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1	Title: Predators, fire or resources: what drives the distribution of herbivores in fragmented
2	mesic forests?
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4	Running title: Drivers of herbivore distributions
5	
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23	
24	Abstract: Trophic interactions and disturbance events can shape the structure and function
25	of ecosystems. However, the effects of drivers such as predation, fire and climatic variables
26	on species distributions are rarely considered concurrently. We used a replicated landscape-
27	scale predator management experiment to compare the effects of red fox Vulpes vulpes
28	control, time-since-fire, vegetation type and other environmental variables on native
29	herbivore distributions. Occurrence data for four native herbivores, and an invasive
30	predator—the red fox—were collected from 240 sites across three baited (for lethal fox
31	control) and three unbaited forest blocks (4659 – 9750 ha) in south-western Victoria,

32 Australia, and used to build species distribution models. The herbivore taxa were: red-33 necked wallaby Macropus rufogriseus, black wallaby Wallabia bicolour, grey kangaroo 34 Macropus fuligenosus and Macropus giganteus. and common brushtail possum Trichosurus 35 vulpecula. Fox control and fire had little effect on herbivore occurrence, despite the 36 literature suggesting it can influence abundance, while climate, proximity to farmland and 37 topography were more influential. This may be because the region's high productivity and 38 agricultural pastures subsidise food resources for both predators and prey within the forest 39 blocks, and so dampen trophic interactions. Alternatively, these drivers may affect 40 herbivore abundance, but not herbivore occurrence. Understanding the drivers of herbivore 41 distributions is an important step in predicting the effects of herbivory on other species, 42 particularly after management interventions such as predator control and prescribed burns. 43

44 **Key Words:** herbivore, fire, predation, trophic relationships, spatial distribution, *Vulpes*

45 vulpes, species distribution model, macropod, predator control, motion-sensing camera

46 Introduction

47 Understanding the processes that drive the distributions of herbivores is fundamental to 48 managing ecosystems (Franklin 2010). Herbivores consume and trample organic matter, and 49 so shape ecosystems globally by simplifying vegetation structure, changing the composition 50 of plant communities and altering ecosystem successional trajectories (Bond 1994; Olofsson 51 et al. 2004; Raffaele et al. 2011). Herbivores are also an important food source for 52 predators, and can be a key driver of predator abundance (Sinclair and Krebs 2002). 53 Management actions that inadvertently affect herbivore populations may therefore have 54 important implications for ecosystem composition and biodiversity conservation. 55

56 Climate, disturbance events and habitat modification by humans can influence food 57 availability for herbivores from the bottom-up (Eby et al. 2014; Muhly et al. 2013). For 58 example, wildfires promote nutrient-rich vegetative growth and attract herbivores 59 (Fuhlendorf and Engle 2004), with cascading effects on the ecosystem (Raffaele et al. 2011). 60 Likewise, management interventions such as prescribed burns can facilitate increased 61 herbivory, with herbivores taking advantage of high-nutrient regrowth and potentially 62 restricting vegetation recovery (Fuhlendorf et al. 2010; Meers and Adams 2003). High food 63 availability may enable herbivore abundance to increase beyond the point where predators 64 can suppress the population (Jedrzejewska et al. 2005).

65

66 Top-down processes such as predation can also strongly influence patterns of herbivory 67 (Sandom et al. 2013). By killing and consuming herbivores, and altering their behaviour, 68 predators can restrict herbivore abundance and cause individuals to graze where they are 69 less vulnerable to predation. For example, small-medium herbivores can hide from 70 predators in dense vegetation cover (Kuijper et al. 2013) and large herbivores can 71 selectively graze in open areas with high visibility (Valeix et al. 2009). Herbivory then 72 becomes concentrated over small areas, producing changes to vegetation (Ford et al. 2014; 73 Ripple et al. 2001). Consequently, reductions in apex predator populations, by lethal control 74 or otherwise, are associated with increases in herbivore abundance and occurrence in 75 forests globally (Colman et al. 2015; Waser et al. 2014). Lethal control of predators can also 76 induce trophic cascades, including herbivore-related changes to vegetation structure 77 (Schmitz et al. 2000). Herbivore-release following invasive predator control can sometimes

