

<sup>1</sup> Mesopredator release among invasive predators: controlling red foxes can  
<sup>2</sup> increase feral cat density and alter their behaviour

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<sup>6</sup> *Data accessibility:* Data and code will be deposited on the Dryad Digital Repository after acceptance and  
<sup>7</sup> can be viewed here: <https://github.com/matt-w-rees/invasive-mesopredator-release>.

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<sup>9</sup> control, mesopredator release, spatial capture-recapture

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10 **ABSTRACT**

- 11 1. The mesopredator release theory predicts that the density of subordinate predators will increase  
12 as dominant predators decline. Persistent debate around mesopredator release in part reflects the  
13 lack of robust, replicated experiments to test this theory, and the use of population indices which  
14 confound changes in mesopredator density and detectability. This uncertainty has immediate impacts  
15 for conservationists who are faced with managing sympatric invasive predators.
- 16 2. We used replicated experimental designs and spatially-explicit models to examine whether mesopredator  
17 release of the feral cat *Felis catus* occurs in response to targeted control of the introduced red fox  
18 *Vulpes vulpes*. We surveyed three Control-Impact paired landscapes in a region with long-term fox  
19 control (1080 poison baiting), and conducted a Before-After Control-Impact Paired-Series experiment  
20 in another region. We used fox occurrence as a simple metric of fox populations and estimated feral  
21 cat density with spatial mark-resight models.
- 22 3. Lethal fox control had varying effects on fox occurrence, consistent with variation in the duration and  
23 intensity of poison baiting. Correspondingly, responses in feral cat density ranged from negligible to a  
24 3.7-fold higher density in fox-baited landscapes. At a fine spatial scale ( $200 \text{ m}^2$ ), feral cat density was  
25 negatively associated with fox occurrence probability across both regions. These results were consistent  
26 with mesopredator release, although uncertainty was high in the region where fox control had only  
27 recently commenced.
- 28 4. Feral cat detectability also varied across the (artificially-manipulated) gradients of fox occurrence  
29 probability. In one region, nonlinear models indicated that feral cats had lower detection and increased  
30 movement rates when foxes were uncommon, giving way to density suppression at high fox occurrence  
31 probabilities.
- 32 5. *Synthesis and applications.* Our study provides replicated, experimental evidence that dominant  
33 predator suppression can be associated with a higher mesopredator density. Mesopredator release  
34 can manifest as changes in both behaviour and density, distorting inference if these processes are not  
35 distinguished. Our results may help explain why fox control does not consistently improve native  
36 prey persistence, suggesting integrated pest management may be necessary to improve conservation  
37 outcomes.

<sup>38</sup> **1. INTRODUCTION**

<sup>39</sup> Understanding species interactions is critical for effective invasive species management (Zavaleta, Hobbs,  
<sup>40</sup> & Mooney 2001). Where several invasive species co-occur, management actions that suppress the dominant  
<sup>41</sup> invasive species may inadvertently benefit subordinate invasive species (Jackson 2015). For example, the  
<sup>42</sup> removal of a dominant invasive predator may increase the density of subordinate invasive predators directly  
<sup>43</sup> by reducing top-down pressure, or indirectly by increasing the availability of shared resources; often referred  
<sup>44</sup> to as mesopredator release (Soulé *et al.* 1988; Prugh *et al.* 2009). The release of subordinate invasive  
<sup>45</sup> predators can have serious negative implications for native taxa and ecosystem function (Doherty & Ritchie  
<sup>46</sup> 2017; Takimoto & Nishijima 2022). However, integrated invasive predator management is often far more  
<sup>47</sup> costly and less feasible than single species control, and so it is important to identify when the extra cost is  
<sup>48</sup> justified (Bode, Baker, & Plein 2015).

<sup>49</sup> Most knowledge of mesopredator release stems from unreplicated ‘natural experiments’ (e.g., range  
<sup>50</sup> contractions - Crooks & Soulé 1999) or ad-hoc management interventions (e.g., invasive species eradication -  
<sup>51</sup> Rayner *et al.* 2007) where dominant predators have become largely absent from the system. It is particularly  
<sup>52</sup> unclear whether mesopredator release still occurs when dominant predators are suppressed but not completely  
<sup>53</sup> removed. The occurrence, nature (positive or negative, direct or indirect) and strength of predator interactions  
<sup>54</sup> can vary among species assemblages, environmental productivity, management regimes and other landscape  
<sup>55</sup> contexts (Finke & Denno 2004; Baum & Worm 2009; Ritchie & Johnson 2009). Replicating management  
<sup>56</sup> programs in an experimental framework is logically challenging, but important for understanding these  
<sup>57</sup> complexities, discriminating between plausible hypotheses and producing generalisable results to inform  
<sup>58</sup> effective pest management (Glen & Dickman 2005; Ford & Goheen 2015).

<sup>59</sup> Another source of uncertainty around the mesopredator release hypothesis stems from the inability of  
<sup>60</sup> traditional survey and modelling approaches to distinguish behavioural from numerical population processes  
<sup>61</sup> (Anderson 2001; Hayward *et al.* 2015). Suppression of a dominant predator may simultaneously change  
<sup>62</sup> the behaviour and the density of a mesopredator, both of which influence detection rates (Broadley *et al.*  
<sup>63</sup> 2019). This makes it difficult to interpret observed changes in naïve indices of mesopredator activity or  
<sup>64</sup> occurrence in relation to changes in dominant predator populations, even if the study has an experimental  
<sup>65</sup> design. Unbiased estimates of invasive predator density are also important for setting meaningful control  
<sup>66</sup> targets and inferring impacts on native prey (Moseby *et al.* 2019). Spatial capture-recapture methods offer a

67 solution by separating behavioural and observational processes from population density, estimated within a  
68 defined spatial unit (Gardner, Royle, & Wegan 2009).

69 Predation by two invasive species, the red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus*  
70 (hereafter ‘cat’), has played a major role in Australia’s high rates of mammalian extinction (Woinarski,  
71 Burbidge, & Harrison 2015). Integrated pest management programs are rare; instead, foxes are far more  
72 commonly controlled than cats, as they are more susceptible to poison baiting, have greater direct economic  
73 impacts and fewer legal impediments to control (Reddiex *et al.* 2007; McLeod & Saunders 2014). Nonetheless,  
74 cats are one of the most widespread and damaging vertebrate predator species (Medina *et al.* 2011; Doherty  
75 *et al.* 2017; Legge *et al.* 2020). As foxes are larger-bodied and have high dietary overlap with cats (Fleming  
76 *et al.* 2022), the mesopredator release hypothesis (Soulé *et al.* 1988) predicts cat density will increase as fox  
77 populations are suppressed (Molsher *et al.* 2017). Mesopredator release of cats would likely dampen the  
78 conservation benefits of fox control, and could even worsen outcomes for some native prey species (Takimoto  
79 & Nishijima 2022), as has previously been suspected (e.g., Wayne *et al.* 2017).

80 Evidence that foxes suppress cats is inconclusive. In parts of Australia where the apex mammalian  
81 predator (the dingo *Canis familiaris*) is locally extinct and introduced foxes are the largest terrestrial  
82 mammalian predator, four studies found that fox control was associated with higher cat detection rates  
83 (Risbey *et al.* 2000; Marlow *et al.* 2015; Norton *et al.* 2015; Stobo-Wilson *et al.* 2020). However, two other  
84 studies in similar systems did not see any change (Towerton *et al.* 2011; Molsher *et al.* 2017). A further  
85 study with spatial replication detected an increase at one site but not another (Davey *et al.* 2006), and  
86 another observed a decrease in cat activity (Claridge *et al.* 2010). No prior studies have directly estimated  
87 changes in cat density in response to fox control. More reliable and standardised population measurements  
88 need to be deployed across different landscapes to understand what factors drive the variable responses of  
89 cats to dominant predator control (Hayward *et al.* 2015).

