

1 **Forecasting patterns of shifting biodiversity refuges in an increasingly flammable world**

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25 **Key words:** spatial prioritisation, megafires, species distribution modelling, multiple threats,
26 fire

27 **Abstract**

28 In a warming and rapidly changing world, biodiversity is increasingly threatened by
29 more frequent, severe, and larger fires. Variation in the life history attributes and habitat
30 preferences of species mean that they may be affected differently by fire, and hence, decision
31 makers must account for this. Understanding how fire affects the distribution of important
32 areas of habitat and refuges for biodiversity can help guide appropriate conservation and
33 management actions. In 2019-20 Australia suffered widespread and devastating megafires,

34 known as the Black Summer, and the East Gippsland region in state of Victoria was heavily
35 affected. To estimate impacts of the fires on fauna within the region, we used a joint species
36 distribution model fitted to data from 967 camera trap sites to estimate variation in the
37 occurrence for 40 native and invasive animal species. We focused on the influence of the fire
38 regime, lethal control of introduced red foxes (*Vulpes vulpes*), timber harvesting,
39 precipitation, and soil gradients, on wildlife. We then predicted the spatial distribution of
40 each native animal species in the dataset for three time periods: 1) in 2017 prior to the Black
41 Summer megafires, 2) in 2022 following the 2019/2020 wildfires and 3) in 2030. This
42 allowed us to estimate changes in the patterns of occurrence for each species attributable to
43 fire. Finally, we used spatial conservation prioritisation to identify priority conservation areas
44 ('fire refuges) and identify where potential threats (e.g. invasive species) might co-occur with
45 these areas. We found that fire regime variables, including time since fire and repeat short-
46 interval fires, influence occurrence patterns for ~50% of species and this meant that the
47 megafires influenced predicted occurrence patterns. Half of the mammal species (mostly
48 small and medium-sized ground-dwelling mammals) were positively associated with a
49 topographic wetness index, as were four bird species. Spatial conservation prioritisation also
50 suggested that while there were some shifts in the location of fire havens due to the
51 megafires, some large areas of high-conservation value persisted after fire. These areas were
52 disproportionately likely to be long-unburnt (≥ 80 years) with fewer repeat burns, have high
53 fox baiting intensity, and low probabilities of introduced red fox and feral cat (*Felis catus*)
54 occurrence. This suggests maintaining older vegetation in landscapes and managing predation
55 pressure by invasive predators will be important to maintaining the identified high priority
56 refuges. Our study presents a useful approach for guiding fire management before and after
57 large disturbance events, and could be expanded to test the response of species and
58 communities to forecasts of future fire regime scenarios. Predictive approaches such as this
59 study will be essential for managers to understand the possible outcomes of management
60 actions on biodiversity during a time of rapid global change.

61

62 **Introduction**

63 Fire affects species' distributions and the community structure of many ecosystems
64 globally (Jones & Tingley 2022). Some plant and animal species are adapted to fire regimes,
65 including the environmental heterogeneity that fire creates (Smith, Bull & Driscoll 2013;
66 Furnas, Goldstein & Figura 2022). However, as fire regimes change, and interact with other

67 threats (Abatzoglou, Williams & Barbero 2019; Keith *et al.* 2022), fire is emerging as a major
68 driver of global extinction risk (Kelly *et al.* 2020; Doherty *et al.* 2024).

69 Animal species show diverse responses to fire due largely to its impact on habitat
70 resources (Fox 1982). As a result, the availability and location of suitable habitat for animal
71 species may change over time in fire-prone landscapes (Reside *et al.* 2019). This poses a
72 significant challenge for conservation, as species' shifting distributions also change the
73 locations of areas with high conservation value, particularly when other dynamic threats—
74 such as invasive species or human land use (e.g., timber harvesting)—co-occur and interact
75 with fire (Doherty *et al.* 2022). The challenge is magnified by extreme fire events, including
76 megafires (>100,000 ha) and gigafires (>1,000,000 ha), which transform species'
77 distributions across vast areas (Linley *et al.* 2022). Extreme wildfires are becoming common
78 across the globe (Cunningham, Williamson & Bowman 2024), including the 2019 Amazon
79 wildfires, Australia's 2019/2020 Black Summer wildfires, and 2020 to 2021 California
80 megafires. During such large, intense fires, it is crucial for managers to identify which
81 species are most affected and which areas of the landscape are impacted (Legge *et al.* 2022).

82 Forecasts are increasingly used in ecology and conservation to guide management
83 (Mouquet *et al.* 2015). Forecasts allow managers to anticipate future conditions, including
84 disturbance, enabling informed decision-making in the face of environmental change (Dietze
85 *et al.* 2018). In ecology, forecasts often link baseline data on species occurrences or
86 abundances across space or time to biophysical or environmental data, and sometimes a
87 management action or disturbance of interest, then project these data to future environmental
88 conditions or possible management scenarios (Penman *et al.* 2015; Briscoe *et al.* 2019;
89 Connell *et al.* 2019). However, robust forecasts require models that are parameterised with
90 robust empirical or field-collected data (Greenville *et al.* 2018). As fire regimes change, there
91 is an increasing need for flexible and adaptive approaches that accurately estimate species'
92 responses to large disturbances (e.g. megafires) and explicitly link these predictions to
93 guidance for managers.

94 Our study aims to a) develop a field data-driven framework for forecasting fauna
95 community responses to future fire regimes using baseline data that can be updated as new
96 data are collected post-disturbance, and b) use these forecasts to identify fire havens where
97 managers should focus management effort at a given point in time, including by potentially
98 excluding future fires (e.g. bushfires and/or planning burning) or managing co-occurring
99 threats. We demonstrate our approach by using it to understand how a wildlife assemblage in
100 East Gippsland, Australia, is shaped by fire, and to forecast how species occurrence patterns

101 and areas of high conservation importance were affected by 2019/2020 wildfires. Finally, we
102 evaluate the quality of fire refuges by predicting their vulnerability to six invasive species
103 known to influence food and shelter resources for native species in East Gippsland.

104 **Methods**

105 *Study region*

106 Our study focussed on the forests of East Gippsland, Victoria, Australia, an area
107 spanning ~1 million hectares. The study region experiences a temperate climate, with mean
108 annual precipitation ranging of 630–1156 mm (BoM 2020), and is made up of numerous
109 vegetation types, including wet eucalypt forest, mixed eucalypt species foothill forest, coastal
110 heathland, rainforest, and dry woodland (Cheal 2010).

111 There are a range of forest management practices that occur within our study area.
112 The fire regime in the region is a mix of wildfires and planned burning of a range of
113 severities. Fire return intervals range from <5 years to ~20 years (DELWP 2020b). In East
114 Gippsland, the frequency and severity of fire influences the structure of vegetation, and
115 therefore, habitat for fauna. Timber harvesting has also occurred within State Forests over
116 several decades at a range of intensities, including both clear fell and regrowth thinning.
117 Predation by introduced red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) is a major threat
118 to native mammals within the study region, and lethal fox control has occurred in the region
119 since the late 1990s, later becoming more extensive through the Southern Ark program
120 (Dexter & Murray 2009).

121

122 *Camera trapping*

123 To understand the distribution of wildlife species in East Gippsland, we used a large
124 camera trapping dataset collected across 967 sites that spanned the range of vegetation types,
125 fire histories and land tenures (e.g. National Parks and State Forests). Cameras were deployed
126 between June 2016 and June 2017 for a minimum of 30 days to maximise detections. Each
127 camera was baited with a lure staked 1-2 metres in front of the camera. For a full summary of
128 camera site selection procedures, refer to Robley *et al.* (2022). From this camera dataset, we
129 then collated presence-absence data for each of the species detected on the camera traps, with
130 the aim of including in community modelling species that were detected at more than 10
131 sites.

132

133 *Covariate development*

134 To understand the drivers of species' distributions in East Gippsland, we developed a
135 series of covariates representing key disturbances and forest management drivers (e.g. fire,
136 timber harvesting and lethal fox control), and biogeographic and habitat variables (e.g. mean
137 annual precipitation, topographic wetness index and soil composition) (Table 1). Because we
138 were interested in predicting species' distributions across the study region and some species
139 in our dataset, such as *Antechinus* spp. have small home ranges (0.5-3 Ha; Lazenby-Cohen &
140 Cockburn 1991), we developed these covariates with pixels at a common resolution of 50 m.

