 \text{TrapHab}_{i,m} + \beta_2 \text{BaitLure}_{i,t}$
10	Controls	85.8	1.00	$\beta_0 + \beta_1 \text{TrapHab}_{i,m} + \beta_2 \text{Date}_{i,t}$
11	Controls	140.8	1.00	$\beta_0 + \beta_1 \text{BaitLure}_{i,t} + \beta_2 \text{Date}_{i,t}$
12	Controls	641.9	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t}$
13	Controls	80.3	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{Date}_{i,t}$
14	Controls	136.1	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{BaitLure}_{i,t} + \beta_3 \text{Date}_{i,t}$
15	Controls	37.4	1.00	$\beta_0 + \beta_1 \text{TrapHab}_{i,m} + \beta_2 \text{BaitLure}_{i,t} + \beta_3 \text{Date}_{i,t}$
16	Controls	36.2	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t}$
17	H_1	5.8	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},i}$
18	H_1	130.7	0.98	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{exfor},i}$
19	H_1	32.1	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{unfor},i}$
20	H_1	120.6	0.97	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{scrub},i}$
21	H_1	59.2	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{grass},i}$
22	H_{2a}	11.4	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},i} + \beta_6 \text{HabEff}_{\text{indfor},i}^2$
23	H_{2b}	128.5	0.99	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{exfor},i} + \beta_6 \text{HabEff}_{\text{exfor},i}^2$
24	H_{2b}	25.8	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{unfor},i} + \beta_6 \text{HabEff}_{\text{unfor},i}^2$
25	H_{3a}	2.1	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},i} + \beta_6 \text{HabEff}_{\text{exfor},i}$
26	H_{3a}	0	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},i} + \beta_6 \text{HabEff}_{\text{indfor},i} \times \text{HabEff}_{\text{exfor},i}$
27	H_{3b}	4.9	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},i} + \beta_6 \text{HabEff}_{\text{unfor},i}$
28	H_{3b}	4.8	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{indfor},i} + \beta_6 \text{HabEff}_{\text{unfor},i} + \beta_7 \text{HabEff}_{\text{indfor},i} \times \text{HabEff}_{\text{unfor},i}$
29	H_{3c}	45.7	1.00	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{exfor},i} + \beta_6 \text{HabEff}_{\text{unfor},i}$
30	H_{3c}	37.5	0.98	$\beta_0 + \beta_1 \text{Rem}_{i,t} + \beta_2 \text{TrapHab}_{i,m} + \beta_3 \text{BaitLure}_{i,t} + \beta_4 \text{Date}_{i,t} + \beta_5 \text{HabEff}_{\text{exfor},i} + \beta_6 \text{HabEff}_{\text{unfor},i} + \beta_7 \text{HabEff}_{\text{exfor},i} \times \text{HabEff}_{\text{unfor},i}$

Note: HabEff suffixes correspond to the following habitats: exfor is exotic forest; indfor is indigenous forest; grass is grassland; scrub is scrub; unfor is unforested (grassland and scrub combined).

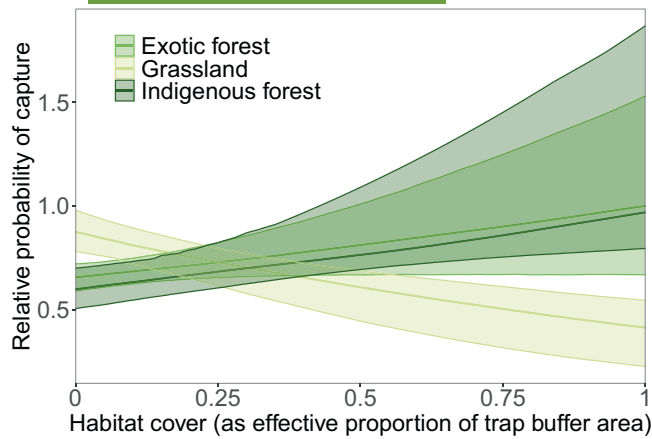


FIGURE 3 Median capture probability relative to maximum given increasing coverage of indigenous forest, exotic forest or grassland. Here, habitat cover is represented as effective proportion of trap buffer area, with $Rem_{i,t}$, $TrapHab_{i,m}$, $BaitLure_{i,t}$ and $Date_{i,t}$ held constant. Marginal predicted lines are shown with 90% credible intervals, using output from models 17, 18 and 19 in [Table 1](#).

