Author/s:
Geary, WL;Hradsky, BA;Robley, A;Wintle, BA

Title:
Predators, fire or resources: What drives the distribution of herbivores in fragmented mesic forests?

Date:
2020-05-01

Citation:
Geary, W. L., Hradsky, B. A., Robley, A. & Wintle, B. A. (2020). Predators, fire or resources: What drives the distribution of herbivores in fragmented mesic forests?. Austral Ecology, 45 (3), pp.329-339. https://doi.org/10.1111/aec.12861.

Persistent Link:
https://hdl.handle.net/11343/275509

MR. WILLIAM GEARY (Orcid ID : 0000-0002-6520-689X)

Article type   : Research Article

Corresponding author mail id : billygeary4@gmail.com

Title: Predators, fire or resources: what drives the distribution of herbivores in fragmented mesic forests?

Running title: Drivers of herbivore distributions

Authors: William L. Geary[1,2,3], Bronwyn A. Hradsky[1,4], Alan Robley[5], Brendan A. Wintle[1,4]

[1]Quantitative and Applied Ecology group, School of BioSciences, University of Melbourne, Parkville, Melbourne, 3010

[2]Biodiversity Division, Department of Environment, Land, Water & Planning, East Melbourne, 3002

[3]Centre for Integrative Ecology, School of Life and Environmental Sciences (Burwood Campus), Deakin University, Geelong, Victoria, Australia

[4]NESP Threatened Species Recovery Hub, School of Biosciences, University of Melbourne, Parkville, Melbourne, 3010

[5]Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, Heidelberg, 3078

Abstract: Trophic interactions and disturbance events can shape the structure and function of ecosystems. However, the effects of drivers such as predation, fire and climatic variables on species distributions are rarely considered concurrently. We used a replicated landscape-scale predator management experiment to compare the effects of red fox *Vulpes vulpes* control, time-since-fire, vegetation type and other environmental variables on native herbivore distributions. Occurrence data for four native herbivores, and an invasive predator—the red fox—were collected from 240 sites across three baited (for lethal fox control) and three unbaited forest blocks (4659 – 9750 ha) in south-western Victoria, Australia, and used to build species distribution models. The herbivore taxa were: red-necked wallaby *Macropus rufogriseus*, black wallaby *Wallabia bicolour*, grey kangaroo *Macropus fuligenosus* and *Macropus giganteus*. and common brushtail possum *Trichosurus vulpecula*. Fox control and fire had little effect on herbivore occurrence, despite the literature suggesting it can influence abundance, while climate, proximity to farmland and topography were more influential. This may be because the region's high productivity and agricultural pastures subsidise food resources for both predators and prey within the forest blocks, and so dampen trophic interactions. Alternatively, these drivers may affect herbivore abundance, but not herbivore occurrence. Understanding the drivers of herbivore distributions is an important step in predicting the effects of herbivory on other species, particularly after management interventions such as predator control and prescribed burns.

Key Words: herbivore, fire, predation, trophic relationships, spatial distribution, *Vulpes vulpes*, species distribution model, macropod, predator control, motion-sensing camera

Introduction

Understanding the processes that drive the distributions of herbivores is fundamental to managing ecosystems (Franklin 2010). Herbivores consume and trample organic matter, and so shape ecosystems globally by simplifying vegetation structure, changing the composition of plant communities and altering ecosystem successional trajectories (Bond 1994; Olofsson *et al.* 2004; Raffaele *et al.* 2011). Herbivores are also an important food source for predators, and can be a key driver of predator abundance (Sinclair and Krebs 2002).

Management actions that inadvertently affect herbivore populations may therefore have important implications for ecosystem composition and biodiversity conservation.

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

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

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).

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

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.