141 To model species' responses to the fire regime, we developed two fire-related
142 covariates due to their hypothesised effect on vegetation structure, which then influences
143 species occurrence (Swan *et al.* 2015). We use a directed acyclic graph to illustrate the
144 hypothesised causal relationship using a causal model with the key relationships between
145 time since fire, repeat fire, vegetation structure and fauna occurrence (Figure S8.1) (Ferraro,
146 Sanchirico & Smith 2019; Arif & MacNeil 2022). First, for each pixel, we calculated the
147 number of years since it had last burnt (i.e. time since fire) using maps of all past fires
148 (DELWP 2020a). For pixels with no fire history, we arbitrarily assigned the year of last fire
149 as 1900 as large (but unmapped) fires occurred throughout Gippsland in the early 1900s. We
150 also used the fire history data to calculate the mean number of times that pixels within 500 m
151 of each camera site that has been burnt in the 20 years prior to survey. Because the maps of
152 past fires can be inaccurate, particularly for fires that had been mapped without considering
153 satellite imagery (i.e. most fires before the 1990s), we used a burn cover model of south-
154 eastern Victoria to mask out vegetation unlikely to burn in most fires from the mapped fire
155 history, such as gullies and other wet vegetation (Bluff & McCarthy 2018). Using this
156 approach to edit the fire history data produces more accurate estimates of burnt locations
157 within East Gippsland (Lucas Bluff & Luke Smith *pers. comm.*). However, it is important to
158 note that many fires from before ~1970 have not been mapped at all and so fire mapping
159 before this time is incomplete for the East Gippsland region (Bluff 2014). This may bias the
160 fire history dataset, in that the fire mapping may mean that some sites identified as ~100
161 years post-fire may be closer to ~50 years post-fire.

162 Timber harvesting is another prominent disturbance within the study region that
163 influences vegetation structure at both the site and landscape-scale (Alexander, Scotts &
164 Loyn 2002). To quantify variation in timber harvesting across the study region, we calculated
165 the proportion of pixels within 500 m of each camera site that were harvested in the 40 years
166 prior to survey using clearfell techniques. Lethal fox control is undertaken throughout the
167 study region by regularly deploying permanent poison bait stations along roadsides, spaced

168 on average every 0.7 km along roads. To quantify the spatial variation in fox baiting
 169 intensity, we quantified the density (number of baits per km²) of poison bait stations within 5
 170 km of each camera site.

171 As a proxy for landscape-scale variation in resource availability and variation in
 172 habitat type, we collated data on the average annual precipitation at each camera site (BoM
 173 2020). To represent local scale variation in resource availability and habitat type, we used the
 174 topographic wetness index at each site (Gallant & Austin 2012). The modelled percentage of
 175 clay and carbon in the soil at each site was also used to represent variation in habitat types
 176 across the study region, as soil type is highly associated vegetation type and structure in the
 177 region (Grundy *et al.* 2015).

178 Finally, before inclusion in further analysis, we assessed whether any pairs of
 179 covariates were strongly correlated (using Spearman’s correlation test, with a threshold of r_s
 180 > 0.7). All covariate pairs had correlation coefficients of $r_s < 0.7$ and $r_s > -0.7$.

181

182 **Table 1:** Description of each covariate included in the joint-species distribution modelling framework, and
 183 the range and units of their values.

Covariate	Description	Range
Time since fire	The time (years) since each site was last burned by fire of any severity. Where no fires had been mapped, we assigned a year of last fire as 1900 (122 years post-fire).	0 – 122
Mean repeat burn	The average number of times a pixel within 500 m of a site has been burnt in the 20 years prior to survey	0 – 2.11
Bait Intensity	The density of fox baiting stations (number per km ²) within 500 m of a site	0 – 20
Harvest prop 40	The proportion of a 500m buffer around each site that has been clear-fell harvested in the 40 years prior to survey.	0 – 0.93
Mean rainfall	The mean annual precipitation at each site (mm per annum)	630.6 – 1156
Topographic wetness index	The topographic wetness index describes the relative wetness of the site, based on how both local and landscape-scale topography (e.g. slope) and placement within a catchment influences water flow (index).	4.95 – 11.26
Clay	The modelled percentage (by mass, 0-0.05 m depth) of soil in a location made up of clay	9.20 – 20.58
Carbon	The modelled percentage (by mass, 0-0.05 m depth) of soil in a location made up of carbon	1.96 – 7.58

184

185 *Joint-species distribution modelling*

186 To identify the key drivers of the spatial distribution of the East Gippsland fauna
 187 community, we used a spatial joint-species distribution model implemented in the R package
 188 *Hmsc*—hierarchical modelling of species communities (Ovaskainen *et al.* 2017; Tikhonov *et*
 189 *al.* 2020). Joint-species distribution models (jSDM) simultaneously estimate species’
 190 responses to model covariates, as well as correlations between the occurrence patterns of each

191 individual species. The approach implemented by Tikhonov *et al.* (2020) uses a spatial factor
 192 dimension reduction approach and a Nearest Neighbour Gaussian Process with 10 nearest
 193 neighbours in a Bayesian framework to efficiently deal with large, spatially-autocorrelated
 194 datasets (e.g. many sites and species). The environmental variable component of our model
 195 included covariates relating to the fire regime, lethal control of red foxes, spatial variation in
 196 precipitation and soil characteristics (Table 1 & 2). We also included a spatial component in
 197 the model to account for spatial autocorrelation between camera trap locations (Table 2). All
 198 covariates were scaled using the base R scale function prior to modelling, and we used
 199 uninformative priors.

200

201 **Table 2:** Environmental and spatial model formulae of the joint species distribution model used to estimate
 202 species' occurrences across the study region in East Gippsland, Victoria

Model Component	Model Formula
Environmental	\sim time since fire + time since fire ² + mean repeat burn + bait intensity + harvest prop 40 + mean rainfall + topographic wetness index + clay + carbon
Spatial covariates	Easting, Northing

203

204 The model was implemented as a spatial factor jSDM using the species' presence-absence
 205 data with a probit error distribution and used Markov Chain-Monte Carlo sampling for four
 206 chains, with 25,000 iterations each, as well as a burn in of 25,000 iterations. We retained
 207 every 100th iteration of each chain, giving a total number of 1000 posterior samples (250 per
 208 chain). To ensure model convergence, we ensured the Gelmin-Rubin statistic was below 1.1
 209 for each parameter (Gelman, Hwang & Vehtari 2014) and examined trace plots for all major
 210 values to ensure adequate mixing. To evaluate model predictive performance for each
 211 species, we report the root mean squared error (RMSE) and the area under the receiver
 212 operating curve (AUC) following *k*-fold cross validation with 4 folds, all implemented within
 213 the *hmsc* package and framework (Ovaskainen *et al.* 2017; Tikhonov *et al.* 2020).

214

215 *Spatial prioritisation*

216 To identify the most important locations within the study area for the 40 native
 217 species in our study (i.e. excluding invasive species) immediately before and after the Black
 218 Summer fires, we used the systematic conservation planning program Zonation (v5)
 219 (Moilanen *et al.* 2005). We produced Zonation rank maps using predicted species occurrence
 220 probabilities for a) fire histories in 2017 (pre-Black Summer), b) fire histories in 2022
 221 (immediately post-Black Summer), and c) fire histories 10 years post-Black Summer
 222 (calculated by adding 8 years to all values in the 2022 fire history map, and assuming no

223 additional fires following 2022). We chose this time horizon as the natural fire return interval
224 in these forests is typically greater than 10 years (Cheal 2010).