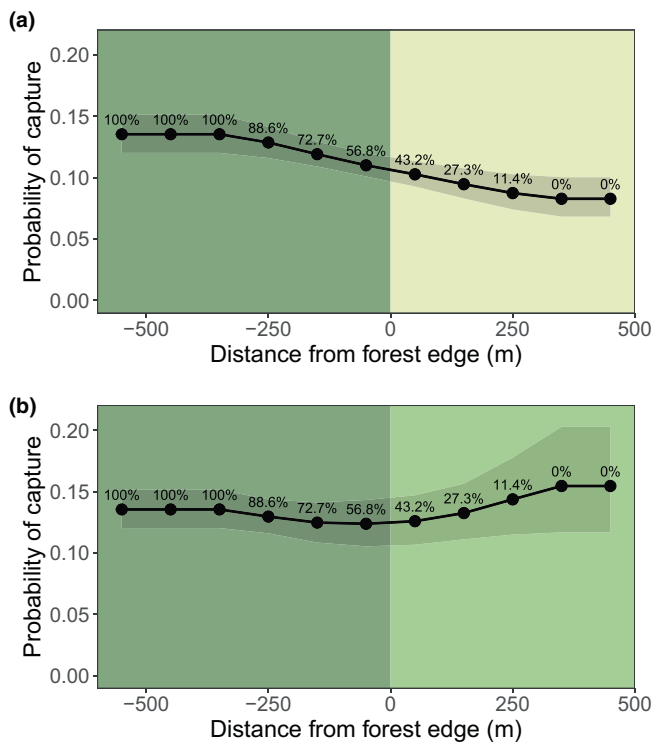


FIGURE 4 Predicted median capture probability across a theoretical indigenous forest-grassland gradient (a) and a theoretical indigenous forest-exotic forest gradient (b). Predictions are fitted across a 1 km range, because at the 500m distance into each habitat, the predicted probability of capture approaches saturation (the size of our buffer radius was 400m, so beyond this distance habitat cover within the buffer does not change). Traps are labelled with the percentage of their neighbourhood buffer in indigenous forest cover. Predicted lines are shown with 90% credible intervals using output from our best-fitting model (model 26 in [Table 1](#)), all else held constant.

calculations of $HabEff_{indfor,j}$ using distances from cell centroids rather than exact trap locations did not qualitatively change our results ([Figure S2](#)).

We calculated $Rem_{i,t}$ to account for any distance-weighted effect of individuals removed by traps from the surrounding area (on any date preceding the night of interest) on capture probability. First, we measured the Euclidean distance between each trap and all other traps that fell within the same 400-m buffer used to calculate $HabEff_{indfor,j}$ (median: 179; range: 1–315). We constructed a history of previous captures and non-captures that occurred in each trap's buffer. The median number of possums removed from a trap's buffer on previous nights was 78 (range: 0–452). We calculated $Rem_{i,t}$ as:

$$Rem_{i,t} = \sum_{k=1}^K \sum_{t'=-1}^{-T'} -y_{k,t'} \times \exp\left(-\frac{d_{i,k}^2}{2\gamma^2}\right), \quad (5)$$

where $d_{i,k}^2$ is the Euclidean distance between trap i and trap k , and γ is a distance-decay parameter (as in [Equation 4](#)) that reduced the effect of neighbour trap k with increasing distance to trap i . We were not able to account for a time decay or seasonality effect in calculating $Rem_{i,t}$, because we had neither the temporal resolution nor extent; 25.1% of the 3,036 traps were measured only once or twice, and only 21.4% of traps were measured for more than 30 days.

The above description included only indigenous forest, but we also included effects of additional habitats in the same form as [Equation \(4\)](#), along with their interactions to account for distraction effects or complementary use of two habitats. We applied a model selection approach to determine which model components were necessary for predicting capture probability ([Table 1](#)). To do this, we explored a range of predictor variables according to our specific hypotheses and assessed model fit using the leave-one-out information criterion (LOOIC) (loo package v2.5.1; Vehtari et al., 2022). Firstly, we compared models 1–16 in [Table 1](#) to determine whether bait type, removal effects, date of trapping event and a trap's local habitat were important for predicting capture and therefore should be included as control variables in all subsequent models that explored habitat effects. Secondly, to assess whether habitat type rankings aligned with H_1 , we compared models 17–21 with the best-fitting control model in [Table 1](#), determining the importance of each habitat individually (exotic forest, indigenous forest, grassland, scrub and the latter two unforested habitats combined as 'unforested'). To address H_{2a-b} , we compared models 17–19 with equivalent models with a quadratic habitat effect term to assess whether effects on capture probability were non-linear (models 22–24 in [Table 1](#)). Next, we ran models including main habitat effects for pairs of habitats with all combinations of two-way interactions to test for non-additivity (H_{3a-c}), and compared each combination of main effects with and without interaction terms (models 25–30 in [Table 1](#)).