have harmful ecological outcomes (Bergstrom *et al.* 2009), causing uncertainty about the
net value of predator control for biodiversity conservation (Doherty and Ritchie 2016). For
example, poison baiting of red foxes *Vulpes vulpes* in Booderee National Park, Australia,
caused an irruption in black wallabies *Wallabia bicolor* that reduced vegetation cover
(Dexter *et al.* 2013).

83

Bottom-up and top-down forces can also interact to shape herbivore distributions (Wisz *et al.* 2013). For example, white-tailed deer *Odocoileus virginianus* select for unburnt areas
post-fire as they offer concealment from predators (Cherry *et al.* 2016). The role of
interactions in determining herbivore distributions is an important knowledge gap for
ecosystem management, particularly as variations in herbivore numbers may influence
vegetation change over multiple decades (Nuttle *et al.* 2011).

90

91 Management interventions such as lethal predator control and prescribed burning are 92 common across Australia, and case-studies indicate that they may promote population 93 growth in native herbivores, with cascading effects for vegetation and other fauna (Dexter 94 et al. 2013; Foster et al. 2016). Historically, grazing or browsing by invasive herbivores has 95 also contributed to the decline of fauna such as the burrowing bettong *Bettongia lesueur* 96 (McKenzie et al. 2007; Newsome 1971). Given that native herbivores can also cause 97 vegetation structural change (Bennett et al. 2019), it is conceivable that overabundant 98 native herbivores may also drive fauna declines. Further, loss of vegetation cover due to 99 grazing and prescribed fire may make native mammals more vulnerable to predators 100 (Hradsky 2019; McGregor et al. 2014). Understanding the indirect effects of management 101 interventions on both invasive and native herbivore populations is therefore important for 102 biodiversity conservation.

103

Species distribution models predict the likelihood of species occurrence based on presence (and sometimes absence) records, and can be useful approach for informing environmental management and planning (Guisan *et al.* 2013). However, they have not been widely used to examine the impacts of management interventions on species' distributions, or to identify areas where unwanted ecological consequences (such as high herbivory pressure) are likely to occur.

110

111 We used a large-scale replicated predator management experiment to examine the relative 112 influence of red fox control, fire, and other environmental and bioclimatic drivers on the 113 landscape-scale distribution of medium and large native herbivores. Our study was 114 conducted in a fragmented mesic forest ecosystem of south-eastern Australia. We predicted 115 that herbivores would be more likely to occur at sites that: (1) were within fox-baited zones; 116 (2) had been recently burnt as these species commonly feed on new post-fire vegetation 117 growth, and (3) were closer to surrounding farmland due to the food resources (e.g. 118 pasture) provided by agricultural areas. We expected that rainfall and temperature 119 gradients would mediate these relationships but that, overall, they would have relatively 120 little influence on herbivore distributions. We also modelled red fox occurrence to confirm 121 that the fox baiting program influenced the distribution of red foxes.

122

123 Methods

124 Field surveys

125 Data were collected across the Glenelg region in far-south-west Victoria, Australia. This

126 43,500 ha landscape comprises patches of mixed sclerophyll woodland forest and heathy

127 forest within an agricultural matrix (Fig. 1, Robley *et al.* 2014). The climate is temperate,

- 128 with a mean annual rainfall of 835 971 mm, and a mean annual temperature of 11.9 –
- 129 17.6 °C (BoM 2017).