225 Zonation ranks pixels across the study region based on their contribution to the
226 conservation of each individual species in the analysis, determined by the probability of
227 occurrence of each species identified by the joint-species distribution models. The output of a
228 Zonation analysis is a complementarity-based ranking of conservation priority for the entire
229 study region of interest, where the highest-ranking cells have values closer to 1 and lowest
230 ranking cells have values closer to 0. In our prioritisation, we used the ‘Core Area Zonation’
231 algorithm which identifies high ranking areas that have a high probability of occurrence for
232 rare species (i.e. species with relatively restricted distributions within the study region being
233 modelled) (Moilanen *et al.* 2014). Therefore, for this algorithm, cells that are relatively less
234 species rich can be ranked highly if they are important for a single species. We did not apply
235 any weightings to any species (e.g. conservation status) for the purposes of our study. As our
236 goal was to rank sites by their relative conservation importance (rather than an explicit
237 management action) immediately before and after the 2019/2020 wildfires (Moilanen *et al.*
238 2014; Selwood, Cunningham & Mac Nally 2019), we did not consider cost in our Zonation
239 problem formulation.

240 We defined ‘high-ranking locations’ as the 20% of the study region with the highest
241 Zonation ranking (i.e. values above 0.8). We used this threshold to identify locations in the
242 study region that were high-ranking before, 1 year after, and 10 years after the 2019/2020
243 wildfires.

244 Finally, to provide some general insight into the potential drivers of the 1 year post-
245 fire Zonation ranking beyond the individual species distributions, we built a beta regression
246 model of 10,000 random spatial point samples of the Zonation rank (as rank data are bounded
247 between 0 and 1) and six scaled covariates—time since fire, baiting intensity, mean repeat
248 burn (Table 1) and predictions from the joint-species distribution model for three invasive
249 species of conservation concern in the study region: the red fox, feral cat and sambar deer
250 (*Rusa unicolor*). All covariates were fitted as 3rd order polynomials to account for non-linear
251 relationships with zonation rank. To account for spatial autocorrelation between residuals, we
252 included an auto-covariate calculated from the zonation ranking using the R package *spdep*
253 (Bivand *et al.* 2015), with a neighbourhood radius of 10,000 cells. The model was fit using
254 the package *brms* with four chains and 3000 iterations (Bürkner 2017). Model convergence
255 was assessed by interpreting the effective sample size, Rhat values and diagnostic plots
256 (Gelman & Rubin 1992).

257 **Results**

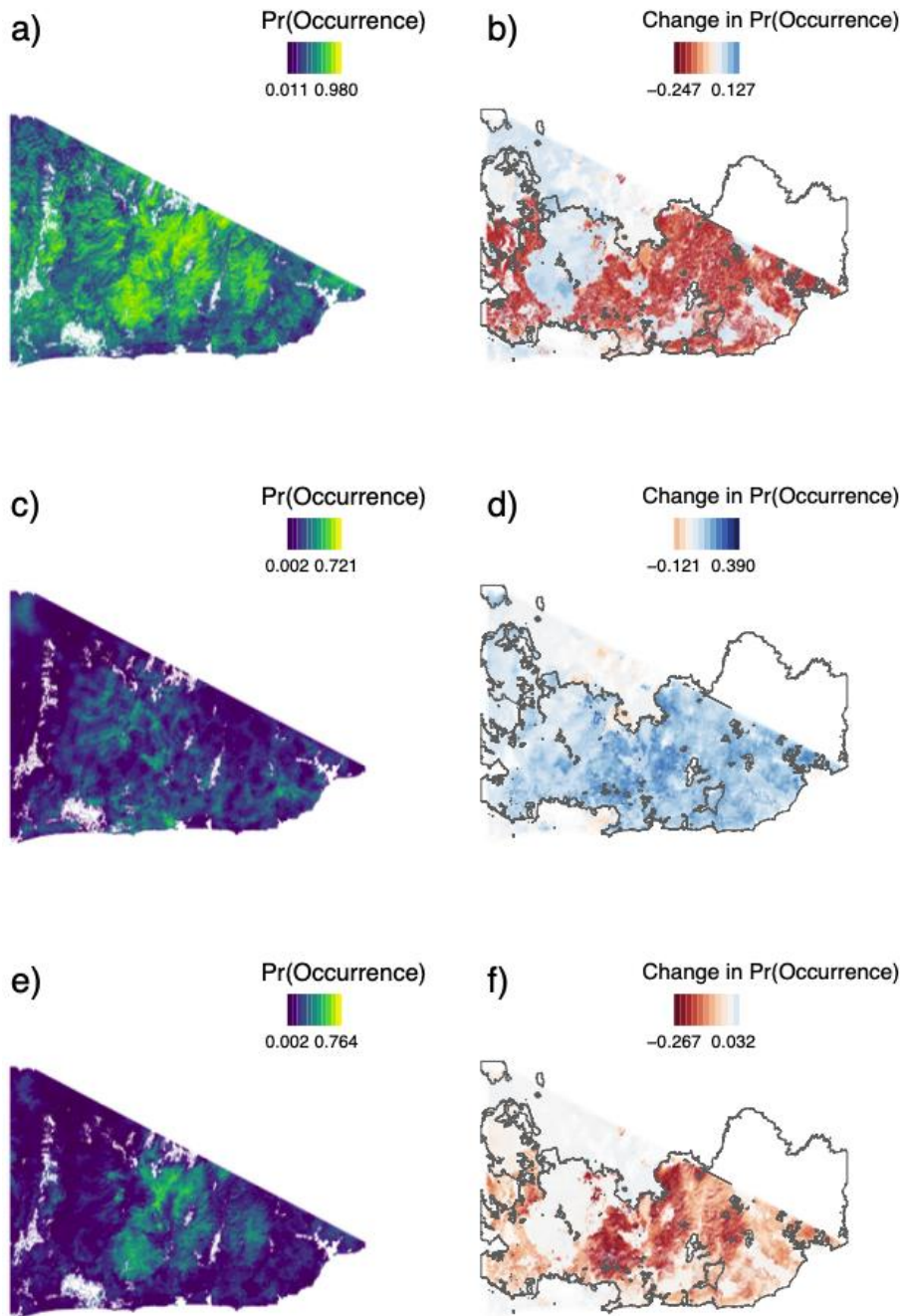
258 *Species modelling*

259 Thirty-four native and six invasive species were detected by the camera traps at 20 or
260 more sites across the study region and were therefore eligible for inclusion in our joint-
261 species distribution model. The most frequently detected species were the black wallaby
262 (*Wallabia bicolor*; 747 sites out of 1196) and superb lyrebird (*Menura novaehollandiae*; 580
263 sites), whereas species such as fallow deer (*Dama dama*) and crimson rosella (*Platycercus*
264 *elegans*) were detected at less than 25 (~2% of sites) sites (Table S1).

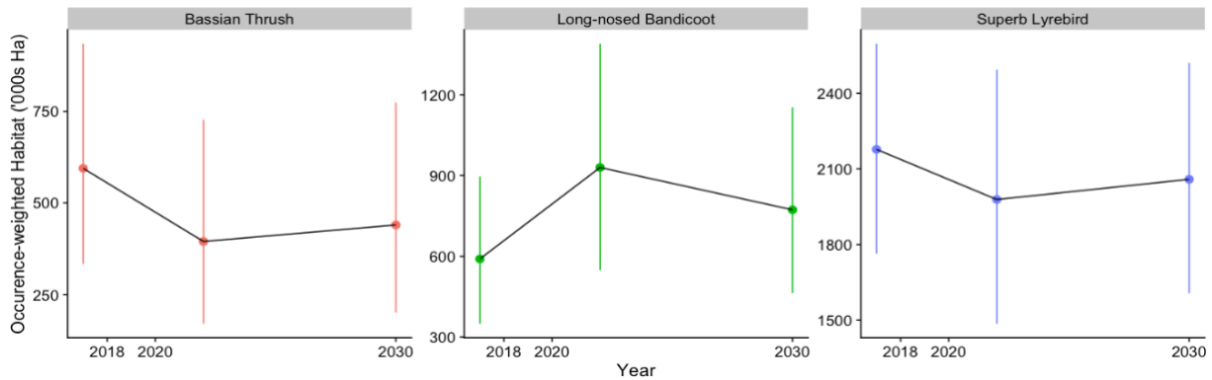
265 The joint-species distribution model revealed a range of influential drivers of species
266 occurrence patterns across the East Gippsland study region. Time since fire had significant
267 associations with one third of mammal species (Figure S3), and 31% of bird species (Figure
268 S4). For most bird and mammal species, the time since fire relationship was a negative
269 quadratic relationship, with occurrence peaking at intermediate time since fire ages (Figures
270 S3 and S4). For the invasive species in the joint-species distribution model, time since fire
271 was only influential for sambar deer (positive quadratic shape) (Figure S5). Eight mammal
272 and reptile species (e.g. long-footed potoroo *Potorous longipes*, long-nosed bandicoot
273 *Perameles nasuta*, and short-beaked echidna *Tachyglossus aculeatus*) and nine bird species
274 (e.g. wonga pigeon *Leucosarcia melanoleuca*, white-browed scrub-wren *Sericornis frontalis*)
275 were positively associated with fox baiting intensity (Figure S3). Of the native species, only
276 dingoes and spot-tailed quolls were negatively associated with fox baiting intensity, whereas
277 all invasive species, except sambar deer, were negatively associated with fox baiting intensity
278 (Figure S5). Soil clay and carbon content and topographic wetness index were important for
279 >50% of native mammal and reptile species (Figure S3). Soil carbon content influenced more
280 bird species distributions than clay content, and 50% of the bird species modelled were
281 positively associated with topographic wetness index (Figure S4). Three-quarters of native
282 mammal, reptile and bird species modelled were associated with rainfall (Figure S3, S4).