90 We experimentally investigated the role of introduced foxes in top-down suppression of cat density across  
91 eight landscapes within two regions of south-eastern Australia. Our experiment had a replicated Control-  
92 Impact design in the region with long-term fox control, and a Before-After Control-Impact Paired-Series  
93 (BACIPS) design in the region with newly implemented fox control. Foxes and cats are the only terrestrial  
94 mammalian predators in these regions heavier than one kilogram. Each region included at least one area in  
95 which foxes were subject to continuous lethal poison baiting (hereafter ‘impact landscape’), and a paired area

96 where foxes were not controlled (hereafter ‘non-impact landscape’). This allowed focus on the associations  
97 between the two invasive predators, across an artificially-manipulated gradient of dominant predator (fox)  
98 occurrence probability. In accordance with mesopredator release theory, we predicted that: (1) fox control  
99 would be associated with higher cat densities at the landscape-scale, and (2) cat density would be negatively  
100 correlated with fox occurrence probability at a fine spatial scale (which could help explain cat responses  
101 to fox control). We based inference on direct estimates of cat density using spatially explicit mark-resight  
102 models.

<sup>103</sup> **2. MATERIALS AND METHODS**

<sup>104</sup> *2.1. Study area*

<sup>105</sup> We conducted our study across two regions of south-west Victoria, Australia (Fig. 1). The native  
<sup>106</sup> temperate forests in both regions are fragmented to varying degrees, primarily by livestock farming and  
<sup>107</sup> timber plantations. Dingoes are now absent throughout southwest Victoria (Cairns *et al.* 2018). A native  
<sup>108</sup> mesopredator, the tiger quoll *Dasyurus maculatus* is long absent from the Glenelg region and extremely rare  
<sup>109</sup> in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial mammalian  
<sup>110</sup> predator guild is therefore depauperate, with foxes and cats being the primary mammalian terrestrial  
<sup>111</sup> predators heavier than one kilogram; birds of prey and snakes are the only other medium-large carnivores  
<sup>112</sup> present.

<sup>113</sup> Our study landscapes in the Glenelg region were primarily lowland forest and heathy woodland (Depart-  
<sup>114</sup> ment of Environment, Land, Water & Planning 2020). The area receives an average annual rainfall of 700 mm  
<sup>115</sup> (Bureau of Meteorology 2021, Cashmore Airport) and has gently undulating terrain. The region frequently  
<sup>116</sup> experiences prescribed burns and wildfires, creating a mosaic of fire histories and vegetation complexity. Our  
<sup>117</sup> study landscapes in the Otway region were in the western section of the Otway Ranges. Rainfall here is  
<sup>118</sup> more than twice as high as the Glenelg region (Bureau of Meteorology 2021, Cape Otway). The vegetation is  
<sup>119</sup> a mosaic of shrubby wet forest and cool temperate rainforest, with the northern landscape bordering on a  
<sup>120</sup> large heathy woodland (Department of Environment, Land, Water & Planning 2020). This region rarely  
<sup>121</sup> experiences fire and is nearly ten times more rugged than the Glenelg region (based on the terrain ruggedness  
<sup>122</sup> index, Riley, DeGlria, & Elliot 1999).

<sup>123</sup> Government land managers conduct ongoing targeted fox control for biodiversity conservation across  
<sup>124</sup> broad landscapes within each region (detailed in Section 2.2 below). In these landscapes, manufactured  
<sup>125</sup> poison baits ('FoxOff', Animal Control Technologies, Somerton) containing 3 mg of sodium fluroacetate  
<sup>126</sup> (compound 1080) are buried at a depth of 12 - 15 cm at 1-km intervals along accessible forest tracks and  
<sup>127</sup> roads (Fig. 1). Different road densities across the two regions result in variable poison bait densities. Other  
<sup>128</sup> large sections within each region are maintained without fox control.

<sup>129</sup> 2.2. Study design and camera-trapping

<sup>130</sup> We designed experiments around the implementation of fox-baiting in each region. We simultaneously  
<sup>131</sup> surveyed one impact and one non-impact landscape at a time. Each pair of impact and non-impact landscapes  
<sup>132</sup> were chosen based on similarity in vegetation groups, while aiming to maximise spatial independence with  
<sup>133</sup> respect to predator daily movements.

<sup>134</sup> In the Glenelg region, we used a spatially replicated Control-Impact design to compare three impact  
<sup>135</sup> landscapes that had been poison baited for foxes at fortnightly intervals for more than 13 years with three  
<sup>136</sup> paired non-impact landscapes. The pairing of these landscapes was based on similarities in vegetation  
<sup>137</sup> classes, and specified in the original design of the Glenelg Ark monitoring program (Robley *et al.* 2014). We  
<sup>138</sup> surveyed Cobboobooonee National Park (impact) and Annya State Forest (non-impact) in January – April  
<sup>139</sup> 2018 ('replicate 1'), Mt Clay State Forest / Narrawong Flora Reserve (hereafter 'Mt Clay'; impact) and  
<sup>140</sup> Hotspur State Forest (non-impact) in April – June 2018 ('replicate 2'), and Lower Glenelg National Park  
<sup>141</sup> (LGNP) South (impact) and LGNP North (non-impact) in March – May 2021 ('replicate 3'). For replicates 1  
<sup>142</sup> and 2, the paired landscapes were separated by at least 8 km, a distance unlikely to be frequently traversed  
<sup>143</sup> regularly by these invasive predators (Hradsky *et al.* 2017). Lower Glenelg National Park South and North  
<sup>144</sup> are separated by the Glenelg River, which is unlikely to be regularly crossed by most terrestrial animals.

<sup>145</sup> In the Otway region, we used a Before-After Control-Impact Paired-Series (BACIPS) design to assess  
<sup>146</sup> changes related to the introduction of a fox control program. We deployed camera-trap grids in a pair of  
<sup>147</sup> impact – non-impact landscapes from June to September in three years (2017, 2018, 2019), in the Great  
<sup>148</sup> Otway National Park and Otway Forest Park. Our first survey occurred approximately three months before  
<sup>149</sup> fox-baiting began. Fox-baiting commenced for the first time in the impact landscape in November 2017.  
<sup>150</sup> Poison baits were replaced weekly for six weeks until December 2017, before changing to monthly bait  
<sup>151</sup> replacement until July 2018. The second survey was conducted six months after fox-baiting commenced,  
<sup>152</sup> however poison bait replacement ceased from near the beginning of the survey until nearly three months  
<sup>153</sup> afterwards. Fox-baiting at monthly intervals recommenced in December 2018, six months prior to the start of  
<sup>154</sup> the final survey (Supporting Information Fig. S1). The impact ('South') and non-impact ('North') landscapes  
<sup>155</sup> were at least 4.2 km apart through dense forest. In this study, and a concurrent study which identified  
<sup>156</sup> individual foxes through genetic sampling (Le Pla *et al.* 2022), we found no evidence that either foxes or cats  
<sup>157</sup> moved between the impact and non-impact landscapes.

158 In each landscape, we established an irregular grid of 49 – 110 sites (mean: 88). We broadly aimed to  
159 space camera-traps 500 m apart, but randomly varied distances from 194 – 770 m (mean spacing: 448 m) to  
160 achieve an irregular spacing design (Rich *et al.* 2019). Larger ‘holes’ in the camera-trap grids were due to  
161 accessibility constraints. We situated each site in the forest interior, at least 30 m from roads and tracks. At  
162 each site, we set up a Reconyx (Holmen, Wisconsin) infrared camera-trap on a tree, facing a tuna oil lure  
163 (Supporting Information S1.1; Fig. S2; Table S1). Overall, we deployed 1,051 functional camera-traps, which  
164 operated for an average of 65 days (range: 12 – 93 days), totalling 68,504 trap nights (Table 1). Surveys  
165 were conducted under approval from the University of Melbourne Animal Ethics Committee (ref: 1714119)  
166 and Victorian Government (ref: 10008273)

167 *2.3. Individual feral cat identification*

168 We sorted the camera-trap images of cats into five categories based on coat type (Supporting Information  
169 Fig. S3), and identified individual feral cats within each category; see Supporting Information S1.2 for details.  
170 In the Otway region, 40% of cat detections were of black cats with few identifiable markings, so we did not  
171 attempt to identify any black cats here. In the Glenelg region, black cats were rarer (not detected at two  
172 landscapes) and often more distinctive, and so we could identify some individuals (Table 1).