We used a large-scale replicated predator management experiment to examine the relative influence of red fox control, fire, and other environmental and bioclimatic drivers on the landscape-scale distribution of medium and large native herbivores. Our study was conducted in a fragmented mesic forest ecosystem of south-eastern Australia. We predicted that herbivores would be more likely to occur at sites that: (1) were within fox-baited zones;

(2) had been recently burnt as these species commonly feed on new post-fire vegetation growth, and (3) were closer to surrounding farmland due to the food resources (e.g. pasture) provided by agricultural areas. We expected that rainfall and temperature gradients would mediate these relationships but that, overall, they would have relatively little influence on herbivore distributions. We also modelled red fox occurrence to confirm that the fox baiting program influenced the distribution of red foxes.

Methods

Field surveys

Data were collected across the Glenelg region in far-south-west Victoria, Australia. This 43,500 ha landscape comprises patches of mixed sclerophyll woodland forest and heathy forest within an agricultural matrix (Fig. 1, Robley *et al.* 2014). The climate is temperate, with a mean annual rainfall of 835 - 971 mm, and a mean annual temperature of 11.9 – 17.6 °C (BoM 2017).

There are two main vegetation types in this region: woodland forest and heathy forest. In the woodland forest, tall *Eucalyptus* trees are mixed with a diverse, open midstorey and understorey. Heathy forests are typified by smaller *Eucalyptus* species and a complex, often dense understory dominated by bracken, shrubs and sedges. Natural and prescribed fires are frequent, creating a complex mosaic of fire histories. Fire in sclerophyll forest impacts vegetation structure, removing understorey and midstorey vegetation (Bradstock *et al.* 2002). High severity fires can also cause loss of canopy cover (Bradstock *et al.* 2002).

The study area comprised six ‘blocks’ of similar size (Fig. 1; Robley *et al.* 2014). Three blocks have undergone an intensive fox baiting program since 2005: southern Lower Glenelg 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.

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

Variables

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

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 were considered 'day'.

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

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).

Model development

We used a two-stage process to develop candidate model sets and identify important drivers of species' distributions. First, we selected a subset of environmental variables to include in the candidate model sets for each species and checked the shape of the univariate relationships. We used generalised additive mixed models (GAMMs) with high degrees of freedom to explore the relationship between each environmental variable and species separately (Wintle *et al.* 2005), using the package gam (Hastie 2013). The purpose of this was to identify the type of environmental variables and their shape that could be used in explaining species occurrence. We fitted the GAMMs with binomial distributions, using 'region' as the random effect. We used the shape of the relationship (e.g. linear, quadratic, cubic) between candidate variables and species occupancy to determine the number of degrees of freedom in the full generalised linear mixed model (GLMM) model selection routine (see below). We checked for correlations between candidate variables using Spearman's rank correlation test. Where two variables were strongly correlated ($R > 0.7$) or represented similar environmental factors (e.g. BioClim temperature-related variables), the variable with the highest univariate GAMM R^2m was retained and the other excluded from further analysis.

Using the variables identified with the GAMM process, we then developed at least 20 candidate GLMMs for each species, based on the hypothesised major drivers of their distributions (predator control, fire, vegetation type, climate, topography and landscape context). The appropriate response shapes for each variable determined in the previous step. We also included a null model in the candidate set. All candidate models were allowed no more than $m/10$ degrees of freedom, where m is the lesser of the number of presences and the number of absences (Wintle *et al.* 2005). GLMMs were fitted with binomial error distributions and logit-link functions, and 'region' was included as a random effect to account for the spatial grouping of sites. For the red-necked wallaby and black wallaby models, 'site' nested within 'region' was used as the random effect to account for repeat sampling of sites between day and night. The full sets of candidate models for each species are listed in Appendix 1. Analyses were conducted using the packages lme4 (Bates *et al.* 2014) and MuMin (Barton 2013).

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).

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 R^2), and fixed and random effects (conditional R^2) (Nakagawa and Schielzeth 2013).

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

For the best model for each species, we used the predict function in dismo to generate raster-based model predictions. We then used these maps to predict each species' 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.

Results

Models

The two top-ranked models of grey kangaroo occurrence received similar support (Table 1). Grey kangaroos were less likely to occur at sites in blocks that had been baited for foxes (Fig 2a); the 95% confidence intervals of all other predictors overlapped zero.