283 Based on the model coefficients, at least ten native mammals and reptiles, and six bird
284 species, are predicted to have experienced changes in their spatial patterns of occurrence
285 when comparing their modelled distribution at the time of survey (2017) with their forecast
286 distribution (2022 and 2030). For example, the superb lyrebird is forecast to have seen large
287 areas decrease in occurrence probability and other parts increase (Figure 1). For other species
288 predicted decreases in occurrence probability are forecast to be as much as 30% (Figure 2;
289 Bassian thrush). Other species are predicted to have increased in occurrence probability (e.g.

290 long-nosed bandicoot), in some places by up to 40%. Model fit for each species was
291 generally good, with almost all (45/48) species having an AUC > 0.7 (Table S2).
292



293
294 **Figure 1:** Predicted distributions of probability of occurrence from the joint-species distribution model for
295 the superb lyrebird (*Menura novaehollandiae*) [a, b], the long-nosed bandicoot [c,d] and the Bassian thrush
296 [e,f] for the the year 2017 (pre-Black Summer) and the predicted change in probability of occurrence
297 between 2017 and 2022 (post-Black Summer), respectively.
298
299



300

301

Figure 2: Predicted area of occurrence-weighted habitat (000's of Ha) for three example species, the Bassian thrush, the long-nosed bandicoot and the superb lyrebird (*Menura novaehollandiae*) for the years 2017 (pre-Black Summer), 2022 (post-Black Summer) and 2030.

303

304
305 *Spatial prioritisation*

306

Our prioritisations using predictions of 34 native species distributions in both 2017 and 2022 revealed shifts in the distribution of high-ranking habitat for the modelled fauna species following the 2019/2020 Black Summer megafires (Figure 3), demonstrated by the areas that became highly ranked habitat in the 2022 and 2030 scenarios (Figure 3).

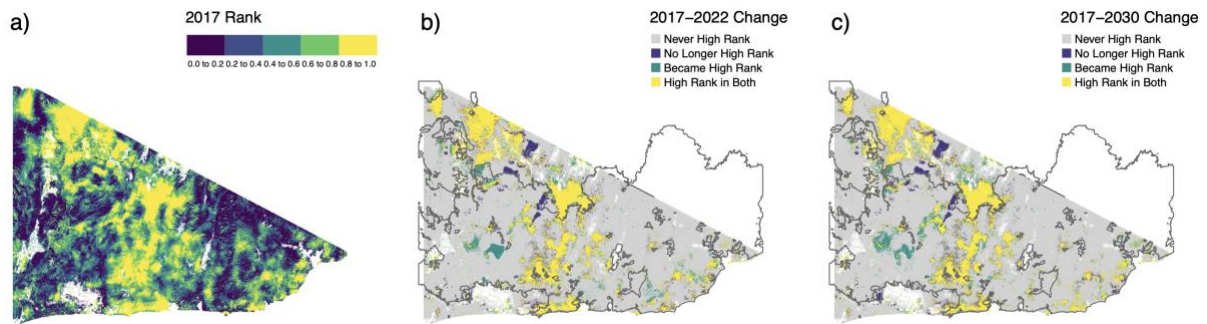
309

Three key areas remained high ranking in both prioritisations—the Errinundra region in the centre of the study region, the Upper Snowy River region in the northwest of the study region, and coastal heathland along the southern coast of the study region (Figure 3). High-ranking locations in the 2017 prioritisation that did not appear in the 2022 prioritisation were scattered throughout the study region, with some larger areas occurring in coastal habitat that was burnt during the 2019/2020 wildfires (Figure 3). Many of the high-ranking locations that only appeared in the 2022 prioritisation were also scattered through the region, aside from a large block of unburnt habitat near the Martins Creek Nature Conservation Reserve in the central west of the study region (Figure 3).

319

High-ranking locations for native species from the 2022 analysis with current fire history information are more likely to have lower feral cat and red fox occurrence, but higher sambar deer occurrence (Figure 4). Further, high ranking locations are more likely to be long-unburnt, have lower repeat fire and higher fox baiting intensity (Figure 4).

323

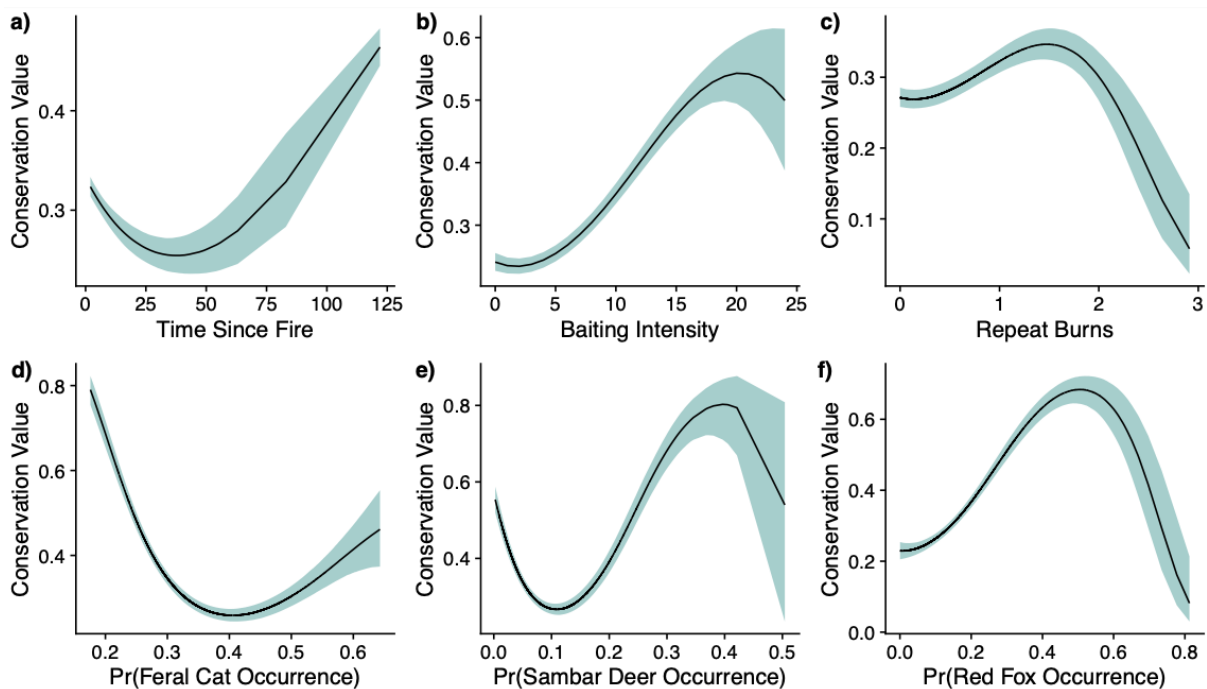


324

325 **Figure 3:** a) Priority rankings from Core Area Zonation analyses using predicted species distributions for
 326 the year 2017 (pre-Black Summer) for a fauna community in East Gippsland, Victoria, Australia. Values
 327 closer to 1 are relatively higher ranked in terms of conservation importance compared with values closer to
 328 0. Rankings for the 2022 and 2030 scenarios are in Figure S6. Locations of change in the highest ranked
 329 (Top 20%) locations by Core Area Zonation between b) 2017 and 2022, and c) 2017 and 2030 for a fauna
 330 community in East Gippsland, Victoria, Australia. Yellow locations are within the Top 20% ranking in
 331 both 2017 and 2022, green locations became highly ranked in 2022, blue locations were highly ranked in
 332 2017 but not in 2022. Grey locations never occurred in the high ranks for either 2017 or 2022.