173 *2.4. Fox spatial occurrence*

174 To (i) investigate effects of poison-baiting on foxes, (ii) test for negative correlations between foxes and  
175 cat density and (iii) account for potential effects of foxes on cat detectability, we modelled fine-scale and  
176 spatially-explicit fox occurrence probabilities. We used fox occurrence probability as a simple metric of fox  
177 populations in lieu of simultaneous, reliable fox density estimates. Foxes are not individually identifiable  
178 from camera-trap images (Güthlin, Storch, & Küchenhoff 2014) and, while density estimates can be derived  
179 from unmarked populations, their reliability remains questionable (Barker *et al.* 2018; Sun *et al.* 2022). We  
180 modelled fox occurrence probabilities (from presence-absence records) rather than detection counts as we  
181 considered this more conservative: a greater change in fox density is likely required to alter occurrence. In  
182 some circumstances, predator occurrence probability scales with population density (e.g., Linden *et al.* 2017),  
183 although this remains unknown in our study.

184 We could not use raw fox presence-absence data from the camera-traps as a response variable for cat

185 density as spatial mark-resight models require covariate values for each grid cell in which density is estimated  
186 (see Section 2.5). Instead, we generated a spatially-interpolated layer of the probability of fox occurrence for  
187 each study landscape, using fox presence-absence data for each camera-trap site and binomial generalised  
188 additive mixed-effects models (Wood 2017). These models allow efficient nonlinear spatial estimates, but do  
189 not account for imperfect detection. Nonetheless, naïve fox occurrence probabilities may relate to how cats  
190 perceive the risk of fox encounter for the survey duration.

191 We built fox occurrence models using the ‘mgcv’ R-package (version 1.3.1, Wood 2011). We modelled fox  
192 presences and absences (response variable) across space (explanatory variable) separately for each region, with  
193 a Duchon spline spatial smooth (which provide better predictions at the edge of surveyed space than other  
194 splines, Miller & Wood 2014). In the Otway region, we included a random intercept for each camera-trap site  
195 to account for repeat sampling and did not share spatial information across years. Differences in camera-trap  
196 deployment lengths were accounted for using a model offset.

197 *2.5. Spatial mark-resight models of feral cat density*

198 We used a spatial capture-recapture approach to estimate cat density (Gardner, Royle, & Wegan 2009).  
199 These models use counts of detections and non-detections of individual animals at trap locations (accounting  
200 for trap-specific survey effort) to estimate the location of each individual’s activity centre. They commonly  
201 assume that individuals have approximately circular home ranges, spend the majority of time in the centre  
202 of their range (‘activity centre’), and that the probability of observing an individual decreases with distance  
203 from the activity centre. Two detectability parameters govern this process:  $g_0$ , the probability of detecting  
204 an individual per occasion in their activity centre, and  $\sigma$ : a spatial scale parameter which relates to  
205 home range size. Multiple candidate shapes for the decline in detectability with distance from the activity  
206 centre (‘detection function’) can be modelled, although half-normal and exponential are most commonly  
207 used. Spatial capture-recapture models have been extended to consider situations where not all individuals  
208 in a population are identifiable (i.e., some are unmarked, Efford & Hunter 2018). These models typically  
209 assume unmarked individuals to be a random sample of the population, sharing the same detection process  
210 as marked individuals, allowing density to be estimated for the entire population.

211 We used sighting-only spatial mark-resight models to estimate cat density using the maximum likelihood  
212 ‘secr’ R-package (version 4.4.4, Efford 2021). We used closed population models as open population spatial

mark-resight models have not yet been developed. Detections of the ‘mark status uncertain’ category (unidentifiable cats), cannot be handled in the ‘secr’ R package; we added them to as ‘unmarked’ detections (black cats) rather than discard them (following Moseby, McGregor, & Read 2020). We condensed unmarked detection histories to a binary presence-absence record per each camera-trap for a 24-hour length duration (‘occasion’), beginning at midday. We ran separate models for each region and treated each camera-trap grid deployment as a ‘session’ within the region-specific model. We created a 4000-m buffer zone around each site (which was truncated by the river in LGNP), and estimated cat density at a 200-m grid cell resolution within this area. These habitat mask specifications were based on initial model trials and our knowledge of cat behaviour in these regions; the aim was to ensure density was estimated over a large enough area to encompass the activity centres of all cats exposed to our camera-traps, at a fine enough spatial scale to minimise bias in density estimates.

For each region, we ran four sets of models. We (1) chose between half-normal and exponential detection functions and (2) chose ‘base model’ covariates to carry through to subsequent model sets. We then (3) evaluated the effect of fox control on cat density at the landscape scale with traditional experimental approaches (prediction 1), and (4) tested for associations between fox occurrence probabilities and cat density at a fine spatial scale (prediction 2). To choose between competing model specifications, we used small-sample corrected Akaike Information Criterion (hereafter ‘AIC<sub>c</sub>’) scores (Burnham & Anderson 2004); carrying forward or presenting the top-ranked model (i.e., model with the lowest AIC<sub>c</sub> score). In addition to examining confidence intervals around estimated model coefficients, we also used AIC<sub>c</sub> scores to assess statistical evidence; models within two AIC<sub>c</sub> units are generally considered equivalent in terms of predictive power (Burnham & Anderson 2004). Steps two to four are described in more detail below.

The second set of models (base models) established the base covariates for each region. We hypothesised that cat detectability might decrease over each survey due to the scent of the tuna oil lure fading. To account for this, we modelled a nonlinear trend in  $g_0$  over the survey duration for each camera-trap. We also used a range of camera-trap models which could have impacted detection rates (Table S1). We tested whether camera-trap model impacted cat detection rates in the Otways, but not the Glenelg region as 97% of cameras here were the HC600 model (3% were the PC900 model which primarily differ only in software settings, Seidlitz *et al.* 2020), using camera-trap model as a categorical variable ( $n = 5$ ) on  $g_0$ . We further hypothesised that cat density might differ between vegetation types. We classed the vegetation into three dominant types for each region: cleared land, heathy vegetation, and either dry forest (Glenelg region) or wet

243 forest (Otway region); see Supporting Information S1.3, Fig. S4, for details. We compared these covariates  
244 as single and additive models, as well as to a ‘null model’ (density and detectability constant), and carried  
245 the supported covariates forward to subsequent model sets.

246 The third set of models inferred the effects of fox-baiting on cat density at a landscape scale within  
247 each region using traditional experimental designs (prediction 1). We fitted models which estimated cat  
248 density separately for each landscape, and used AIC<sub>c</sub> scores to choose whether to model detectability as a  
249 function of predicted fox occurrence probability or constant. For the top-ranked model, we then calculated  
250 the estimated difference in cat density between paired landscape surveys (via the ‘contrasts’ argument in the  
251 ‘secr.fit’ function). We assessed the weight of statistical evidence using confidence intervals of the estimated  
252 difference and a p-value threshold of 0.05. In CI experiments (Glenelg region), a p-value below 0.05 is  
253 achieved when the 95% confidence interval of the estimated difference between the two independent samples  
254 does not cross zero on the natural logarithmic scale (Cumming & Finch 2005). We repeated this confidence  
255 interval assessment three times in the Glenelg region, once for each spatially replicated landscape pair. In  
256 ‘repeated measures’ designs such as BACI experiments (Otway region), changes in successive estimates of  
257 difference provide inference of an effect (Cumming & Finch 2005); here a p-value below 0.05 is approximately  
258 reached once 83% confidence intervals do not overlap each other (Goldstein & Healy 1995; Austin & Hux  
259 2002). We therefore assessed whether the 83% confidence interval of the estimated difference between the  
260 Otway region paired landscapes in 2017 (before fox control) overlapped the respective 83% confidence interval  
261 of the estimated difference in 2018 (approximately six months after fox control first commenced), as well as  
262 in 2019 (approximately 18 months after fox control first commenced).