130

131 There are two main vegetation types in this region: woodland forest and heathy forest. In 132 the woodland forest, tall *Eucalyptus* trees are mixed with a diverse, open midstorey and 133 understorey. Heathy forests are typified by smaller *Eucalyptus* species and a complex, often 134 dense understory dominated by bracken, shrubs and sedges. Natural and prescribed fires 135 are frequent, creating a complex mosaic of fire histories. Fire in sclerophyll forest impacts 136 vegetation structure, removing understorey and midstorey vegetation (Bradstock et al. 137 2002). High severity fires can also cause loss of canopy cover (Bradstock et al. 2002). 138 139 The study area comprised six 'blocks' of similar size (Fig. 1; Robley et al. 2014). Three blocks

140 have undergone an intensive fox baiting program since 2005: southern Lower Glenelg

141 National Park (8954 ha), Mt Clay State Forest (4703 ha) and Cobboboonee National Park

(9750 ha). The other three blocks have never been baited: northern Lower Glenelg National
Park (4659 ha), Annya State Forest, (8520 ha) and Hotspur State Forest (6940 ha). Blocks
were at least 10 km apart except for the southern and northern sections of Lower Glenelg
National Park, which are separated by the Glenelg River, forming a barrier to fox movement.

147 To quantify the patterns of red fox and native herbivore distribution, camera trap data were 148 collected annually between October and November from 2013 to 2015 across 40 survey 149 sites in each block (240 sites in total – Fig. 1; Robley et al. 2014). Camera traps are 150 commonly used to study fauna occurrence, and are triggered by animal movement through 151 the camera's detection range (Rovero et al. 2013). During each survey, camera traps were 152 deployed for at least 28 days. Camera traps were baited with a mixture of peanut butter, 153 oats and honey fixed in a small, ventilated container 2 m in front of camera. Full site 154 selection and camera trapping procedures are described in Robley et al. (2014).

155

156 Variables

157 We collated presence-absence data for four medium-large native herbivores (black wallaby 158 Wallabia bicolor, red-necked wallaby Macropus rufogriseus, eastern and western grey 159 kangaroo Macropus giganteus and Macropus fuliginosus, and common brushtail possum 160 Trichosurus vulpecula) that were recorded from at least 150 sites across the study period 161 (2013-2015), as well as the red fox. The two species of grey kangaroo were grouped as they 162 were difficult to distinguish from camera trap images. We aimed to model species' 163 occurrence over the whole study period, and so merged occurrence data at each camera 164 site across years.

165

We used species' presence/absence to test for associations between environmental variables and the occurrence of grey kangaroos, common brushtail possums and red foxes. An absence was defined as no records of the species over the three-year survey period. We were unable to use this approach for black wallabies or red necked wallabies, as they had few, or no, recorded absences across the study sites. However, black wallaby habitat use varies with time of day (Hradsky 2014), so we separated presences and absences for each wallaby species at each site into day and night datasets. 'Night' presences were recorded

between one hour before sunset and one hour after sunrise, and the remainder wereconsidered 'day'.

175

176 We used time-since-fire (categorical: ≤ 2 years post-fire, 2-15 years post-fire, 15-35 years 177 post-fire, or >35 years post-fire), fox control (categorical: baited or unbaited), and the 178 distance of the camera site from farmland to test our primary hypotheses. These time-since-179 fire groupings were selected because they represent the key post-fire growth stages of the 180 vegetation types in the study area (Cheal 2010). We also included a suite of environmental 181 variables, relating to vegetation type (categorical: woodland forest or heathy forest), 182 terrain, soil type, and climate (precipitation and temperature) variables that were 183 hypothesized to influence distribution (Table S1). Environmental variables that exhibited 184 little or no variation across the study region were not included (e.g. isothermality). Predictor 185 variables were stored and manipulated in the statistical freeware R v3.3.1 (R Core 186 Development Team 2017) using the packages raster (Hijmans and van Etten 2014), rgdal 187 (Keitt et al. 2011) and maptools (Bivand and Lewin-Koh 2013), and software ArcMap v10.3 188 (ESRI 2014).