The top-ranked model of red-necked wallaby occurrence had strong support (Table 1), indicating a positive association of the species with soil thorium, and a higher likelihood of red-necked wallabies occurring in woodland forest vegetation than heathy forest during the day (Fig 2b) and either vegetation type at night.

Two candidate models were highly ranked and explained a moderate amount of variation in common brushtail possum occurrence (Table 1). Brushtail possums were more likely to occur in woodland forest. There was also some evidence that brushtail possum occurrence was positively related to precipitation in the coldest quarter and negatively related to distance from farmland, but confidence intervals were wide (Fig 2c).

The distribution of the black wallaby could not be modelled as it was present at nearly all sites during both day and night.

Three similar candidate models for the red fox had predictive value, each explaining at least 45% of variation in red fox occurrence (Table 1). All top-ranked models indicated that red foxes were half as likely to occur at sites within baited blocks than unbaited blocks, and were more likely to occur in woodland forest vegetation than heathy forest (Table 1, Fig. 2d).

The full set of candidate models for red fox (Table S2), red-necked wallaby (Table S3), grey kangaroo (Table S4) and common brushtail possum (Table S5) are detailed in the Supplementary Information.

Model evaluation

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

Discussion

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

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

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

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

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

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

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

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

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

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

Acknowledgements

We thank those who assisted with the data collection for this work, specifically Georgie Neave and the Glenelg Ark team. We thank Matt White for discussions about modelling. This work was supported by the Victorian Government Department of Environment, Land, Water & Planning, Parks Victoria and the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub.

References

Akçakaya H. R., McCarthy M. A. & Pearce J. L. (1995) Linking landscape data with population viability analysis: management options for the helmeted honeyeater *Lichenostomus melanops cassidix*. *Biological Conservation* **73**, 169-76.

Avitabile S. C., Callister K. E., Kelly L. T., Haslem A., Fraser L., Nimmo D. G., Watson S. J., Kenny S. A., Taylor R. S. & Spence-Bailey L. M. (2013) Systematic fire mapping is critical for fire ecology, planning and management: A case study in the semi-arid Murray Mallee, south-eastern Australia. *Landscape and Urban Planning* **117**, 81-91.

Banks P. B., Newsome A. E. & Dickman C. R. (2000) Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology* **25**, 283-91.

Barton K. (2013) MuMIn: Multi-model inference. R package version 1.9. 5. *R Project for Statistical Computing, Vienna, Austria*.

Bates D., Maechler M., Bolker B. & Walker S. (2014) lme4: Linear mixed-effects models using Eigen and S4. *R package version* **1**.

Bennett A., Duncan D. H., Rumpff L. & Vesk P. (2019) How do rabbits and kangaroos limit restoration of endangered woodland ecosystems?

Bergstrom D. M., Lucieer A., Kiefer K., Wasley J., Belbin L., Pedersen T. K. & Chown S. L. (2009) Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology* **46**, 73-81.

Bivand R. & Lewin-Koh N. (2013) maptools: Tools for reading and handling spatial objects. *R package version 0.8–27*.

Bjørnstad O. (2008) The ncf Package: spatial nonparametric covariance functions. R package Version 1.1.1.

BoM. (2017) Bureau of Meteorology. Commonwealth Government of Australia.

Bond W. J. (1994) Keystone Species. In: *Biodiversity and Ecosystem Function* (eds E.-D. Schulze and H. A. Mooney) pp. 237-53. Springer Berlin Heidelberg, Berlin, Heidelberg.

Bowman D. M., Perry G. L., Higgins S. I., Johnson C. N., Fuhlendorf S. D. & Murphy B. P. (2016) Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. *Phil. Trans. R. Soc. B* **371**, 20150169.

Bradstock R. A., Williams J. E. & Gill M. A. (2002) *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, Cambridge.

Burnham K. P. & Anderson D. R. (2003) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media, New York.