333

334



335

336 **Figure 4:** Expected conservation value from the 2022 Zonation analysis against six covariates, including
 337 a) time since fire (years), b) baiting intensity, c) repeat burns, d) feral cat occurrence, e) sambar deer
 338 occurrence, f) red fox occurrence. Shaded bands represent 95% confidence intervals, and the black line
 339 represents the mean predicted relationship.

340 **Discussion**

341 Large, intense fires are become increasingly common across much of the world
342 (Cunningham, Williamson & Bowman 2024). As such, land managers must employ planning
343 approaches that are dynamic, flexible and adaptable to changing conditions (Rhodes *et al.*
344 2022). Our study provides a framework for using field data and spatial conservation planning
345 to forecast the effects of megafire on individual species and animal communities. To achieve
346 this, we bring together methods developed to forecast species' responses to disturbances such
347 as fire (Connell *et al.* 2019; Verdon & Clarke 2022), and conservation planning approaches
348 that informed the short-term responses to the Australian 2019/2020 wildfires (Geary *et al.*
349 2021; Ward *et al.* 2022). Our results show that, while a large portion of the study region
350 remained high ranking in the years following the megafires, there was also considerable
351 turnover (i.e. some areas lowering in ranking and some areas increasing in ranking) due to the
352 forecasted changes in species' occurrences.

353 Species' responses to fires and the overall fire regime are often highly contextual
354 (Nimmo *et al.* 2019) and modelling them often assumes a causal relationship between fire
355 variables and species occurrence, driven by the effect of fire on vegetation structure (Figure
356 S1) (Swan *et al.* 2015). Our model forecasts help to identify species expected to have been
357 positively or negatively affected by the 2019/2020 wildfires as well as their potential
358 recovery trajectories. By explicitly modelling the correlative relationships between species
359 occurrences, fire regime variables (such as time since fire and fire interval), and other
360 environmental factors, our approach enables managers to better understand fine-scale patterns
361 of refuges and provides critical insights for their management. Further, these forecasts can be
362 readily updated with newly collected data from subsequent post-fire surveys (Dietze *et al.*
363 2018).

364 Our prioritizations using the species' forecasts revealed that locations of conservation
365 importance following the Black Summer wildfires were more likely to contain vegetation that
366 was over 80 years post-fire and had been burnt less than three times in the previous 20 years.
367 Vegetation older than 80 years is considered mature for several of the vegetation types within
368 this region (Cheal 2010). Therefore, maintaining sufficient vegetation within this age range
369 and reducing fire frequency may be important actions for conserving fauna species in this
370 study, such as the Bassian thrush and superb lyrebird.

371 Co-occurring threats, such as invasive species, can influence the value of fire refuges
372 (Robinson *et al.* 2013; Reside *et al.* 2019). By jointly modelling occurrence of native species,

373 as well as invasive species that threaten these species, we are also able to identify the
374 invasive species that are likely to co-occur in identified areas of high conservation
375 importance. Our results suggest that feral cats and red foxes were less likely to occur in high-
376 ranking locations after the 2019/2020 wildfires, compared with lower ranking locations. For
377 red foxes, this is likely reflective of decades of lethal fox control that has reduced fox
378 occurrence and abundance in the study region and subsequent increases in the abundance of
379 some native fauna (Dexter & Murray 2009; Robley *et al.* 2022). To maximise the persistence
380 of native species, ensuring that feral cats remain excluded from high-value locations should
381 be a key consideration for managers, under both normal conditions and during post-fire
382 recovery.

383 The results of our joint-species distribution model also revealed some insights
384 relevant to the management of the fauna community considered in our study. Our results
385 confirm the results of previous studies in the region that fox baiting is negatively associated
386 with fox occurrence, and positively associated with the occurrence of some small and
387 medium-sized mammals (e.g. long-footed potoroo) (Dexter & Murray 2009). It is also worth
388 noting that a negative association between baiting intensity and the probability of dingo and
389 spot-tailed quoll occurrence does not demonstrate a causal relationship. For example, spot-
390 tailed quoll presences were geographically concentrated in the north-west of the study area.
391 While this area has lower baiting intensity for logistical reasons, it is also distinctive across a
392 range of environmental variables beyond the scope of this study. For both bird and mammal
393 species in our analysis, topographic wetness index was an important covariate, suggesting a
394 preference for gullies and other wet areas typically characterised by dense vegetation with
395 favourable microclimates and abundant food resources (Reside *et al.* 2019). As feral cat and
396 feral pig occurrence was also positively associated with wetter areas, this requires
397 management attention as feral pigs are predators of small vertebrates, and can simplify
398 vegetation structure (Bengsen, West & Krull 2017), which may in turn aid feral cat hunting
399 success (McGregor *et al.* 2015).

400 While our approach has generated some insights into the management of the East
401 Gippsland fauna community following the 2019/2020 wildfires, care is needed when
402 interpreting our results, especially in a management context. Our intention was to
403 demonstrate a method, rather than to develop an accurate management plan. The spatial
404 prioritisation component of our study assumes that each species' relationship with time since
405 fire has been characterised accurately (see Figure S1). As our approach uses a single
406 historical field dataset collected using one survey method (camera trapping) to model

407 correlative relationships, there may be considerable uncertainty in the relationships between
408 some species' occurrences and time since fire, especially when camera traps are not an
409 effective survey method (e.g. arboreal mammals). Further, our analysis only considers 35
410 mammal and bird species, and one reptile species, for which data were available, and so the
411 identified high-ranking locations are only relevant for these species. Lastly, the severity of
412 the Black Summer megafires were extreme, having been preceded by significant rainfall
413 deficits over three years in East Gippsland (Nolan *et al.* 2020). As our model was
414 parametrised by relating fire history characteristics with species occurrences, forecasting
415 responses to fires outside the historical fire regime will be uncertain.

416 Rapid and substantial climate and environmental change will require conservation
417 managers to explicitly build flexibility into conservation planning approaches and
418 acknowledge that conservation priorities might need to change in response to large events,
419 such as fires (Rhodes *et al.* 2022), or incursions of invasive species. Our study outlines a
420 dynamic framework for forecasting individual species responses to a range of drivers and
421 identifying how locations of conservation importance shift following a large wildfire. As our
422 approach is easily updateable with new field data and can also be used to forecast individual
423 species and community responses to future fire regimes (*sensu* Connell *et al.* 2019), it
424 provides land managers with the ability to pre-plan and make decisions before the next fires
425 occur as well as closely manage the identified important refuges in the interim. Two
426 particular future applications are of interest to fire managers: 1) Using scenario analysis to
427 identify areas for protection from future fire or areas that need to be burnt to maintain an
428 appropriate mix of fire age classes in the landscape, and 2) Ensuring important areas are
429 spread geographically throughout the region to maintain species' metapopulations and
430 minimise the risk of losing all important locations during a single large, severe disturbance in
431 the future. This information will be vital to help managers to better prepare biodiversity for a
432 future of climate and disturbance extremes (Wintle, Legge & Woinarski 2020).