189

To control for the spatial arrangement of the study blocks, we grouped the study area into
three distinct, ecologically similar regions, each including a baited and unbaited block: *Region 1* encompassed sites in southern and northern Lower Glenelg National Park, *Region*2 the sites in Cobobboonee National Park and Hotspur State Forest, and *Region 3* the sites in
Mt Clay State Forest and Annya State Forest (Figure 1).

195

196 *Model development*

197 We used a two-stage process to develop candidate model sets and identify important 198 drivers of species' distributions. First, we selected a subset of environmental variables to 199 include in the candidate model sets for each species and checked the shape of the 200 univariate relationships. We used generalised additive mixed models (GAMMs) with high 201 degrees of freedom to explore the relationship between each environmental variable and 202 species separately (Wintle et al. 2005), using the package gam (Hastie 2013). The purpose of 203 this was to identify the type of environmental variables and their shape that could be used 204 in explaining species occurrence. We fitted the GAMMs with binomial distributions, using

205 'region' as the random effect. We used the shape of the relationship (e.g. linear, quadratic, 206 cubic) between candidate variables and species occupancy to determine the number of 207 degrees of freedom in the full generalised linear mixed model (GLMM) model selection 208 routine (see below). We checked for correlations between candidate variables using 209 Spearman's rank correlation test. Where two variables were strongly correlated (R > 0.7) or 210 represented similar environmental factors (e.g. BioClim temperature-related variables), the 211 variable with the highest univariate GAMM R²m was retained and the other excluded from 212 further analysis.

213

214 Using the variables identified with the GAMM process, we then developed at least 20 215 candidate GLMMs for each species, based on the hypothesised major drivers of their 216 distributions (predator control, fire, vegetation type, climate, topography and landscape 217 context). The appropriate response shapes for each variable determined in the previous 218 step. We also included a null model in the candidate set. All candidate models were allowed 219 no more than m/10 degrees of freedom, where m is the lesser of the number of presences 220 and the number of absences (Wintle et al. 2005). GLMMs were fitted with binomial error 221 distributions and logit-link functions, and 'region' was included as a random effect to 222 account for the spatial grouping of sites. For the red-necked wallaby and black wallaby 223 models, 'site' nested within 'region' was used as the random effect to account for repeat 224 sampling of sites between day and night. The full sets of candidate models for each species 225 are listed in Appendix 1. Analyses were conducted using the packages Ime4 (Bates et al. 226 2014) and MuMin (Barton 2013).

227

228 Model selection & evaluation

We used an information-theoretic approach to select the best model(s) in the set, by using
Akaike's Information Criterion adjusted for small sample size (AICc) and Akaike weights to
evaluate the relative support for alternative candidate models (Burnham and Anderson
2003). We considered that the model with the lowest AICc was the most highly-ranked, and
those within 2 AICc of the top-ranked model as strong candidates (Burnham and Anderson
2003).

The most highly-ranked models were checked for over dispersion ($\varphi > 1.5$), which can arise through higher than expected variance in the model (Quinn and Keough 2002). Models were also checked for spatial autocorrelation of the residuals by plotting spline correlograms of Moran's I for the residuals of the most highly-ranked model (Dormann *et al.* 2007). For all models, the 95% confidence intervals overlapped zero at the distances between sites, indicating that residuals were not spatially autocorrelated. This was done in the package ncf (Bjørnstad 2008).

243

To check that merging species' occurrence data across years did not mask any effects of between-year variation in fire history on model predictions, we built the same set of candidate models for each species by treating the 13 sites that changed fire history (i.e. were burnt) during the study period as separate sites. Model ranks and coefficients were not substantially different to the merged dataset, and so results are not presented. To evaluate how well the most highly-ranked models fitted the data, we calculated the

variance explained by the fixed effects (marginal R²), and fixed and random effects
(conditional R²) (Nakagawa and Schielzeth 2013).