Callister K. E., Griffioen P. A., Avitabile S. C., Haslem A., Kelly L. T., Kenny S. A., Nimmo D. G., Farnsworth L. M., Taylor R. S., Watson S. J., Bennett A. F. & Clarke M. F. (2016) Historical maps from modern images: Using remote sensing to model and map century-long vegetation change in a fire-prone region. *PLoS ONE* **11**, e0150808.

Catling P., Coops N. & Burt R. (2001) The distribution and abundance of ground-dwelling mammals in relation to time since wildfire and vegetation structure in south-eastern Australia. *Wildlife Research* **28**, 555-65.

Cheal D. C. (2010) *Growth stages and tolerable fire intervals for Victoria's native vegetation data sets*. Victorian Government Department of Sustainability and Environment, Melbourne, Australia.

Cherry M. J., Warren R. J. & Conner L. M. (2016) Fear, fire, and behaviorally mediated trophic cascades in a frequently burned savanna. *Forest Ecology and Management* **368**, 133-9.

Colman N. J., Crowther M. S. & Letnic M. (2015) Macroecological patterns in mammal abundances provide evidence that an apex predator shapes forest ecosystems by suppressing herbivore and mesopredator abundance. *Journal of Biogeography* **42**, 1975-85.

Colman N. J., Gordon C. E., Crowther M. S. & Letnic M. (2014) Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceedings of the Royal Society B: Biological Sciences* **281**.

Davis N. E., Forsyth D. M., Triggs B., Pascoe C., Benshemesh J., Robley A., Lawrence J., Ritchie E. G., Nimmo D. G. & Lumsden L. F. (2015) Interspecific and geographic variation in the diets of sympatric carnivores: dingoes/wild dogs and red foxes in south-eastern Australia. *PLoS ONE* **10**, e0120975.

Dexter N., Hudson M., James S., MacGregor C. & Lindenmayer D. B. (2013) Unintended consequences of invasive predator control in an Australian forest: overabundant wallabies and vegetation change. *PLoS ONE* **8**, e69087.

Doherty T. S., Dickman C. R., Nimmo D. G. & Ritchie E. G. (2015) Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation* **190**, 60-8.

Doherty T. S. & Ritchie E. G. (2016) Stop jumping the gun: a call for evidence-based invasive predator management. *Conservation Letters* **10**, 15-22.

Dormann C., McPherson J., Araújo M., Bivand R., Bolliger J., Carl G., Davies R., Hirzel A., Jetz W. & Daniel Kissling W. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609-28.

Eby S. L., Anderson T. M., Mayemba E. P. & Ritchie M. E. (2014) The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *Journal of Animal Ecology* **83**, 1196-205.

Elmhagen B., Ludwig G., Rushton S. P., Helle P. & Lindén H. (2010) Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* **79**, 785-94.

ESRI. (2014) ArcGIS 10.3. 1. Environmental Systems Research Institute Redlands, USA.

Ford A. T., Goheen J. R., Otieno T. O., Bidner L., Isbell L. A., Palmer T. M., Ward D., Woodroffe R. & Pringle R. M. (2014) Large carnivores make savanna tree communities less thorny. *Science* **346**, 346-9.

Foster C. N., Barton P. S. & Lindenmayer D. B. (2014) Effects of large native herbivores on other animals. *Journal of Applied Ecology* **51**, 929-38.

Foster C. N., Barton P. S., Sato C. F., MacGregor C. I. & Lindenmayer D. B. (2015) Synergistic interactions between fire and browsing drive plant diversity in a forest understorey. *Journal of Vegetation Science* **26**, 1112-23.

Foster C. N., Barton P. S., Sato C. F., Wood J. T., MacGregor C. I. & Lindenmayer D. B. (2016) Herbivory and fire interact to affect forest understory habitat, but not its use by small vertebrates. *Animal Conservation* **19**, 15-25.

Franklin J. (2010) *Mapping species distributions: spatial inference and prediction*. Cambridge University Press.

Fuhlendorf S. & Engle D. (2004) Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* **41**, 604-14.

