

1 Interactions among body size, trophic level and dispersal traits predict
2 beetle detectability and occurrence responses to fire

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19 Running title: Trait interactions predict fire response

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21

22 **Abstract**

23 1. Testing the extent to which traits act alone or in combination with other traits to influence
24 responses to fire informs the trade-off between increased generalisation using single-traits
25 and increased predictive power using interactions. We asked: do four traits (body size,
26 trophic group, dispersal ability and stratum of the ecosystem), alone, or in combination best
27 explain changes in beetle occurrence with time since fire?

28 2. Our data from four years and 15 independent fires in southern Australia were analysed
29 using generalised linear mixed models (GLMM). We also assessed whether detectability
30 depends on time since fire using multi-year detection models because detectability has
31 potential to confound occurrence patterns.

32 3. The best model included the three-way combination of size, flight and trophic level
33 interacting with time since fire and with year. The relationship of detectability with time
34 since fire was similar to the occurrence relationship in six of the ten trait-combination groups,
35 with flightless species generally showing reduced detection probability as time-since-fire
36 increased. Detectability did not confound occurrence responses for four trait groups, with
37 three increasing with time since fire while one decreased.

38 4. Generalisation using main effects of traits risks oversimplifying animal responses to fire
39 because combinations of traits influence the direction and magnitude of the response. Also,
40 taking detectability into account is critical to correctly interpret occupancy data. Three-way
41 trait combinations that differ by just one trait, particularly dispersal ability, can result in either
42 negligible effects of disturbance on detectability, or strong effects that influence observed
43 occurrence.

44

45 **Keywords.** functional groups, detectability, dispersal ability, body size, trophic group, trait
46 syndrome

47 **Introduction**

48 Fire is a common disturbance in ecosystems around the world, and our understanding of how
49 species respond to fire has been substantially advanced by applying a functional-trait
50 approach (Syphard et al., 2013). Functional traits, which here refer to any characteristic that
51 is generalisable across species and reflects variation in fitness or ecological function, offer a
52 potentially valuable framework for understanding the responses of wildlife to fire (Kearney &
53 Porter, 2009; McGill et al., 2006). For plants, the functional-trait approach has substantially
54 advanced our ability to predict plant community composition given a particular fire regime
55 (Keith, 2012; Pausas & Bradstock, 2007; Syphard et al., 2013). Traits that predict fire
56 responses for fauna are proving more elusive (Blaum et al., 2011; Moretti et al., 2013). Work
57 on beetles (Driscoll et al., 2010a), cockroaches (Arnold et al., 2017), spiders (Langlands et
58 al., 2011), reptiles (Driscoll et al., 2012; Smith et al., 2013) and frogs (Westgate et al., 2012)
59 found little evidence that traits were reliably associated with particular responses to fire.
60 Based on reptile habitat use, Nimmo *et al.* (2012) predicted fire responses in nine of 17
61 species, but most of these were not consistent across regions. A general framework for using
62 animal traits to predict responses to fire is emerging (Fountain-Jones et al., 2015; Fountain-
63 Jones et al., 2017; Koltz et al., 2018; Pausas & Parr, 2018; Smith, 2018; van Mantgem et al.,
64 2015) but is yet to provide predictive power across animal communities (Driscoll et al.,
65 2010b).

66

67 To hasten development of a predictive framework for fire ecology, research is needed that
68 examines links between traits and the fire response of animals (Moretti et al., 2013). There
69 are grounds to expect that trophic level, body size, dispersal capacity and habitat stratum are
70 expected to be useful traits to explore beetle responses to disturbance and there will influence
71 how animals respond to major ecosystem changes caused by fire. Trophic group can

72 influence animal responses to fire but the patterns are inconsistent. For example, herbivorous
73 arthropods had high species richness and abundance shortly after fire in Mediterranean-type
74 ecosystems (Kaynas & Gurkan, 2008; Parmenter et al., 2011; Pausas et al., 2018), but in a
75 high rainfall ecosystem, herbivorous beetles were least common shortly after fire (Sasal et al.,
76 2015). Increasing, decreasing, and no response to time since fire have all been reported for
77 predatory arthropods (Bargmann et al., 2016; Parmenter et al., 2011; Sasal et al., 2015). It is
78 possible that predatory beetles have muted responses to disturbance compared with
79 herbivores because predators tend to be generalist feeders (Wang et al., 2018). Scavengers
80 feeding on dead plant or animal material have shown no response to fire severity (Menz et al.,
81 2016; Sasal et al., 2015), had highest abundance shortly after fire when predator numbers
82 were low (Hanula & Wade, 2003), or can increase with time since fire as dead wood
83 accumulates (Moretti & Legg, 2009).