253

254 To evaluate model performance, we calculated the area under the receiver operating curve 255 (AUC) statistic using the k-fold cross-validation technique, using ten folds, following the 256 process outlined in Hijmans and Elith (2013). For each species, we present the mean AUC 257 value and standard error across the ten folds. AUC indicates the ability of a model to rank 258 locations of presences more highly than locations of absences when predicting the 259 probability of occurrence at a location. Models with an AUC between 0.5 and 0.7 have a 260 better than random predictive capacity, and models with an AUC between 0.7 and 0.9 have 261 good predictive capacity (Pearce and Ferrier 2000). Analysis was done using the dismo 262 package (Hijmans et al. 2015).

263

264 For the best model for each species, we used the predict function in dismo to generate

265 raster-based model predictions. We then used these maps to predict each species'

266 probability of occurrence across the study area. For these maps, we defined the study area

as the broad baited and unbaited blocks in which the camera surveys were undertaken.

268	
269	Results
270	Models
271	The two top-ranked models of grey kangaroo occurrence received similar support (Table 1).
272	Grey kangaroos were less likely to occur at sites in blocks that had been baited for foxes (Fig
273	2a); the 95% confidence intervals of all other predictors overlapped zero.
274	
275	The top-ranked model of red-necked wallaby occurrence had strong support (Table 1),
276	indicating a positive association of the species with soil thorium, and a higher likelihood of
277	red-necked wallabies occurring in woodland forest vegetation than heathy forest during the
278	day (Fig 2b) and either vegetation type at night.
279	
280	Two candidate models were highly ranked and explained a moderate amount of variation in
281	common brushtail possum occurrence (Table 1). Brushtail possums were more likely to
282	occur in woodland forest. There was also some evidence that brushtail possum occurrence
283	was positively related to precipitation in the coldest quarter and negatively related to
284	distance from farmland, but confidence intervals were wide (Fig 2c).
285	
286	The distribution of the black wallaby could not be modelled as it was present at nearly all
287	sites during both day and night.
288	
289	Three similar candidate models for the red fox had predictive value, each explaining at least
290	45% of variation in red fox occurrence (Table 1). All top-ranked models indicated that red
291	foxes were half as likely to occur at sites within baited blocks than unbaited blocks, and
292	were more likely to occur in woodland forest vegetation than heathy forest (Table 1, Fig.
293	2d).
294	
295	The full set of candidate models for red fox (Table S2), red-necked wallaby (Table S3), grey
296	kangaroo (Table S4) and common brushtail possum (Table S5) are detailed in the
297	Supplementary Information.
298	
299	Model evaluation

- 300 The highest ranked GLMM had good predictive capacity for grey kangaroos (AUC = 0.72 \pm
- 301 0.05, Deviance Explained by fixed effects (DE) = 0.12), common brushtail possums (AUC =
- $302 \quad 0.80 \pm 0.02$, DE = 0.26) and red foxes (AUC = 0.83 ± 0.03, DE = 0.26). The predictive capacity
- 303 of the red-necked wallaby model was good during the day (AUC = 0.70 ± 0.07 , DE = 0.11),
- 304 but low for night (AUC = 0.65 ± 0.05 , DE = 0.04).
- 305

306 **Discussion**

307 Our study highlights the importance of climatic and habitat-related factors as drivers of 308 native herbivore occurrence in south-eastern Australia. Although fox baiting substantially 309 reduced fox occurrence, herbivore distributions were generally more strongly associated 310 with climate, soil chemistry, topography and proximity to agricultural land than predator 311 management. Time-since-fire also did not affect the occurrence of any target herbivore 312 species, or foxes. These findings contrast strongly with other Australian studies that have 313 found that variation in predation rates and fire strongly influence the abundance (rather 314 than occurrence) of native herbivores (Dexter et al. 2013; Foster et al. 2015), although 315 effects on native herbivore occurrence are less well understood. Our findings are, however, 316 consistent with other studies that have found little influence of time-since-fire on fox 317 distribution at a landscape scale (Hradsky et al. 2017; Payne et al. 2014) and broader trends 318 across other predators species (Geary et al. 2019).