Fuhlendorf S. D., Townsend D. E., Elmore R. D. & Engle D. M. (2010) Pyric-herbivory to promote rangeland heterogeneity: evidence from small mammal communities. *Rangeland Ecology & Management* **63**, 670-8.

Gallien L., Douzet R., Pratte S., Zimmermann N. E. & Thuiller W. (2012) Invasive species distribution models–how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography* **21**, 1126-36.

Geary, W.L., Doherty, T.S., Nimmo, D., Tulloch, A.I. and Ritchie, E.G. (2019) Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology*, In Press.

Greenville A., Wardle G., Tamayo B. & Dickman C. (2014) Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia* **175**, 1349-58.

Guisan A., Tingley R., Baumgartner J. B., Naujokaitis-Lewis I., Sutcliffe P. R., Tulloch A. I. T., Regan T. J., Brotons L., McDonald-Madden E. & Mantyka-Pringle C. (2013) Predicting species distributions for conservation decisions. *Ecology Letters* **16**, 1424-35.

Hale S., Nimmo D. G., Cooke R., Holland G., James S., Stevens M., De Bondi N., Woods R., Castle M., Campbell K., Senior K., Cassidy S., Duffy R., Holmes B. & White J. G. (2016) Fire and climatic extremes shape mammal distributions in a fire-prone landscape. *Diversity and Distributions* **22**, 1127-38.

Hastie T. (2013) gam: Generalized Additive Models, R Package, version 0.98. *URL http://CRAN. R-project. org/package= gam*.

Hijmans R. J. & Elith J. (2013) Species distribution modeling with R. *R package version 0.8-11*.

Hijmans R. J., Phillips S., Leathwick J. & Elith J. (2015) dismo: Species distribution modeling. R package version 1.0-12. *The R Foundation for Statistical Computing, Vienna http://cran. r-project. org*.

Hijmans R. J. & van Etten J. (2014) raster: Geographic data analysis and modeling. *R package version* **2**, 15.

Hradsky B. (2019) Conserving Australia's threatened native mammals in predator-invaded, fire-prone landscapes. *Wildlife Research* **In press**.

Hradsky B. A. (2014) More than just presence–absence: camera traps reveal fine scale resource partitioning by the ubiquitous swamp wallaby (*Wallabia bicolor*). In: *Camera Trapping: Wildlife Management and Research* (eds P. Meek, P. J. S. Fleming, G. Ballard, P. B. Banks, A. W. Claridge, J. Sanderson and D. Swann) p. 181. CSIRO PUBLISHING, Australia.

Hradsky B. A., Penman T. D., Ababei D., Hanea A., Ritchie E. G., York A. & Di Stefano J. (2017) Bayesian networks elucidate interactions between fire and other drivers of terrestrial fauna distributions. *Ecosphere* **8**, e01926-n/a.

Jedrzejewska B., Jedrzejewski W., Ray J., Redford K. & Steneck R. (2005) Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. *Large carnivores and the conservation of biodiversity*, 230-46.

Kearney M. & Porter W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**, 334-50.

Keeley J. E., Bond W. J., Bradstock R. A., Pausas J. G. & Rundel P. W. (2011) *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge University Press.

Keitt T. H., Bivand R., Pebesma E. & Rowlingson B. (2011) rgdal: bindings for the Geospatial Data Abstraction Library. *R package version 0.7-1, URL http://CRAN. R-project. org/package= rgdal*.

Kelly L. T., Haslem A., Holland G. J., Leonard S. W. J., MacHunter J., Bassett M., Bennett A. F., Bruce M. J., Chia E. K., Christie F. J., Clarke M. F., Di Stefano J., Loyn R., McCarthy M. A., Pung A., Robinson N., Sitters H., Swan M. & York A. (2017) Fire regimes and environmental gradients shape vertebrate and plant distributions in temperate eucalypt forests. *Ecosphere* **8**, e01781.

Kirkpatrick J. B., Marsden-Smedley J. B., Di Folco M.-B. & Leonard S. W. J. (2016) Influence of grazing and vegetation type on post-fire floristic and lifeform composition in Tasmania, Australia. *Plant Ecology* **217**, 57-69.