263 The fourth set of models directly tested the associations between fine-scale fox occurrence and cats  
264 within each region (prediction 2). We tested three models where (i) fox occurrence probability affected cat  
265 density, (ii) fox occurrence probability affected cat detectability (both  $g_0$  and  $\sigma$  concurrently, Efford &  
266 Mowat 2014), (iii) fox occurrence probability affected both the density and the detectability of cats, against  
267 the null model with no association between fox occurrence and cats. We used the spatial fox occurrence  
268 probability estimates (detailed in Section 2.4) as the explanatory variable. As predator associations may be  
269 nonlinear (Johnson & VanDerWal 2009), we tested these effects as linear and nonlinear terms using regression  
270 splines (generalised additive models called within the ‘secr’ R-package). We included year as a cat density  
271 covariate in all the Otway region models to account for repeat sampling. A limitation of this approach is  
272 that uncertainty from fox occurrence probability models was not propagated into the spatial mark-resight

<sup>273</sup> models - a full Bayesian integration of the fox occurrence analysis and the spatial mark-resight model to  
<sup>274</sup> address this is not yet implemented.

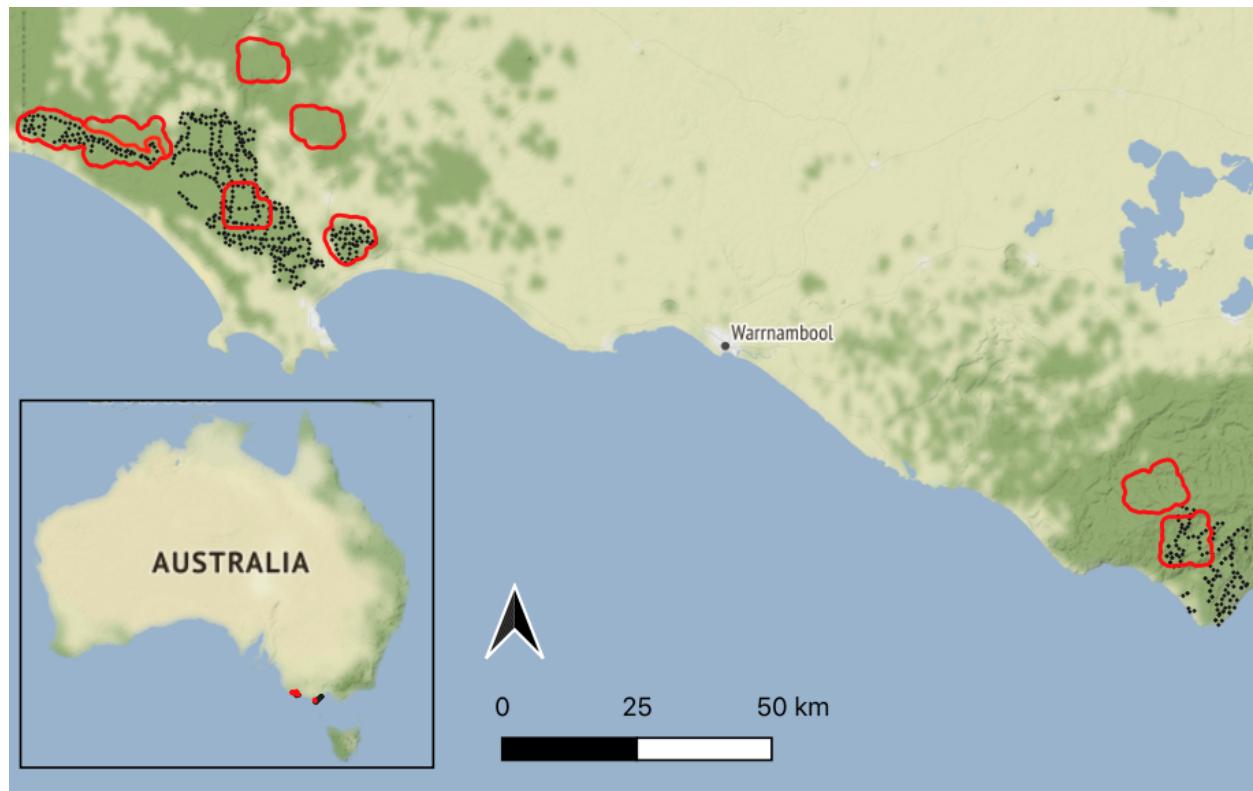


Figure 1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Locations of fox poison bait stations are denoted by black dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 3.0, map data by OpenStreetMap, under CC BY SA.*

275 **3. RESULTS**

276 *3.1. Glenelg region*

277 *3.1.1. Red Fox*

278 In the Glenelg region, foxes were detected at 48 – 57% of sites (i.e., naïve occupancy) within the three  
279 non-impact (unbaited) landscapes (Table 1). Naïve occupancy rates were more than two and three times  
280 lower in the paired impact (poison baited) landscape for replicates 1 and 3, respectively, but only 27% lower in  
281 replicate 2 (Table 1). The fox spatial occurrence probability model explained 13.1% of the null deviance, with  
282 an adjusted R-squared value of 0.13 (spatial standard error estimates are shown in Supporting Information  
283 Fig. S5). The fox occurrence model highlighted fine-scale variation in fox occurrence probabilities within  
284 landscapes (for example, fox occurrence probability was low in the centre of Mt Clay, but higher closer to  
285 the forest edge) and demonstrated a strong effect of the Glenelg River in separating fox populations in the  
286 Lower Glenelg National Park landscapes (Fig. 2).

287 *3.1.2. Feral cat*

288 Across the six landscapes in the Glenelg region, we recorded 251 cat detections from 32,232 camera-trap  
289 nights (Table 1). We were able to identify 64% of cat detections to the individual-level; a total of 67 cats (6 –  
290 13 individuals per landscape; Supporting Information Fig. S7; S8; S9). The exponential detector function  
291 was supported over the half-normal function (Table S2). The null model was marginally supported over  
292 models with vegetation impacts on cat density and linear time trends on  $g_0$  (Supporting Information Table  
293 S3).

294 Our prediction (1) that cat density would be higher in landscapes with fox control was supported for  
295 the first and third spatial replicates: estimated cat densities were 2.5 (95% CI: 1.5 - 4.2) and 3.7 (95% CI:  
296 1.4 - 9.5) times higher in the impact landscape than the paired non-impact landscape, respectively (Fig. 3).  
297 There was no difference in cat density between landscape pairs in the second spatial replicate (1.1; 95% CI:  
298 0.69 - 1.69; Fig. 3); this pair also had the smallest difference in naïve fox occupancy occurrence rates (Table  
299 1). At the landscape-level, there was little evidence that cat detectability was associated with fox occurrence;  
300 although this model ranked more highly than the constant detectability model (Supporting Information  
301 Table S4), the difference in AICc scores was only 0.95 units and the estimated effects were weak with high

302 uncertainty, i.e., detectability ( $g_0$ ): 0.24 (95% CI: -0.32 - 0.80); movement ( $\sigma$ ): 0.13 (95% CI: -0.14 -  
303 0.41).

304 Our prediction (2) that cat density would be negatively correlated with fox occurrence probability at a  
305 fine spatial scale was supported (4.26 AIC<sub>c</sub> units better than the null; Supporting Information Table S5). The  
306 top-ranked model indicated that cat density declined as the probability of fox occurrence increased (-0.32;  
307 95% CI: -0.57 - -0.07; Fig. 5), and that there was no association between fox occurrence and cat detectability  
308 (Supporting Information Table S5). Nonlinear regression splines added additional model parameters without  
309 changing predictions (Fig. 5); all nonlinear models ranked below their linear counterparts (Supporting  
310 Information Table S5).