319

320 Red foxes were significantly less likely to occur in fox-baited blocks than unbaited blocks 321 across Glenelg. Red foxes prey heavily on small and medium-sized macropods (e.g. black 322 wallaby) and brushtail possums (Davis et al. 2015), and so we expected that these 323 herbivores would respond positively to fox control and be more likely to occur at sites 324 within the baited blocks. However, we found no evidence of a positive association with fox 325 baited areas. This contrasts with findings from other mesic forest systems in Australia on 326 changes in herbivore abundance after fox and dingo removal, respectively (Colman et al. 327 2014; Dexter et al. 2013), and suggests that in the Glenelg region, either: (1) foxes do not 328 exert top-down pressure on herbivore occurrence (as they may not be predating on a 329 significant proportion of the herbivore population, and/or their top-down pressure of fox 330 predation on herbivores is relatively weak compared to dingo predation), (2) fox densities in 331 baited areas have not been reduced enough to release herbivores from top-down control 332 and lead to increases in occurrence, or (3) any effects of fox baiting on herbivore occurrence 333 were masked by the north-south spatial configuration of baited and unbaited blocks (Fig. 1), 334 which may correlate with a relatively dryer climate in the north of the study area compared 335 with the south. Given the widespread occurrence of the herbivore species and the 336 fragmented nature of the ecosystem, we suspect the former: the suppressive effects of 337 predators can be reduced in high productivity systems of agriculture-forest matrices

(Pasanen-Mortensen *et al.* 2017). This is despite top-down control typically being stronger
in intact, productive landscapes compared with unproductive landscapes (Elmhagen *et al.*2010; Greenville *et al.* 2014). However, the north-south gradient may explain why grey
kangaroos were less likely to occur at baited sites, contrary to our expectations – we are not
aware of a reasonable mechanism that would cause grey kangaroo occurrence to decrease
in response to fox-baiting.

344

345 Although fox baiting had no effect on the occurrence of herbivores, more subtle effects of 346 predator baiting on herbivore populations (e.g. changes in abundance) may not have been 347 apparent from our presence-absence data. For example, differences in predation pressure 348 could influence herbivore abundance and herbivory pressure, without affecting herbivore 349 distributions. Recent studies that have reported positive herbivore responses to dingo or fox 350 control have used abundance, fecundity and activity indices to measure herbivore 351 responses, rather than presence-absence data (e.g. Banks et al. 2000; Colman et al. 2015; 352 Dexter et al. 2013).

353

354 Our second hypothesis—that herbivores would be more likely to occur at recently-burnt 355 sites was also not supported. Other studies have highlighted the importance of fire in 356 determining herbivore distributions (Bowman et al. 2016; Eby et al. 2014; Meers and Adams 357 2003), yet we found no evidence of this within the Glenelg region. Similarly, Kelly et al. 358 (2017) found that temperature and precipitation were more important drivers of vertebrate 359 distributions than fire history in foothill forests. There are several possible explanations. 360 First, relationships between herbivore abundance and fire history may have been reflected 361 by changes in abundance, but not changes in occurrence. Second, herbivores may respond 362 more strongly to fires in ecosystems with grassy understories, rather than those in mesic 363 forests (Kirkpatrick et al. 2016). Alternatively, consistently high resource availability from 364 the surrounding farmland might dampen the effect of stochastic changes in resources (such as those caused by fire) on herbivore occurrence: high-nutrient vegetation in recently burnt 365 366 patches may not provide greater sustenance than surrounding vegetation in highly 367 productive environments (Styger et al. 2011).