Kuijper D., Sahlén E., Elmhagen B., Chamaillé-Jammes S., Sand H., Lone K. & Cromsigt J. (2016) Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. In: *Proc. R. Soc. B* p. 20161625. The Royal Society.

Kuijper D. P. J., de Kleine C., Churski M., van Hooft P., Bubnicki J. & Jedrzejewska B. (2013) Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Bialowieża Primeval Forest, Poland. *Ecography* **36**, 1263-75.

McGregor H. W., Legge S., Jones M. E. & Johnson C. N. (2014) Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE* **9**, e109097.

McKenzie N., Burbidge A., Baynes A., Brereton R., Dickman C., Gordon G., Gibson L., Menkhorst P., Robinson A. & Williams M. (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* **34**, 597-611.

Meers T. & Adams R. (2003) The impact of grazing by Eastern Grey Kangaroos (*Macropus giganteus*) on vegetation recovery after fire at Reef Hills Regional Park, Victoria. *Ecological Management and Restoration* **4**, 126-32.

Mernagh T. P. & Miezitis Y. (2008) *A review of the geochemical processes controlling the distribution of thorium in the Earth's crust and Australia's thorium resources*. Citeseer.

Molloy S. W., Davis R. A. & van Etten E. J. B. (2016) Incorporating field studies into species distribution and climate change modelling: a case study of the koomal *Trichosurus vulpecula hypoleucus* (Phalangeridae). *PLOS ONE* **11**, e0154161.

Monamy V. & Fox B. J. (2000) Small mammal succession is determined by vegetation density rather than time elapsed since disturbance. *Austral Ecology* **25**, 580-7.

Muhly T. B., Hebblewhite M., Paton D., Pitt J. A., Boyce M. S. & Musiani M. (2013) Humans Strengthen Bottom-Up Effects and Weaken Trophic Cascades in a Terrestrial Food Web. *PLoS ONE* **8**, e64311.

Nakagawa S. & Schielzeth H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**, 133-42.

Newsome A. E. (1971) Competition between wildlife and domestic livestock. *Australian Veterinary Journal* **47**, 577-86.

Newsome T. M., Fleming P. J. S., Dickman C. R., Doherty T. S., Ripple W. J., Ritchie E. G. & Wirsing A. J. (2017) Making a New Dog? *BioScience* **67**, 374-81.

Nimmo D. G., Kelly L. T., Farnsworth L. M., Watson S. J. & Bennett A. F. (2014) Why do some species have geographically varying responses to fire history? *Ecography* **37**, 805-13.

Nuttle T., Yerger E. H., Stoleson S. H. & Ristau T. E. (2011) Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere* **2**, 1-11.

Olofsson J., E Hulme P., Oksanen L. & Suominen O. (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* **106**, 324-34.

Pasanen-Mortensen M., Elmhagen B., Lindén H., Bergström R., Wallgren M., der Velde Y. & Cousins S. A. O. (2017) The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. *Journal of Animal Ecology* **86**, 566-76.

Payne C. J., Ritchie E. G., Kelly L. T. & Nimmo D. G. (2014) Does fire influence the landscape-scale distribution of an invasive mesopredator? *PLoS ONE*.

Pearce J. & Ferrier S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* **133**, 225-45.

Pollock L. J., Tingley R., Morris W. K., Golding N., O'Hara R. B., Parris K. M., Vesk P. A. & McCarthy M. A. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* **5**, 397-406.

Quinn G. P. & Keough M. J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press.

R Core Development Team. (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaele E., Veblen T. T., Blackhall M. & Tercero-Bucardo N. (2011) Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *Journal of Vegetation Science* **22**, 59-71.

Ripple W., Larsen E., Renkin R. & Smith D. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* **102**, 227-34.

Ritchie E. G., Martin J. K., Krockenberger A. K., Garnett S. & Johnson C. N. (2008) Large-herbivore distribution and abundance: intra-and interspecific niche variation in the tropics. *Ecological Monographs* **78**, 105-22.