Finally, to answer Question 3, we used our best-fitting model in [Table 1](#) for prediction, firstly along simulated indigenous forest-to-grassland and indigenous forest-to-exotic forest gradients (H_4), then

in a subset of our real landscape, to explore how capture probability changed along a gradient from indigenous forest core to fragment (H_5).

Models were fitted with a Bayesian approach using the greta package v0.4.3 (Golding, 2019) in R v4.0.4 (R Core Team, 2021). We assigned priors for all β parameters as $\text{Normal}(0, 1)$. We scaled and centred $\text{Date}_{i,t}$, and scaled $\text{HabEff}_{h,i}$ and $\text{Rem}_{i,t}$ by dividing them by the maximum effective number of cells ($\frac{\text{buffer area}}{\text{grid area}} = \frac{400^2 \times \pi}{100^2}$) and the maximum number of trap nights (452), respectively. We used Hamiltonian Monte Carlo sampling across four parallel chains, each with 3,000 warmup (which were discarded) and 1,000 post-warmup samples, which resulted in a total of 4,000 posterior samples. All models achieved convergence based on visual assessment of trace plots and the potential scale reduction factor ($\hat{R} < 1.05$) using the coda package v0.19.4 (Plummer et al., 2006). We calculated the residuals as Dunn–Smyth randomised quantile residuals (Dunn & Smyth, 1996) and confirmed that errors were normally and identically distributed with residual and Q-Q plots. A variogram showed that there was no residual spatial autocorrelation. Our data were processed using the sf package v1.0.5 (Pebesma, 2018) and visualised using the ggplot2 v3.4.1 (Wickham, 2016) and bayesplot v1.10.0 packages (Gabry et al., 2019).

3 | RESULTS

Overall, we found that the area of indigenous forest and exotic forest drives variation in possum capture probability. Models that allowed for non-linearity in habitat effects of exotic forest or grassland, but not indigenous forest, were better at predicting relative possum density than equivalent simpler models. We found the long-term landscape-level effect of trapping efforts through time (negative) was opposite from the localised effect of increasing removals (weak but positive). These findings are presented in further detail below.

3.1 | Question 1: Which habitats need most to be included in predictions of possum capture probability?

In support of hypothesis H_1 , we found that indigenous forest was the most important habitat for predicting possum capture probability (models 17–19 in Table 1). Goodness of fit for our best-fitting model was better when predicting at the trap-level rather than the trap-night level (trap-level: conditional $r^2 = 0.48$; trap-night-level: conditional $r^2 = 0.14$; Tjur, 2009), due to the high incidence of zeros typical of capture data. Holding the removal effect, $\text{TrapHab}_{i,m}$, $\text{BaitLure}_{i,t}$ and $\text{Date}_{i,t}$ constant, being surrounded by more indigenous forest cover or more exotic forest cover increased a trap's mean capture probability (indigenous: no cover, 0.095; half cover, 0.12; full cover, 0.15; exotic: no cover, 0.104; half cover, 0.13; full cover, 0.16; Figure 3). We found that considering habitat effects of grassland and scrub separately fitted more poorly than considering them together as an unforested habitat effect (models 19–21 in Table 1). Accounting for this unforested habitat effect also improved model fit relative to

the best-fitting controls-only model (models 19 vs. 16 in Table 1), and we found that capture probability fell as grassland cover increased (no cover, 0.14; half cover, 0.097; full cover, 0.066; Figure 3), suggesting that large areas of grassland or scrub were unfavourable for possums. However, the model with unforested habitats still fitted more poorly than the equivalent model with indigenous forest habitats (models 19 vs. 17 in Table 1). Therefore, the explanatory power of unforested habitats is likely to be largely determined by its negative relationship with indigenous forest cover. Although accounting for exotic forest alone did not improve fit relative to the best-fitting control model, the inclusion of an exotic forest habitat effect in models along with an indigenous forest habitat effect improved model fit (model 25 or with interaction: model 26 vs. model 18 in Table 1).