368

369 Time-since-fire metrics, such as the one used in our study, have limited use in predicting 370 faunal responses to fire (Sitters et al. 2014). Fire often indirectly influences fauna through its 371 effects on habitat structure, meaning that habitat complexity is more strongly associated 372 with faunal occurrence than time-since-fire (Monamy and Fox 2000; Swan et al. 2015). In 373 addition, environmental variables that influence habitat recovery after fire can cause 374 divergent responses at sites with similar fire histories (Hale et al. 2016; Keeley et al. 2011; 375 Nimmo *et al.* 2014). The quality of spatial fire history information may also limit our 376 understanding the effects of fire on ecosystems (Avitabile et al. 2013; Callister et al. 2016). 377

378 Our third hypothesis—that herbivores would be more likely to occur at sites closer to 379 farmland—was partially supported. We found some evidence that common brushtail 380 possums were more likely to occur at sites closer to farmland, but no evidence of a 381 relationship for grey kangaroos or red-necked wallabies. Some herbivores use agricultural-382 forest matrices (Molloy et al. 2016), and can be released from top-down suppression in 383 highly productive anthropogenic landscapes that provide abundant food resources 384 (Pasanen-Mortensen et al. 2017). Food is also more readily available to some predators in 385 modified landscapes (Kuijper et al. 2016; Newsome et al. 2017), further weakening 386 predator-prey interactions (Rodewald et al. 2011). Given that the study area is in an 387 agricultural matrix, this might explain why there was no evidence that herbivores were 388 more likely to occur in fox-baited blocks at Glenelg.

389

390 Climate, soil and vegetation-related variables can be important drivers of herbivore 391 distributions as they influence resource availability (Ritchie et al. 2008). Contrary to our 392 predictions, these variables were the most important predictors of herbivore occurrence in 393 our study region. Red-necked wallabies, common brushtail possums and foxes were all 394 more likely to occur in woodland forest than heathy forest. Woodland forests are likely to 395 provide more food resources for herbivores, and facilitate easier movement of both 396 herbivores and predators due to the more open understorey (Catling *et al.* 2001). 397 Precipitation was positively associated with the occurrence of common brushtail possums. 398 positive relationship with soil thorium for red-necked wallabies and brushtail possums may 399 also relate to resource availability, as high soil thorium concentrations are associated with 400 nutrient-rich clay soils favourable for the growth of palatable plants (Mernagh and Miezitis

- 401 2008). Topography was an important predictor of occurrence for grey kangaroos, with this
- 402 species being more likely to occur at higher elevations. These associations could reflect the
- 403 influence of environmental gradients on the food plants for each species, and/or direct
- 404 ecophysiological constraints (Kearney and Porter 2009; Sunday *et al.* 2014).
- 405

406 The role of predators in ecosystems, hypothesized interactions between ecological 407 processes (e.g. trophic interactions, disturbance) and the potential unintended 408 consequences of lethal predator control are increasingly relevant for ecosystem 409 management (Doherty et al. 2015). Evidence is required to inform changes in management 410 regimes. In our study, herbivore distributions appeared to be most influenced by vegetation 411 type and topographic factors, rather than disturbance or red fox control. While predator 412 and fire management actions may influence herbivore occurrence or abundance at a finer 413 spatial or temporal resolution than explored here, our study suggests that habitat features 414 play a more important role at the broad-scale.

415

416 Pairing herbivore distribution models with distribution models of species that are 417 potentially vulnerable to increased herbivory, such as small and medium-sized mammals 418 (Foster et al. 2014), could help managers prioritise locations where interventions may be 419 needed. Species distribution models have been applied in similar fashion elsewhere globally 420 to predict, among other things, the impacts of invasive species (Gallien *et al.* 2012). Further 421 developments that incorporate biotic interactions into spatial models and decision tools, 422 such as joint species distribution models (Pollock et al. 2014) or spatially explicit population 423 dynamic models (Akçakaya et al. 1995) would provide additional insight into the trophic 424 dynamics and optimal management of fragmented forest ecosystems.