Robley A., Gormley A. M., Forsyth D. M. & Triggs B. (2014) Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation* **180**, 262-9.

Rodewald A. D., Kearns L. J. & Shustack D. P. (2011) Anthropogenic resource subsidies decouple predator–prey relationships. *Ecological Applications* **21**, 936-43.

Rovero F., Zimmermann F., Berzi D. & Meek P. (2013) "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix, the Italian Journal of Mammalogy* **24**, 148-56.

Sandom C., Dalby L., Flojgaard C., Kissling W. D., Lenoir J., Sandel B., Trojelsgaard K., Ejrnas R. & Svenning J. C. (2013) Mammal predator and prey species richness are strongly linked at macroscales. *Ecology* **94**, 1112-22.

Schmitz O. J., Hambäck P. A. & Beckerman A. P. (2000) Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *The American Naturalist* **155**, 141-53.

Sinclair A. R. E. & Krebs C. J. (2002) Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **357**, 1221-31.

Sitters H., Christie F., Di Stefano J., Swan M., Collins P. & York A. (2014) Associations between occupancy and habitat structure can predict avian responses to disturbance: Implications for conservation management. *Forest Ecology and Management* **331**, 227-36.

Styger J., Kirkpatrick J., Jon M. S. & Leonard S. (2011) Fire incidence, but not fire size, affects macropod densities. *Austral Ecology* **36**, 679-86.

Sunday J. M., Bates A. E., Kearney M. R., Colwell R. K., Dulvy N. K., Longino J. T. & Huey R. B. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences* **111**, 5610-5.

Swan M., Christie F., Sitters H., York A. & Di Stefano J. (2015) Predicting faunal fire responses in heterogeneous landscapes: the role of habitat structure. *Ecological Applications* **25**, 2293-305.

Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. and Macdonald, D.W. (2009) Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* **90**: 23-30.

Waser N. M., Price M. V., Blumstein D. T., Arózqueta S. R., Escobar B. D. C., Pickens R. & Pistoia A. (2014) Coyotes, deer, and wildflowers: diverse evidence points to a trophic cascade. *Naturwissenschaften* **101**, 427-36.

Wintle B. A., Elith J. & Potts J. M. (2005) Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecology* **30**, 719-38.

Wisz M. S., Pottier J., Kissling W. D., Pellissier L., Lenoir J., Damgaard C. F., Dormann C. F., Forchhammer M. C., Grytnes J.-A., Guisan A., Heikkinen R. K., Høye T. T., Kühn I., Luoto M., Maiorano L., Nilsson M.-C., Normand S., Öckinger E., Schmidt N. M., Termansen M., Timmermann A., Wardle D. A., Aastrup P. & Svenning J.-C. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* **88**, 15-30.

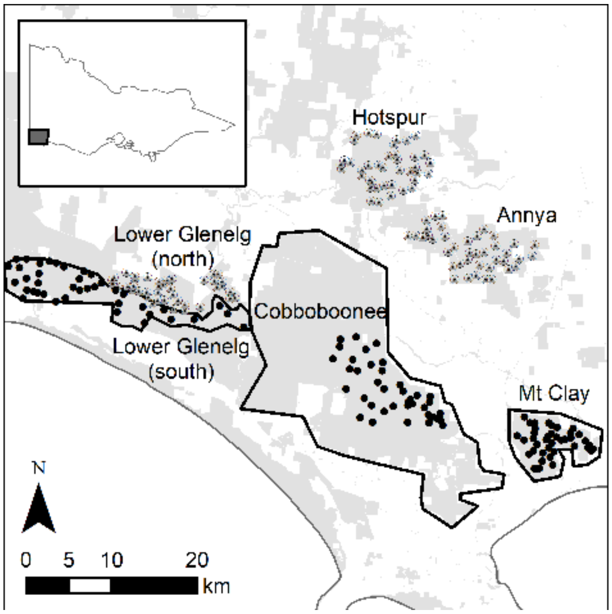
Figure Captions

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.