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434 **Competing Interests**

435 The authors have no competing interests to declare.

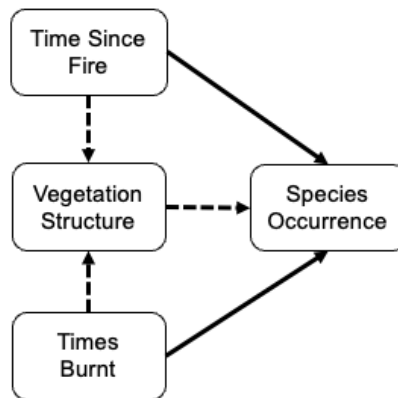
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443

444 **Supplementary Information 1**



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447 **Figure S1:** Directed acyclic graph illustrating the hypothesised causal relationship between time-since-
448 fire, vegetation structure and the number of times a site was burnt in this study, and their effects on species
449 occurrence probabilities. Dashed lines indicate hypothesised causal relationships assumed but not
450 explicitly tested in this study, and solid lines indicate the associations tested in this study that are assumed
451 to be representative of the causal relationships.

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453 **Table S1:** Number of sites each species that was included in the joint-species distribution model was
454 detected. Total number of sites in the analysis was 967.

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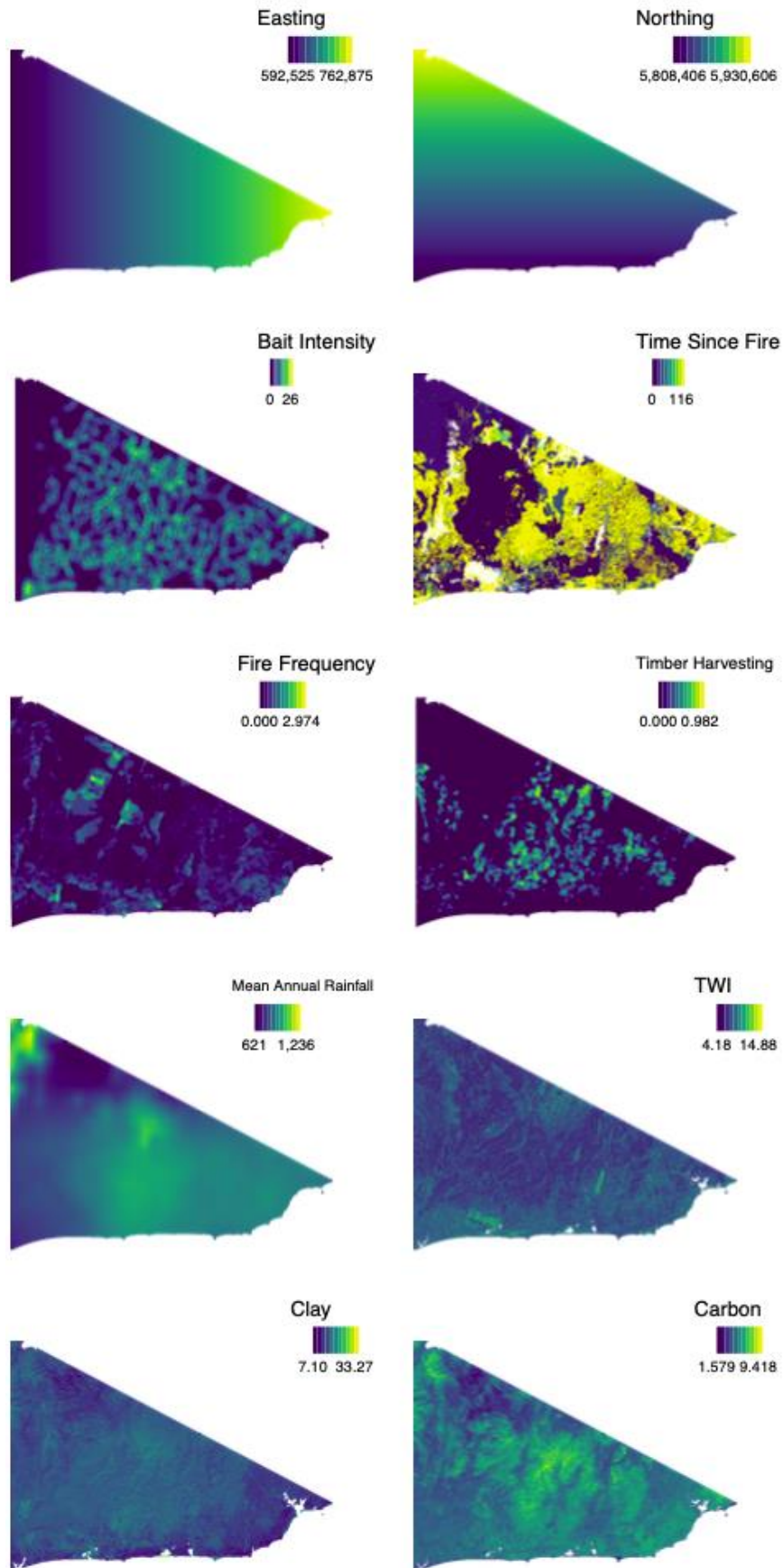
Species Common Name	Species Scientific Name	Count of Sites Detected
Black Wallaby	<i>Wallabia bicolor</i>	747
Superb Lyrebird	<i>Menura novaehollandiae</i>	580
Common Wombat	<i>Vombatus ursinus</i>	516
Mountain Brushtail Possum	<i>Trichosurus cunninghami</i>	440
Feral Cat	<i>Felis catus</i>	371
Common Brushtail Possum	<i>Trichosurus vulpecula</i>	344
Long-footed Potoroo	<i>Potorous longipes</i>	285
Agile Antechinus	<i>Antechinus agilis</i>	242
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	228
Lace Monitor	<i>Varanus varius</i>	184
Long-nosed Bandicoot	<i>Perameles nasuta</i>	184
Bassian Thrush	<i>Zoothera lunulata</i>	174
Short-beaked Echidna	<i>Tachyglossus aculeatus</i>	167
Wonga Pigeon	<i>Leucosarcia melanoleuca</i>	140
Red-necked Wallaby	<i>Macropus rufogriseus</i>	128
White-browed Scrubwren	<i>Sericornis frontalis</i>	120
Pied Currawong	<i>Strepera graculina</i>	116
Eastern Yellow Robin	<i>Eopsaltria australis</i>	102
Red Fox	<i>Vulpes vulpes</i>	94
Superb Fairy-wren	<i>Malurus cyaneus</i>	89
Dusky Antechinus	<i>Antechinus swainsonii</i>	88
Sambar Deer	<i>Rusa unicolor</i>	86
Pilotbird	<i>Pycnoptilus floccosus</i>	70
Dingo	<i>Canis dingo</i>	66
Spotted Quail-thrush	<i>Cinclosoma punctatum</i>	64
Horse	<i>Equus ferus caballus</i>	59

Satin Bowerbird	<i>Ptilonorhynchus violaceus</i>	46
White-throated Treecreeper	<i>Cormobates leucophaea</i>	45
Eastern Grey Kangaroo	<i>Macropus giganteus</i>	44
European Rabbit	<i>Oryctolagus cuniculus</i>	43
Laughing Kookaburra	<i>Dacelo novaeguineae</i>	43
White-winged Chough	<i>Corcorax melanorhamphos</i>	43
Eastern Whipbird	<i>Psophodes olivaceus</i>	40
Bush Rat	<i>Rattus fuscipes</i>	35
Grey Currawong	<i>Strepera versicolor</i>	35
Long-nosed Potoroo	<i>Potorous tridactylus</i>	29
Feral Pig	<i>Sus scrofa</i>	25
Spot-tailed Quoll	<i>Dasyurus maculatus</i>	25
Common Ringtail Possum	<i>Pseudocheirus peregrinus</i>	23
Eastern Pygmy-possum	<i>Cercartetus nanus</i>	21