311 *3.2. Otway region*

312 *3.2.1. Red fox*

313 In the Otway region, the probability of fox occurrence declined by 43% over three years in the impact  
314 landscape, and increased by 22% in the non-impact landscape (where they were not lethally controlled) over  
315 the same period (averaged at each camera-trap site in the landscape; Fig. 2b). Fox occurrence probability in  
316 the Otway region was generally lower than the Glenelg region and had less fine-scale spatial variation. For  
317 example, fox occurrence was predicted to be spatially consistent across the entire Otway region in 2018 (i.e.,  
318 fox occurrence probability was the same in both the impact and non-impact landscape, Fig. 2; as were naïve  
319 occupancy rates, Table 1). The fox spatial occurrence model explained 27.8% of the null deviance, with an  
320 adjusted R-squared value of 0.24 (spatial standard error estimates are shown in Supporting Information Fig.  
321 S6).

322 *3.2.2. Feral cat*

323 In the Otway region, we recorded 970 cat detections from 36,272 camera-trap nights (Table 1). We were  
324 able to identify 53% of cat detections to the individual-level; a total of 93 cats (20 – 30 individuals per  
325 camera-trap grid deployment, with some individual detected in multiple years, Supporting Information Fig.  
326 S10; S11; S12). The exponential detector function was strongly supported over the half-normal function  
327 (Table S7). The null model was more strongly supported than the models with vegetation impacts on cat

328 density, or camera-trap model or linear time trends on  $g_0$  (Table S8).

329 Our prediction (1) that fox control would be associated with higher cat densities was supported in 2019  
330 (~1.5 years after fox baiting commenced), but not 2018 (six months after fox-baiting commenced, and during  
331 a break in the baiting program). Within each year, there was no statistical evidence that cat densities  
332 differed between the impact and non-impact landscapes (95% confidence intervals overlapped zero; Fig.  
333 4a). However, a consistent upward trend in cat density in the impact landscape over three years and a  
334 simultaneous downward trend in the non-impact landscape (Fig. 4a), meant that there was a significant  
335 increase in cat density in the impact landscape 1.5 years after fox-baiting commenced, relative to changes  
336 in the non-impact landscape (i.e., 83% CIs for the estimated difference for 2017 and 2019 do not overlap;  
337 Fig. 4b). There was strong evidence that cat detectability was associated with fox occurrence probability  
338 (Supporting Information Table S9), detailed below.

339 Our prediction (2) that cat density would be negatively correlated with fox occurrence probability at a  
340 fine spatial scale had some support. The top-ranked model included a negative linear association between  
341 cat density and fox occurrence, supporting our prediction. However, statistical evidence was weak: this  
342 model had similar predictive performance to a model without the association between cat density and fox  
343 occurrence probability ( $dAIC_c = 0.80$ ; Table S10). In addition, the 95% confidence interval around the linear  
344 coefficient from the top-ranked model marginally overlapped zero (-0.26; 95% CI: -0.55 - 0.02). The nonlinear  
345 version of this model also marginally ranked above the null model ( $dAIC_c = 0.47$ ; Table S10). This nonlinear  
346 model predicted that cat density only declined (at a steeper rate) in the mid-high range of fox occurrence  
347 probability (greater than ~0.25 on the response scale; Fig. 5).

348 There was strong support for an effect of fox occurrence probability on cat detectability at a fine spatial  
349 scale (Fig. 6; Supporting Information Table S9). Where fox occurrence probability was higher, cats were less  
350 detectable in their activity centres (i.e., negative association with  $g_0$ ; -0.69; 95% CI: -1.11 - -0.27; Fig. 6a)  
351 and ranged further (i.e., positive association with  $\sigma$ ; coefficient 0.30; 95% CI: 0.13 - 0.47; Fig. 6b). The  
352 equivalent nonlinear model predicted that detectability changes occurred only in the low-mid range of fox  
353 occurrence probabilities (less than ~0.25 on the response scale; Fig. 6).

Table 1: Summary of experimental camera-trap surveys and invasive predator detections in the Glenelg and Otway regions, Australia.

Region	Landscape	Replicate	Treatment	Start date	End date	Camera-traps	Trap-nights	Red fox		Feral cats (max. 1 detection per 24-hr)				Total detections
								Naïve occupancy	Individuals	Moves	Prop. unidentified	Prop. unmarked		
Glenelg	Cobboboonee	1	impact	2018-02-13	2018-04-29	110	7752	0.26	13	19	0.11	0.46	81	
	Annya	1	non-impact	2018-01-26	2018-04-13	110	8000	0.55	9	11	0.07	0.43	46	
	Mt Clay	2	impact	2018-04-30	2018-06-27	106	5451	0.35	10	16	0.13	0.00	38	
	Hotspur	2	non-impact	2018-04-16	2018-06-21	99	6085	0.48	8	12	0.08	0.34	38	
	LGNP South	3	impact	2021-03-25	2021-05-12	64	2842	0.17	21	4	0.00	0.00	37	
	LGNP North	3	non-impact	2021-03-30	2021-05-14	49	2102	0.57	6	3	0.00	0.00	11	
	Otways	South	1	impact	2017-06-23	2017-08-30	73	4543	0.36	20	18	0.04	0.42	114
		North	1	non-impact	2017-07-05	2017-09-02	67	3565	0.13	26	12	0.07	0.40	114
		South	2	impact	2018-06-28	2018-09-13	85	6077	0.27	24	37	0.11	0.39	151
		North	2	non-impact	2018-07-09	2018-09-21	103	7099	0.27	30	32	0.07	0.38	164
		South	3	impact	2019-06-07	2019-09-17	86	7150	0.17	25	69	0.11	0.27	214
		North	3	non-impact	2019-06-13	2019-09-15	99	7838	0.43	27	39	0.10	0.47	213

*Note:*

Naïve occupancy - proportion of camera-trap sites which detected foxes

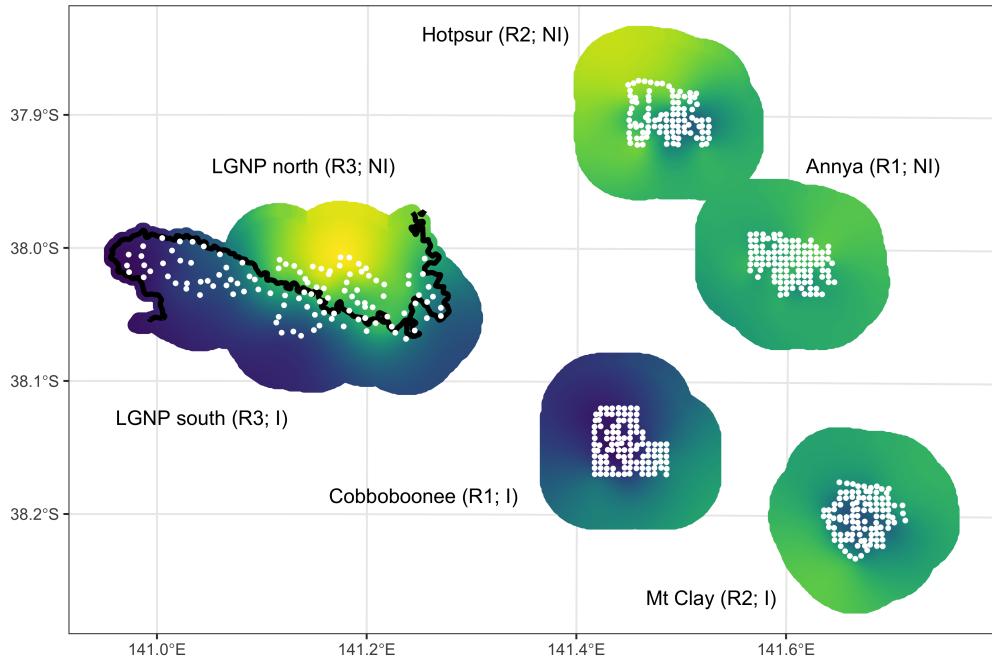
Individuals - Number of identified feral cat individuals