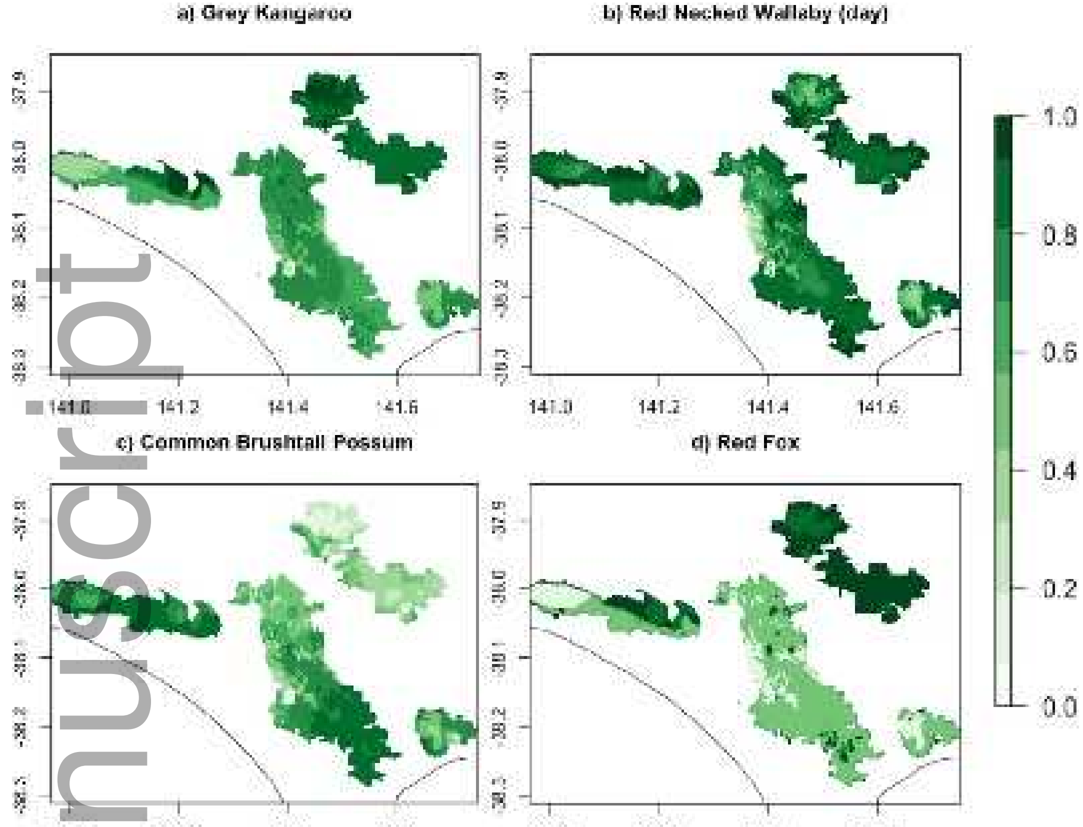
Figure 2: Mapped predicted probability of occurrence for the most highly-ranked distribution model (fixed effects only) for a) grey kangaroo *Macropus sp.*, b) red-necked wallaby *M. rufogriseus* (day time model), c) common brushtail possum *Trichosurus vulpecula* and d) red fox *Vulpes vulpes*.

Table 1: Coefficients, 95% confidence intervals and sum of Akaike weights ($\sum w_i$) for each predictor in the highly ranked species distribution models (ΔAICc < 2.0). 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 the top-ranked model (ΔAICc), the Akaike weight (w), and the marginal (R^{2}m) and conditional (R^{2}c) R^2 of each model. Bolded coefficients are those whose 95% confidence intervals do not overlap zero.

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				
Common brushtail possum		Vegetation type (woodland)	Treatment (baited)	Paddock Distance	Precipitation in Coldest Q	Mean Temp in Coldest Q	Elevation					
	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
	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



aec_12861_f1.tif



aec_12861_f2.png