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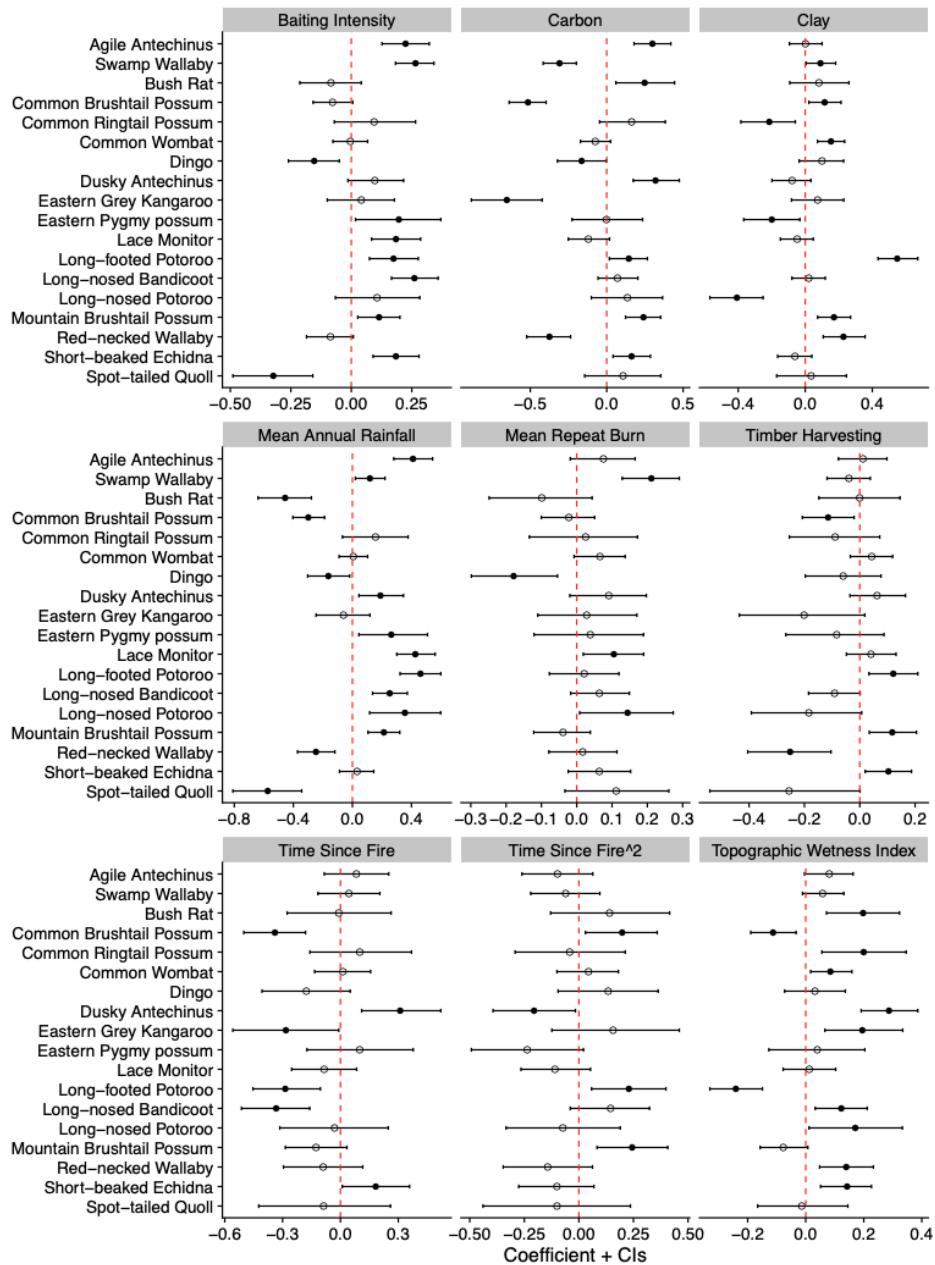
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Figure S2: Covariates included in the joint species distribution model used to predict the occurrence of fauna species throughout the study region in East Gippsland, Australia.



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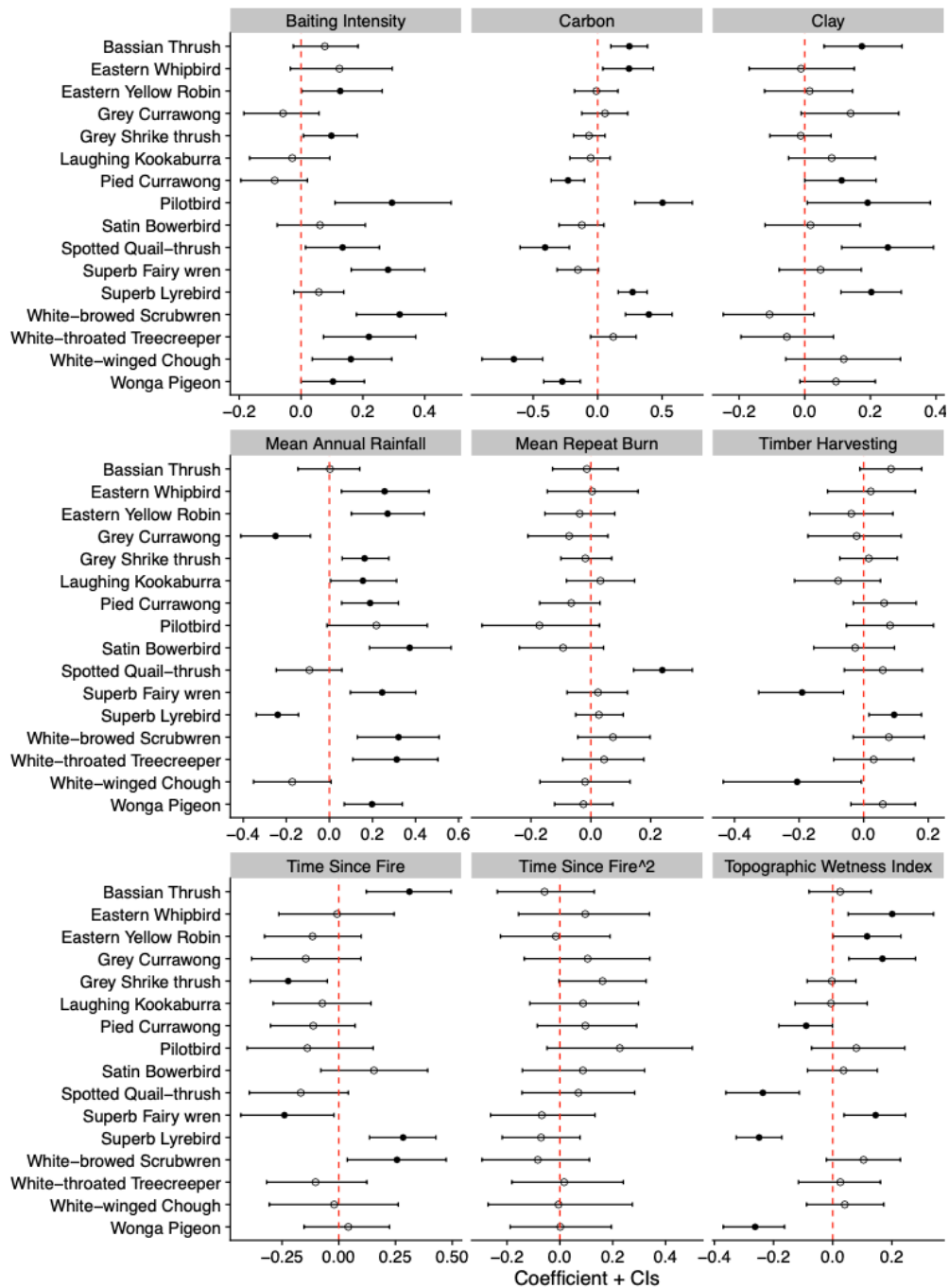
463 **Figure S3:** Model coefficients and 90% credible intervals for each native mammal and reptile species and
 464 environmental covariate within the joint-species distribution model for the East Gippsland fauna

465 community in Victoria, Australia. Coefficients with closed circles indicate covariates where the credible

466 intervals do not overlap zero, and open circles indicate covariates where the credible intervals do overlap

467 zero.