Moves - successive recaptures of individuals at different sites

Prop. unidentified - proportion of feral cat detections in the 'marked' spatial mark-resight category which could not be identified to the individual-level

Prop. unmarked - proportion of feral cat detections in the 'unmarked' spatial mark-resight category

(a) Glenelg region



(b) Otway region

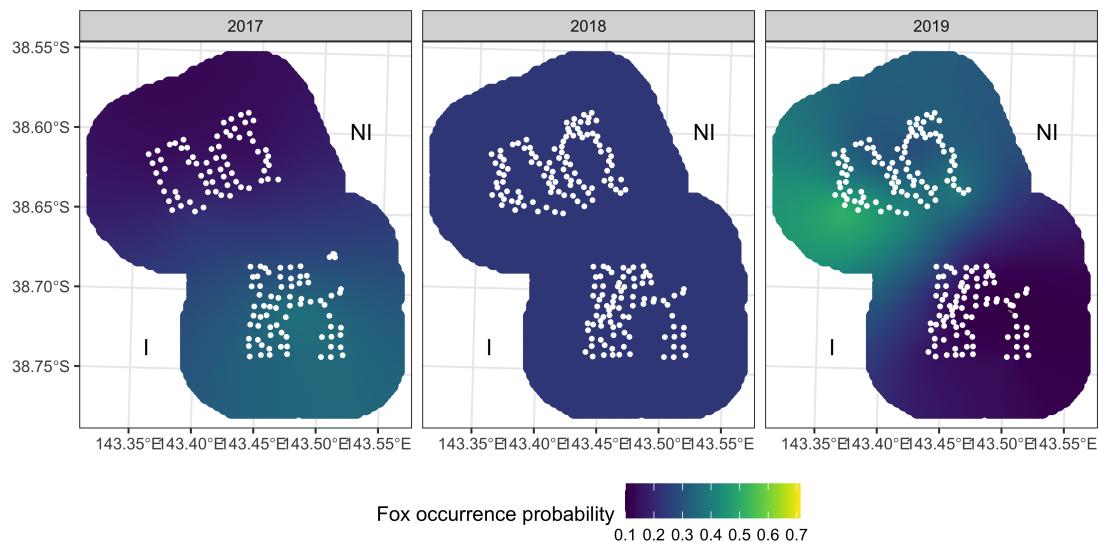


Figure 2: Predicted red fox *Vulpes vulpes* occurrence probabilities derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. White dots represent camera-trap sites. The black line (a) represents the Glenelg River which separates the impact (south) and non-impact (north) landscape pair in the Lower Glenelg National Park.

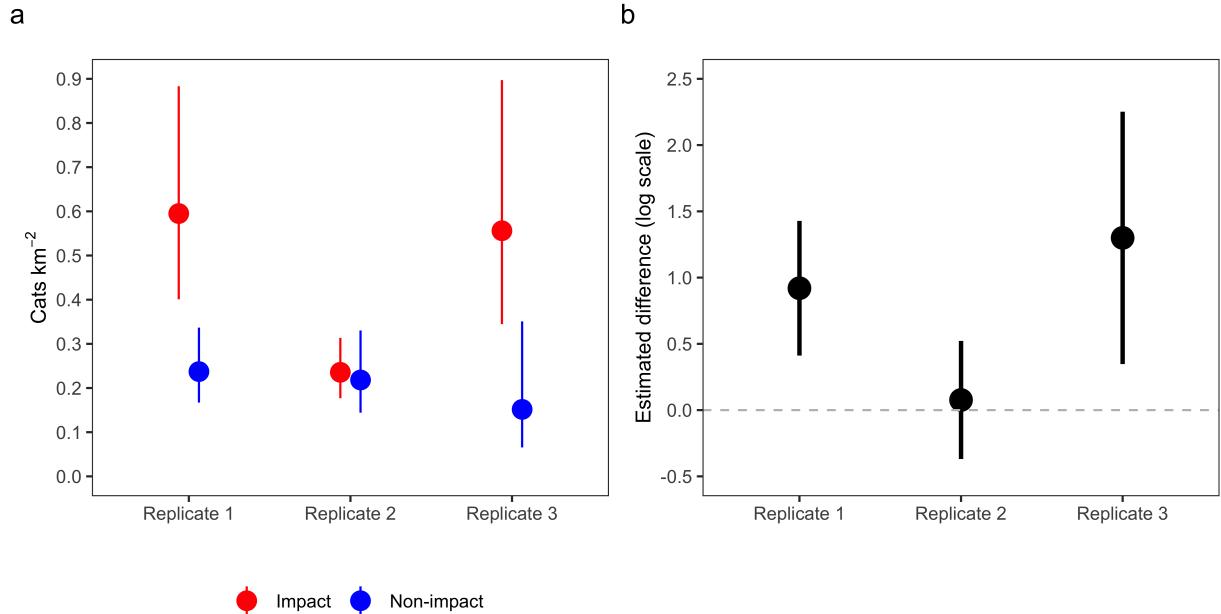


Figure 3: Feral cat *Felis catus* density in response to long-term fox control in the Glenelg region, Australia (replicated Control-Impact analysis). Poison baiting for foxes *Vulpes vulpes* had been conducted continuously in the impact landscapes for more than 13 years for the first two replicates, and 16 years for the third replicate. (a) Cat density estimates with 95% confidence intervals for each landscape derived from spatial mark-resight models. (b) Estimates of difference in cat density (impact landscape relative to the paired non-impact landscape) for each replicate. Error bars show 95% confidence intervals. In (b), confidence intervals that do not overlap 0 (grey dashed line) indicate that that cat density was higher in the impact landscape than the associated non-impact landscape ( $p < 0.05$ ).

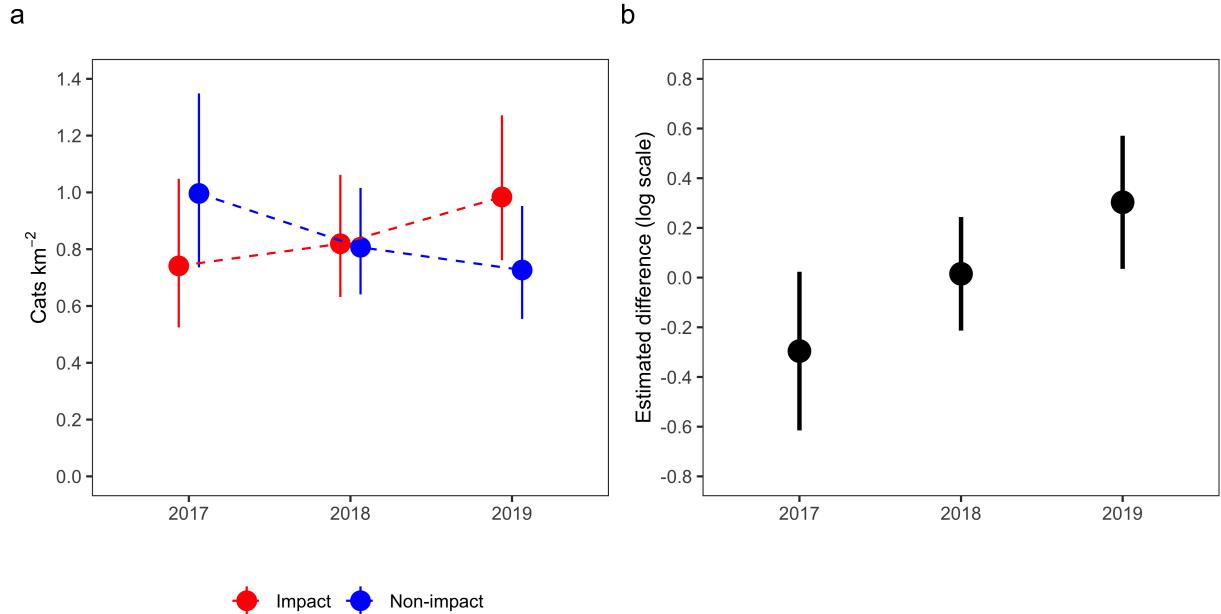


Figure 4: Feral cat *Felis catus* density in response to fox control in the Otway Ranges, Australia (Before-After Control-Impact Paired-Series analysis). The 2017 surveys were conducted approximately two months before lethal red fox *Vulpes vulpes* control began in the impact landscape. Baiting ceased July - November 2018 before resuming approximately five months prior to the 2019 survey. (a) Cat density estimates with 95% confidence intervals for each survey, derived from spatial mark-resight models. (b) Estimates of the difference (on the natural logarithmic scale) between landscape pairs in each survey year (impact landscape relative to the non-impact landscape) with 83% confidence intervals. In (b), confidence intervals that do not overlap each other (visualised horizontally) indicates evidence for a change in cat density at the impact landscape relative to change at the non-impact landscape ( $p < 0.05$ ).