425

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688 Figure Captions



Figure 1: Camera survey sites within the three baited (black dots) and three unbaited (grey
circles) blocks within Victoria (inset), south-eastern Australia. The solid black line indicates
areas where poison baits are deployed for red fox *Vulpes vulpes* control. Grey shading
shows public land.





695 **Figure 2:** Mapped predicted probability of occurrence for the most highly-ranked

696 distribution model (fixed effects only) for a) grey kangaroo Macropus sp., b) red-necked

697 wallaby *M. rufogriseus* (day time model), c) common brushtail possum *Trichosurus vulpecula*

698 and d) red fox *Vulpes vulpes*.

Table 1: Coefficients, 95% confidence intervals and sum of Akaike weights ($\sum w_i$) for each predictor in the highly ranked species distribution models (Δ AICc < 2.0).

700 Coefficients are relative to the reference level of unbaited heathy forest. Also shown is the difference in Akaike Information Criterion adjusted for small sample size from

701 the top-ranked model (ΔAICc), the Akaike weight (w), and the marginal (R²m) and conditional (R²c) R² of each model. Bolded coefficients are those whose 95% confidence

intervals do not overlap zero.

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Species	Rank				Coefficients				ΔAICc	w	R ² m	R ² c
Red- necked wallaby		Vegetation type (woodland)	Diel period (night)	Diel : veg	Thorium							
	1	1.59 [0.75, 2.46]	-0.58 [-1.29, 0.09]	-1.10 [-2.01, -0.22]	0.44 [0.21, 0.67]				0.00	0.99	0.15	0.36
	$\sum w_i$	1.00	1.00	1.00	1.00							
Grey kangaroo	_	Vegetation type (woodland)	Treatment (baited)	Veg : treatment	Thorium	Ruggedness	Elevation	Precipitation during driest Q				
	1	-1.23[-3.34, 0.88]	-3.14[-5.26, -1.03]	1.95 [-0.31, 4.21]	-	-	0.38 [-0.02,0.78]	-	0.00	0.22	0.27	0.27
	2	-	-2.05[-2.81, -1.29]	-	0.22 [-0.14, 0.59]	-0.19 [-0.53, 0.15]	-	0.28 [-0.04,0.59]	1.36	0.11	0.24	0.24
	$\sum w_i$	0.57	1.0	0.37	0.48	0.46	0.48	0.29				
		Vegetation type	Treatment (baited)	Paddock Distance	Precipitation in	Mean Temp in	Elevation					
Common		(woodland)			Coldest Q	Coldest Q						
brushtail	1	1.77 [0.88,2.65]	-	-0.33 [-0.72, 0.06]	0.34 [-0.06, 0.75]	0.39 [-0.14,0.92]	-		0.00	0.28	0.15	0.50
possum	2	1.80 [0.92,2.68]	-0.92 [-2.40, 0.66]	-0.35 [-0.75, 0.05]	0.67 [0.06, 1.29]	-	-0.79 [-1.65, 0.07]		0.95	0.17	0.24	0.45
	$\sum w_i$	1.0	0.5	1.0	0.88	0.55	0.54					
Red fox		Vegetation type (woodland)	Treatment (baited)	Tree Density	Precipitation in Coldest Q							
	1	1.36 [0.59, 2.12]	-2.95 [-3.76, -2.13]	-0.45 [-1.05, 0.14]	-				0.00	0.29	0.48	0.48
	2	1.33 [0.57, 2.09]	-2.98 [-3.78, -2.17]	-	-				0.84	0.19	0.45	0.45
	3	1.31 [0.55, 2.08]	-2.54 [-3.65, -1.44]	-	-0.32 [-0.91, 0.27]				1.75	0.12	0.46	0.46
	$\sum w_i$	1.0	1.0	0.40	0.14							

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