We hypothesised that the habitat effects on capture probability would saturate (indigenous forest; hypothesis H_{2a}) or be offset by increasing loss of food or shelter (exotic forest and grassland respectively; hypothesis H_{2b}). Our results do not support H_{2a} ; we found that the model with a nonlinear indigenous forest effect (quadratic term for habitat effect) was no better at predicting capture probability than its respective more parsimonious linear model (models 22 vs. 17 in Table 1); that is, the quadratic term had relatively low explanatory power. Although the addition of quadratic terms to models of the main habitat effects of exotic forest or grassland did improve model fit relative to simpler models (in support of hypothesis H_{2b}), all remained worse at predicting capture probability than the simplest indigenous forest habitat effect model (models 18, 19, 23 and 24 vs. 17 in Table 1). Furthermore, we did not find evidence of strong distance-decay effects (Table 2). This lack of difference was visible in our exploration of how predicted $\text{HabEff}_{\text{indfor},i}$ varied for combinations of cells in indigenous forests at increasing distance from a focal trap (Figure S3).

3.2 | Question 2: Is the strength of habitat effects influenced by neighbouring habitats?

In support of hypothesis H_{3a} , our best-fitting model retained the two-way habitat effect interaction term of indigenous forest with exotic forest (models 26 vs. 25 in Table 1). Adding the grassland habitat

TABLE 2 Posterior means and 90% credible intervals of model coefficients of our best-fitting model (Model 26 in Table 1).

Coefficient	Equation	Mean	5% CI	95% CI
β_0	3	-2.817	-3.006	-2.624
β_1	5	0.244	0.032	0.472
β_2	3	0.885	0.643	1.128
β_3	3	-0.293	-0.375	-0.208
β_4	3	-1.049	-1.127	-0.972
β_5	4	0.689	0.341	1.056
β_6	4	0.875	0.444	1.294
β_7	4	-1.022	-2.314	0.303
γ	4 & 5	1.820	0.294	5.423

effect to models of either indigenous forest or exotic forest never improved model fit (models 27–30 vs. 26 in Table 1). The interaction we observed between indigenous forest and exotic forest habitat effects suggests that the indigenous forest habitat effect was influenced by neighbouring exotic forest habitat, and that information about the amount of indigenous forest and exotic forest together is required to generate suitable predictions of capture probability at given trap locations (Figure S4).

3.3 | Question 3: How does the spatial configuration of the surrounding landscape influence capture probability?

We found that capture probability was driven by the total area of nearby indigenous forest and its proximity to exotic forest areas. Across an indigenous forest-exotic forest edge, predictions using our best-fitting model (model 26 in Table 1) showed that capture probability was lowest at the edge and increased as either indigenous forest or exotic forest cover increased (Figure 4). Across an indigenous forest-grassland edge, however, capture probability decreased almost linearly with distance from the edge, in support of hypothesis H_4 (Figure 4). Comparing capture probability across indigenous forest patches in a matrix of grassland within a subset of the Māhia peninsula further supports the importance of total indigenous forest area, rather than the arrangement of, or distance to, patches (Figures S3 and S5).

3.4 | Control variables

We found that accounting for trapping habitat, capture history, bait type and trapping date all improved predictions of capture probability relative to the intercept-only model (models 1–16 in Table 1). Capture probability was higher in traps located in indigenous forests relative to other habitats, and in traps baited with flour blaze (rather than a visual lure) on a given night (Figure S6A,B). Capture probability decreased strongly through time, suggesting a reduction in possum density at the landscape-level (Figure S6D). Interestingly, at the local-level (i.e. in a trap's neighbourhood buffer), capture probability increased slightly as the cumulative number of possums captured nearby increased, but the increase was approximately linear in the response scale within the observed range of removal values (Figure S6C).

4 | DISCUSSION

In this research, we explored how spatial habitat patterns influenced the provision of an NCP (quantified through the probability of possum capture) across a heterogeneous landscape in Aotearoa New Zealand. We expected that predicted NCP provision would vary in non-linear ways in response to the amount of, and proximity to, different habitat types because possums utilise different

habitats for different purposes (i.e. trading off between shelter and food resources; Figure 1; Clout, 2006; Warburton, 1978). We found some evidence of interaction effects between neighbouring habitats, with our main model retaining the main habitat effects of indigenous forest and exotic forest, with which capture probability was positively associated, and their interaction (Figures 3 and 4; Figure S5). This suggests that indigenous forest area in a trap's neighbourhood and its proximity to exotic forest areas were the most important factors in determining possum density, with implications for management decisions that prioritise indigenous afforestation for other positive NCP that this habitat supports (Brockerhoff et al., 2017; Gómez-Creutzberg et al., 2021). By utilising methods from other research fields, we have mapped predictions of this NCP's provision across our focal landscape (Figure 5), in a way that can be easily extended to predict the provision of, and interactions among, multiple NCP in future landscapes. Further explanations are detailed below.