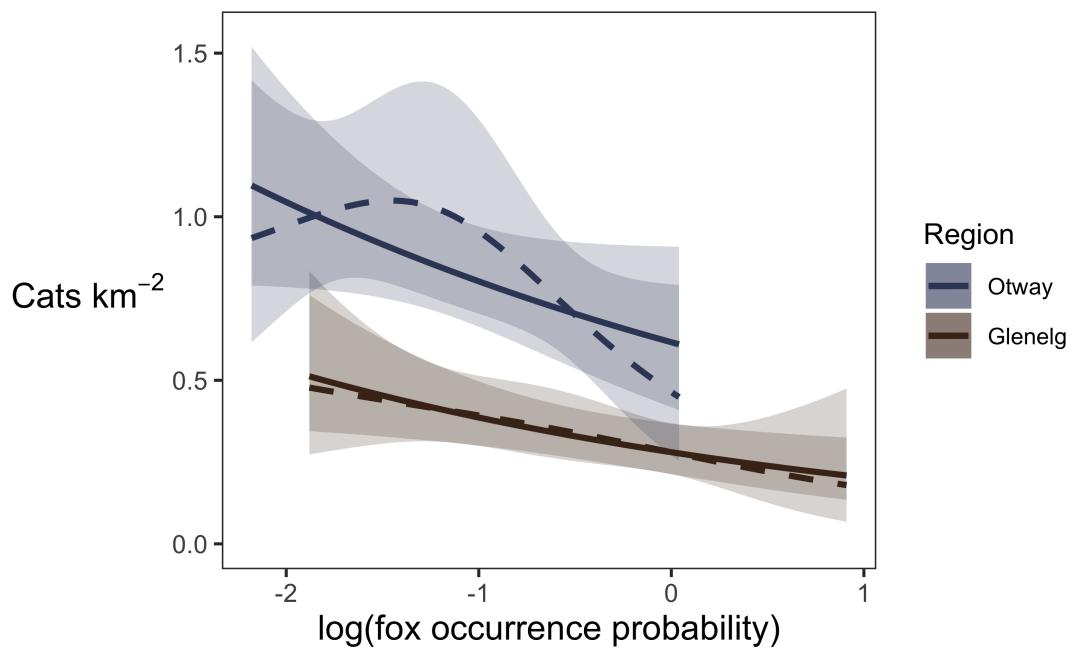


Figure 5: Feral cat *Felis catus* density in relation to the probability of red fox *Vulpes vulpes* occurrence, Glenelg and Otway regions, Australia. Lines show estimates from top-ranked linear (solid) and nonlinear (dashed) models, shaded areas indicate 95% confidence intervals

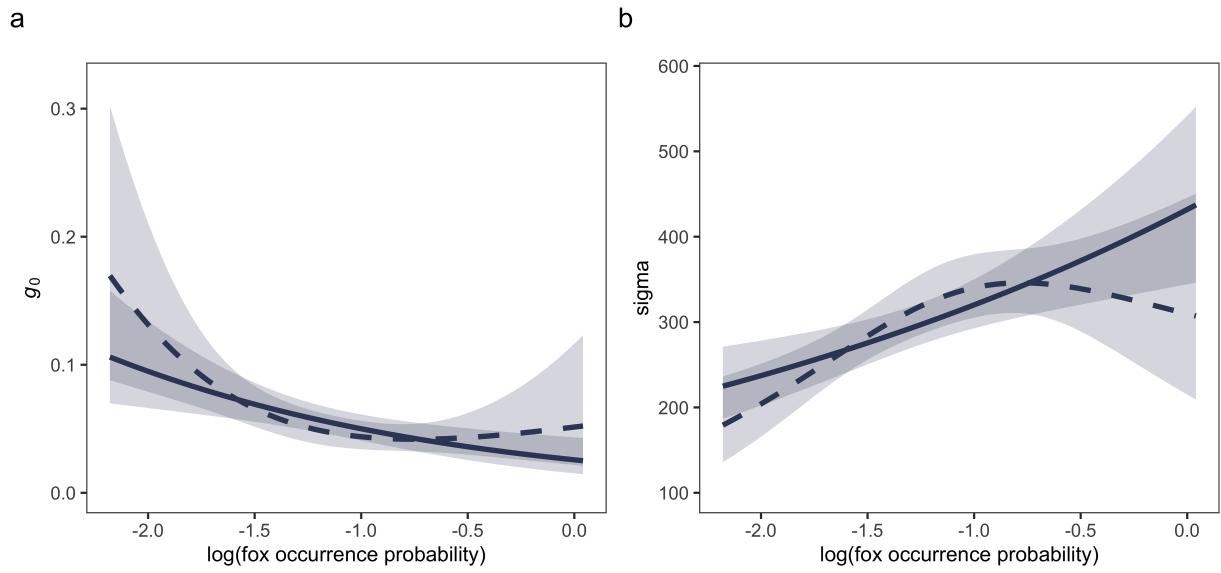


Figure 6: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-scaled red fox *Vulpes vulpes* occurrence probability in the Otway region, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion ( $g_0$ ) decreased with the probability of fox occurrence (a), while  $\sigma$  (which is related to home range size; exponential detection function) increased (b). Shaded areas indicate 95% confidence intervals.

354    **4. DISCUSSION**

355    Our study is one of the first to provide replicated, experimental evidence that dominant predator  
356 suppression can be associated with higher mesopredator densities. We provide two lines of evidence that  
357 foxes can exert top-down control on feral cats in the forests of south-eastern Australia: feral cat density  
358 was (1) commonly higher in landscapes where fox control occurred, and (2) higher where fine-scale fox  
359 occurrence probability was lowest, although this association was only weakly supported in the Otway region.  
360 Targeted fox control is a widely used conservation strategy in Australia and so unintended mesopredator  
361 release of feral cats is concerning, as it is likely to increase impacts on some native prey (e.g., Marlow *et al.*  
362 2015). More broadly, our study illustrates how experimental (landscape-scale) and correlative (fine-scale)  
363 approaches provide complementary lines of evidence when investigating interactions between predator species,  
364 and highlights the importance of disentangling changes in mesopredator density from changes in detectability.

365    In the Glenelg region where fox-baiting had occurred for more than 13 years, feral cat density was  
366 considerably higher in two out of three replicate baited landscapes than their unbaited pairs. The lack of  
367 difference for pair 2 was likely due to limited suppression of foxes at Mt Clay despite ongoing fox control  
368 (Fig. 2a). Mt Clay is a small forest block surrounded entirely by unbaited farmland; simulation modelling  
369 indicates that the size of the baited area is a key driver of the degree of reduction in the fox population  
370 (Francis, Robley, & Hradsky 2020), including at Mt Clay (Hradsky *et al.* 2019). There was also strong  
371 support for a negative association between cat density and fox occurrence probability at a fine spatial scale  
372 in this region, consistent with the mesopredator release hypothesis. Studies of fox-cat (and other intraguild  
373 predator) interactions often use the presence of a management program as a proxy for dominant predator  
374 suppression (e.g., Hunter *et al.* 2018). Our findings indicate the need to directly measure the dominant  
375 predator population to reliably interpret the responses of subordinate species (Salo *et al.* 2010).