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Figure S4: Model coefficients and 90% credible intervals for each native bird species and environmental

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covariate within the joint-species distribution model for the East Gippsland fauna community in Victoria,

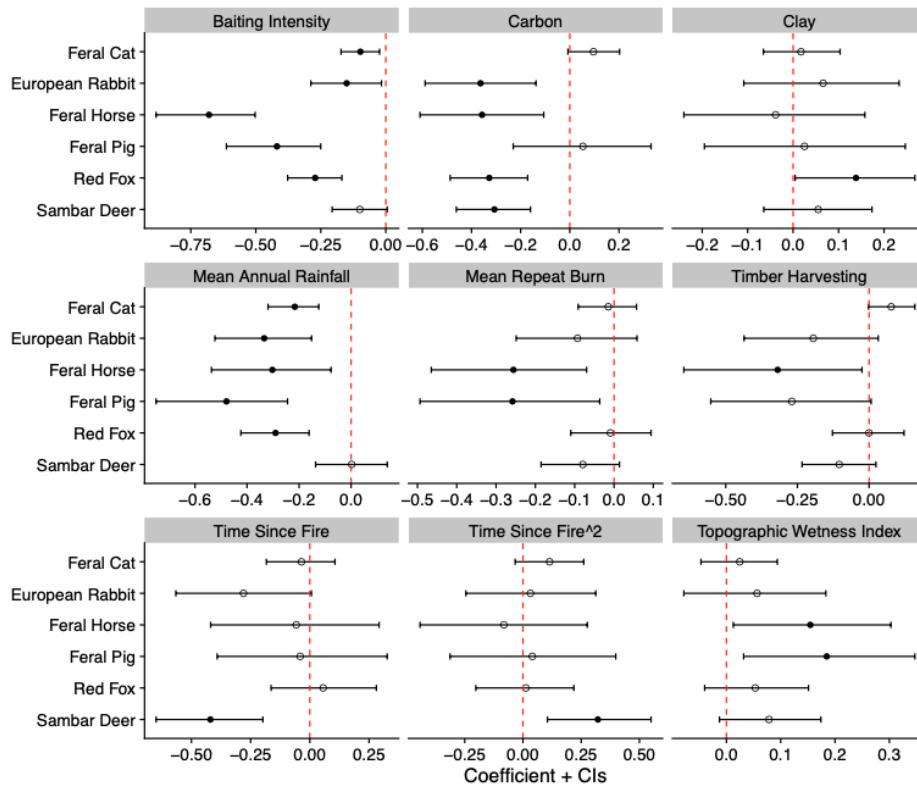
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Australia. Coefficients with closed circles indicate covariates where the credible intervals do not overlap

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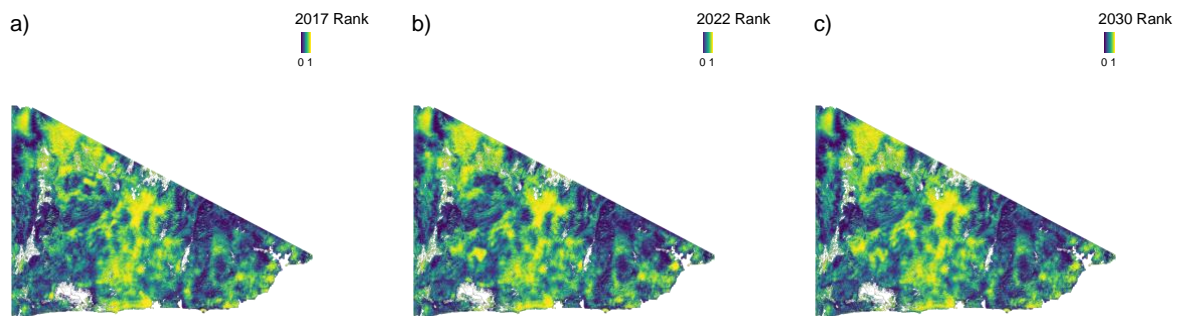
zero, and open circles indicate covariates where the credible intervals do overlap zero.

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Figure S5: Model coefficients and 90% credible intervals for each invasive species and environmental covariate within the joint-species distribution model for the East Gippsland fauna community in Victoria, Australia. Coefficients with closed circles indicate covariates where the credible intervals do not overlap zero, and open circles indicate covariates where the credible intervals do overlap zero.



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Figure S6: Priority rankings from Core Area Zonation analyses using predicted species distributions for a) the year 2017 (pre-Black Summer), b) the year 2022 (post-Black Summer) and c) 2030 (10 years post-Black Summer) for a fauna community in East Gippsland, Victoria, Australia. Values closer to 1 are relatively higher ranked in terms of conservation importance compared with values closer to 0. Rankings for the 2022 and 2030 scenarios are in Figure S6.

489 **Table S2:** Model diagnostics for each species contained within the joint-species distribution
 490 model. AUC: Area Under the Curve, RMSE: Root Mean Squared Error, TjurR²: Tjur R².
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Species	AUC	RMSE	TjurR ²
Horse	0.98	0.17	0.45
Pilotbird	0.97	0.18	0.34
Pig	0.95	0.14	0.17
Spot-tailed Quoll	0.93	0.15	0.11
Eastern Yellow Robin	0.92	0.25	0.2
White-browed Scrubwren	0.92	0.26	0.25
Eastern Pygmy-possum	0.92	0.14	0.07
European Rabbit	0.91	0.18	0.19
Long-nosed Potoroo	0.91	0.15	0.08
Eastern Grey Kangaroo	0.91	0.18	0.17
White-winged Chough	0.89	0.18	0.16
Eastern Whipbird	0.88	0.18	0.1
Long-footed Potoroo	0.87	0.35	0.31
Bassian Thrush	0.86	0.31	0.22
Red-necked Wallaby	0.86	0.29	0.2
Superb Fairy-wren	0.85	0.25	0.12
Red Fox	0.83	0.27	0.16
Common Brushtail Possum	0.83	0.39	0.29
Satin Bowerbird	0.83	0.2	0.07
Mountain Brushtail Possum	0.82	0.41	0.25
Wonga Pigeon	0.82	0.31	0.11
White-throated Treecreeper	0.81	0.2	0.05
Spotted Quail-thrush	0.79	0.23	0.07
Lace Monitor	0.79	0.35	0.12
Dusky Antechinus	0.79	0.27	0.08
Agile Antechinus	0.78	0.38	0.16
Superb Lyrebird	0.78	0.44	0.2
Bush Rat	0.77	0.18	0.04
Common Ringtail Possum	0.77	0.14	0.02
Dingo	0.76	0.24	0.07
Sambar Deer	0.76	0.27	0.08
Long-nosed Bandicoot	0.76	0.35	0.1
Grey Shrike-thrush	0.75	0.39	0.08
Pied Currawong	0.72	0.3	0.05
Grey Currawong	0.72	0.18	0.02
Short-beaked Echidna	0.72	0.35	0.07
Black Wallaby	0.7	0.45	0.1
Feral Cat	0.68	0.46	0.06
Common Wombat	0.62	0.49	0.03
Laughing Kookaburra	0.61	0.2	0.01

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Table S3: Estimated regression coefficients, error and credible intervals from the beta regression model used to explain patterns of conservation value identified in the Zonation analysis. Q2.5 and Q97.5 represent the lower and upper 95% credible intervals, respectively.

	Estimate	Est.Error	Q2.5	Q97.5
Intercept	0.01	0.01	-0.01	0.03
polyCat_s31	-20.93	1.92	-24.66	-17.21
polyCat_s32	25.10	0.97	23.20	27.01
polyCat_s33	-5.01	0.95	-6.84	-3.17
polySambar_s31	0.19	2.57	-4.77	5.11
polySambar_s32	30.37	1.22	28.05	32.82

polySambar_s33	-13.35	1.04	-15.37	-11.38
polyRed.Fox_s31	50.13	3.27	43.67	56.65
polyRed.Fox_s32	-1.73	1.36	-4.38	0.97
polyRed.Fox_s33	-11.84	1.27	-14.26	-9.27
polytsf_s31	17.77	1.05	15.78	19.84
polytsf_s32	12.57	1.17	10.34	14.86
polytsf_s33	-1.59	0.88	-3.33	0.16
polybait_s31	30.52	1.15	28.27	32.75
polybait_s32	9.13	0.93	7.29	10.94
polybait_s33	-5.51	0.83	-7.11	-3.93
polyrepeatburn_s31	6.78	0.88	5.05	8.44
polyrepeatburn_s32	-1.43	0.87	-3.12	0.27
polyrepeatburn_s33	-4.88	1.01	-6.90	-2.93
polyautocov_s31	53.94	1.09	51.86	56.11
polyautocov_s32	-6.49	0.92	-8.27	-4.69
polyautocov_s33	-2.00	0.87	-3.71	-0.30

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