We built upon existing approaches that relate landscape features to NCP provision in order to generate realistic predictions that can inform landscape management decisions. Our novel approach based on methods previously applied for estimating dispersal shadows (Clark et al., 1999; Ribbens et al., 1994) overcomes two main limitations. Firstly, we moved beyond a transect-based approach of measuring a unidirectional relationship between NCP provision and distance from source habitat (Ricketts et al., 2008) to determine whether predictions are improved when multiple habitat patches concurrently contribute (and receive) mobile NCP providers (Goedhart et al., 2018). Secondly, we overcome the limitations of regression approaches that assess distance effects using arbitrary concentric circles of habitat features, which effectively restrict animal movement to be unidirectional (Goedhart et al., 2018). Instead, we allowed any habitat to be a source and/or recipient of NCP. Although our approach enables tests for more realistic nuance to spatial distance-decay of NCP provision, in this particular application to possums in Aotearoa New Zealand, we found surprisingly weak distance-decay effects (our fitted γ value was large). Nevertheless, total indigenous forest area and its proximity to exotic forest patches were the most important variables for explaining differences in capture probability (Figures S3 and S5). The strong role of forest cover and the weak distance-decay relationship we observe have implications for the conclusions we can draw from transect-based studies. As shown in Figure 4b, each point along a forest-grassland transect will by necessity be surrounded by progressively less forest. This reduction in forested habitat may in fact generate an apparent distance-decay function that is inconsistent with evidence from our focal system that the importance of indigenous forest for possum capture does not decay rapidly with distance.

Predictions from our best-fitting model suggest that capture probability will be greatest in landscapes dominated by indigenous forest and exotic forest, and lower in mixed forest-grassland landscapes (Figure 5). Although it is unclear how well our best-fitting model can predict relative possum density in landscapes outside the

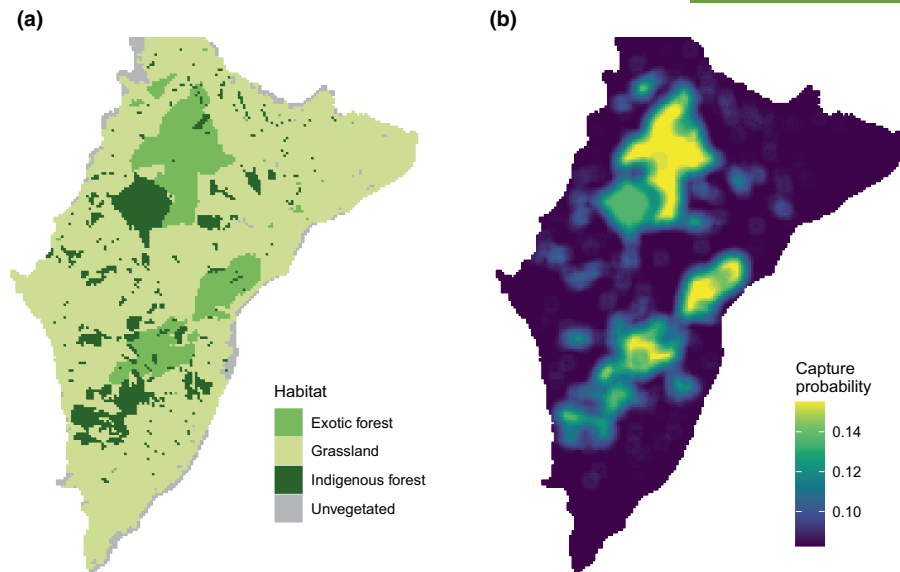


FIGURE 5 Application of our approach to the Māhia Peninsula. Panel (a) shows habitat cover across the study area, panel (b) shows median capture probability at each 100-m grid cell, predicted using output from model 26 in Table 1, all else held constant.