376    In the Otway region, cat density increased significantly in the impact landscape two years after baiting  
377 commenced, relative to changes in the non-impact landscape. However, this increase was relatively small  
378 compared to differences between cat densities in impact and non-impact landscapes in Glenelg. Evidence  
379 for a fine-scale negative association with fox occurrence was also much weaker. There are two possible  
380 explanations for this. Firstly, changes in fox and adult cat density may not have fully manifested yet. Fox  
381 occurrence rates in the impact landscape continued to decline over our three years of surveys. We found  
382 some evidence for a sequential response: a reduction in fox occurrence probability may relax cat behaviour,

383 potentially improving hunting success, leading to higher recruitment rates, subsequently higher cat densities.  
384 Also, younger cats are more vulnerable to fox predation than adult cats (Sogliani & Mori 2019), and so  
385 foxes may have a greater impact on recruitment rates than the adult population, leading to a delayed effect  
386 on density. Further, cats may respond to an increase in shared prey availability following fox suppression  
387 (Stobo-Wilson *et al.* 2020). A time-lagged release of cats following fox control would explain eruptions and  
388 subsequent crashes commonly observed in shared mammalian prey populations two to ten years following fox  
389 control commencement (Duncan *et al.* 2020).

390 Secondly, foxes may have a weaker suppressive effect on cats in the highly productive Otway region than  
391 the dry forests of Glenelg. Fox occurrence was already relatively low prior to fox control in the Otways  
392 compared to Glenelg (Fig. 2). Competition theory predicts competitive interactions to be weaker with high  
393 prey availability: there may be less imperative for foxes to be aggressive towards or prey upon cats when  
394 there is enough food to share (Dickman 1996; Johnson & VanDerWal 2009; Greenville *et al.* 2014; Sogliani &  
395 Mori 2019). Conversely, foxes may have a higher capacity to maintain vigilance against cats when they are  
396 not food stressed, and top-down control from dominant predators could be the primary limiting factor for  
397 feral cats (a generalist mesopredator) in resource-rich environments (Oksanen & Oksanen 2000; Feit, Feit,  
398 & Letnic 2019). Prey availability is likely a strong mediator of mesopredator release, although it remains  
399 unclear whether mesopredator release would be stronger where prey availability is low or high—severely  
400 limiting our ability to predict mesopredator release across different landscapes.

401 Because subordinate predators may only be suppressed when dominant predator abundance is high, there  
402 is contention around whether linear regression is appropriate for investigating correlations between different  
403 predator species (Johnson & VanDerWal 2009; Letnic *et al.* 2011). We found no evidence of nonlinear  
404 associations between foxes and cats in the Glenelg region, while linear and nonlinear models performed  
405 equally well in the Otway region. Nonlinear models in the Otway region predicted that cat density declined  
406 only in the mid-high range of fox occurrence (Fig. 5), while behavioural changes were seen in the low-mid  
407 range of fox occurrence probability (Fig. 6). Perhaps cats can successfully avoid foxes through behavioural  
408 change where foxes are rare, but this is ineffective where foxes are common. This could explain the lack of  
409 evidence for foxes impacting cat detectability in the Glenelg region where fox occupancy was relatively high.  
410 Alternatively, behavioural changes may be untenable for cats in the Glenelg region because small mammal  
411 abundance is relatively low (M.Rees, unpublished data) and fox avoidance strategies likely come at the  
412 expense of hunting success (Sih 1980; Wilson *et al.* 2010). Alternatively, negative spatial associations between

413 species may simply reflect differences in niche preference rather than exclusion or avoidance, although is less  
414 likely in our case given we observed the relationship across an artificial gradient of fox occurrence probability  
415 caused by lethal control.

416 In the Otway region, we observed opposing trends in fox occurrence probabilities and cat densities in  
417 the impact and non-impact landscapes over time (Fig. 2b; Fig. 4). We are unsure what drove the increase  
418 in fox occurrence probability in the non-impact landscape and whether it was related to fox control in the  
419 nearby impact landscape. The effects observed in our BACIPS study may therefore only partly be due to  
420 mesopredator release in the strict sense (i.e., due to fox suppression in the impact landscape), although may  
421 demonstrate reciprocity in responses of cats to both increases and declines in foxes, which is rarely observed  
422 (Alston *et al.* 2019). Perhaps changes in the non-impact landscape were due to changes in prey availability,  
423 however we do not expect large fluctuations in prey here given the low seasonality and consistent climatic  
424 conditions relative to other parts of the country.

425 Where fox occurrence probabilities were higher at a fine spatial scale in the Otway Ranges, cats were  
426 less detectable in their activity centres and ranged further (Fig. 6). Low detectability is likely to correlate  
427 with fewer dominant predator encounters, and has been observed in other predator interaction studies (e.g.,  
428 Lombardi *et al.* 2017). An increase in cat ranging distances (*sigma*) with fox control supports observations  
429 made by Molsher *et al.* (2017) using telemetry, and may reflect a direct avoidance strategy. Animal movement  
430 rates are expected to increase in response to unpredictable threats (Riotte-Lambert & Matthiopoulos 2020).  
431 Alternatively, cats may consider foxes predictable and avoid locations they frequent, thus having to range  
432 further to obtain the same amount of food. In a similar forest habitat, Buckmaster (2012) observed large  
433 ‘holes’ in the home range of each GPS-collared cat; he confirmed that this was not due to an absence of prey  
434 and hypothesised it was due to dominant predator avoidance. In contrast, cats in another similar forest  
435 habitat without foxes or dingoes had compact home ranges within which intensity of use was reasonably  
436 uniformly spread (Hamer *et al.* 2021), suggesting this to be an optimal strategy for cats. Regardless of the  
437 cause, changes in mesopredator detectability and movement rates when dominant predators are suppressed  
438 have serious implications for the interpretation of studies that simply compare relative activity, occurrence or  
439 spatial overlap indices of predator species (Efford & Dawson 2012; Broadley *et al.* 2019).

440 Our findings may explain why pest management that only targets foxes—one of the most prevalent  
441 conservation actions in Australia—does not consistently improve native prey persistence (Dexter & Murray

442 2009; Robley *et al.* 2014; Wayne *et al.* 2017; Lindenmayer *et al.* 2018; Duncan *et al.* 2020). More evidence is  
443 required to understand the circumstances in which lethal fox control increases cat density, particularly the  
444 role of baseline fox and prey densities. A more integrated approach to invasive predator management, where  
445 foxes and cats are simultaneously or otherwise optimally controlled could substantially improve biodiversity  
446 outcomes (Risbey *et al.* 2000; Comer *et al.* 2020). If this is not feasible, changes in invasive mesopredator  
447 density and native prey populations should be closely monitored as part of invasive predator control programs,  
448 with triggers for ceasing dominant predator control or commencing integrated management if single-species  
449 control proves counter-productive for threatened native prey.

450 This study is among very few which have used a direct measure of density to test mesopredator release.  
451 Previous studies have mostly used live capture-rates to infer population density, without accounting for  
452 behavioural or detectability changes (e.g., Arjo *et al.* 2007; Karki, Gese, & Klavetter 2007; Thompson &  
453 Gese 2007; Berger, Gese, & Berger 2008; Jones, Van Vuren, & Crooks 2008). Contention about mesopredator  
454 release has centred on such methods (Hayward *et al.* 2015), as well as unaccounted species interactions  
455 in complex predator guilds (Levi & Wilmers 2012; Jachowski *et al.* 2020). In contrast, our study tests  
456 the mesopredator release theory using a combined behavioural and numerical approach, in a system with  
457 a simplified carnivore guild. Further replication of our approach in new landscapes, as well as explicitly  
458 accounting for dominant predator density, prey availability and landscape productivity is a priority for  
459 improving understanding of mesopredator release.

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