Māhia peninsula, the fact that including more specific habitat types (grassland and scrub considered as separate habitats; models 11–13 in Table 1) did not improve model fit is encouraging. Finally, we found that bait choice was important in predicting trapping outcomes, and although the removal effect was retained in model selection, capture probability at a given trap increased only weakly as the number of removals increased (Figure S6). This implies that some individuals may spread out their home ranges in response to localised removals around a trap (Rouco et al., 2017), but this effect is weakened by the strong population decline at the landscape level (the coefficient of $Date_{i,t}$ is large and negative).

To meet trapping programme objectives to limit possum populations, deployment effort must be proportional to possum risk. Based on our findings, we therefore recommend focusing trapping efforts in the indigenous forest and exotic forest core to align with the predicted possum risk (Figure 5). These predictions have clear implications for management (through optimising trap deployment), and have been requested by the local government (Hawke's Bay Regional Council) as inputs for their proof-of-absence modelling on the Māhia peninsula. However, decisions about resource allocation must also consider the feasibility and cost-effectiveness of potential trapping locations. For possum monitoring, it is important to understand how both fixed and variable costs vary non-linearly with increasing spatial coverage (Gormley et al., 2015). Even though our results suggest that moving trapping efforts even 500m into the forest core can improve capture probability relative to the forest-grassland edge (Figure 4), we could expect that the locations with some of the highest predicted capture probability (i.e. dense forest) may be inaccessible for trap deployment. Incorporating these data was beyond the scope of our study, but we suggest that future research that extends our modelling approach considers other factors relevant to the focal landscape and the NCP-providing species.

Our exploration of the NCP associated with possum density adds to the small but growing literature that examines negative NCP provided by vertebrates, such as squirrels, rodents, birds and bats, with implications for the broader challenge of managing landscapes for multiple NCP (Kross et al., 2012; Pyšek & Richardson, 2010; Tschumi et al., 2018; Vansynghel et al., 2022). Indigenous forest supports multiple other NCP, including other mobile species (Brockerhoff et al., 2017; Gómez-Creutzberg et al., 2021). Additionally, extensive grassland not only can mitigate the negative NCP possums provide but supports multiple positive NCP (Bengtsson et al., 2019). Managing for the negative NCP from possums will therefore need to consider these multiple trade-offs and synergies, to ensure that decisions made to promote positive NCP from indigenous forest are not outweighed by an increased negative NCP provision such as invasive pest abundance. Because each of these habitats supports unique NCP, landscape management for multifunctionality will need to carefully consider their relative contributions to each NCP and their trade-offs (Gómez-Creutzberg et al., 2021), along with diverse stakeholder preferences (Neyret et al., 2023). Furthermore, classifying NCP as 'positive' or 'negative' depends on worldview and can differ across communities (Pascual et al., 2022); alongside possums' negative contributions to culturally significant indigenous species, possums also make positive economic and cultural contributions via fur harvesting for some small rural Māori communities (Díaz et al., 2018; Jones et al., 2012). Fortunately, our modelling approach is designed to be applied to other NCP provided by mobile species and has the flexibility to make spatial predictions about bundles of multiple positive or negative NCP considered together (Le Provost et al., 2023). By overlaying landscape-level predictions as in Figure 5 for multiple NCP, decision-makers can explore whether trade-offs or synergies arise in particular habitat arrangements with ease. Such research will aid land-use decision-makers to confidently predict the extent

to which current and future landscape arrangements can provide multiple NCP in ways that can be equitably delivered to local communities (Kass et al., 2023; Neyret et al., 2023).

AUTHOR CONTRIBUTIONS

Sophie A. O'Brien, Jason M. Tylianakis and Sandra Lavorel conceived the ideas. Jason M. Tylianakis and Sandra Lavorel secured the funding. Sophie A. O'Brien, Jason M. Tylianakis, Sandra Lavorel and Dean P. Anderson designed the methodology; Natalie de Burgh coordinated the field programme that provided the data; Sophie A. O'Brien processed the data and led the writing of the manuscript. Sophie A. O'Brien, Dean P. Anderson and Hao Ran Lai analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw land cover data are publicly available and can be accessed from <https://iris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-version-50-mainland-new-zealand>. Processed trapping data are available from the Figshare repository <https://doi.org/10.6084/m9.figshare.c.7392709> (O'Brien et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Steps to prepare trapping data.

Appendix S2: Land cover categorisation.

Appendix S3: Habitat effect recalculated using a range of buffer widths.

Appendix S4: Habitat effect recalculated using grid cell centroids.

Appendix S5: Further supporting figures.

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