84

85 Disturbance may be more likely to disadvantage large-sized species because they can have
86 small population sizes and lower reproductive rates (Brown, 1971), whereas small species
87 with fast life histories can rapidly recover after disturbance (Koltz et al., 2018; Romiguiet et
88 al., 2014). However, other mechanisms related to size have been reported. For example, cool
89 temperatures in late successional habitat (Roe et al., 2017) might favour large body sizes
90 (Horne et al., 2018). Further, the type of disturbance interacts with size and taxonomic
91 group, so large species are not always the most vulnerable to disturbance-driven declines
92 (McKinney, 1997; Pedley & Dolman, 2014). Indeed, empirical research on insects suggests
93 that smaller species may increase as succession proceeds because these are better able to
94 move through structurally complex habitats (Chown & Gaston, 2010), they are poorer
95 colonisers than large species and are less able to survive dry conditions shortly after fire
96 (Buckingham et al., 2019; Love & Cane, 2016).

97

98 Behavioural traits are expected to have an important influence on animal responses to fire,
99 including dispersal ability and the stratum of the environment in which the animal lives
100 (Driscoll & Weir, 2005; Koltz et al., 2018; Love & Cane, 2016; Pausas & Parr, 2018; Smith
101 et al., 2014). Recovery after fire may depend on high dispersal, enabling escape from fire
102 (Swengel, 2001) and subsequent rapid colonisation (Altermatt et al., 2011; Banks et al., 2011;
103 Hutchinson, 1951; Pedley & Dolman, 2014; Tilman, 1988). Species that are common shortly
104 after disturbance are often good dispersers (Moretti et al., 2004; Ribera et al., 2001), whereas
105 poor dispersers become more common as time after the disturbance elapses (Buddle et al.,
106 2006; Holliday, 1991). Through micro-habitat specialisation, some species will be more
107 vulnerable to certain disturbances than others (Martin & Possingham, 2005; Swengel, 2001).
108 Species that live in the stratum of the environment that is most impacted by disturbance
109 should be most at risk of decline (Kelly et al., 2010; Moretti et al., 2006; Orgeas & Andersen,
110 2001). For example, soil macrofauna in deep soil layers had better survival after fire than
111 surface-dwelling species (Gongalsky & Persson, 2013), while beetles living underground
112 were more vulnerable to agriculture than those able to use the canopy or on the ground
113 (Driscoll & Weir, 2005).

114

115 Although traits like trophic group, size, dispersal and stratum can act independently, traits can
116 also interact with one another (Driscoll & Weir, 2005). For example, Laughlin et al. (2017)
117 and Hammill et al. (2016) predicted plant species distributions and fire responses,
118 respectively, from combinations of three traits. Flying carnivorous arthropods were
119 associated with recent fires while small arthropods feeding on dead wood were associated
120 with unburnt sites (Moretti & Legg, 2009). Although greater predictive power may be
121 obtained by considering interactions of traits, there is a trade-off in the breadth of

122 generalisation. The extent to which multiple traits must be combined to explain animal
123 responses to disturbance helps to define the limitations to generalisation.

124

125 In this study we used a four-year beetle data set from fire-prone woodlands in southern
126 Australia to ask: what level of trait complexity best explains how beetle occurrence is
127 influenced by time since fire, considering size, flight ability, trophic level, habitat stratum and
128 their interactions? Given the range of reported insect responses to fire, we expect higher level
129 interactions will best explain fire response. However, the diversity of responses mean it is
130 not possible to meaningfully predict how combinations of traits might respond to time since
131 fire; hypotheses would be arbitrary and misrepresent the state of knowledge. Because we
132 used passive traps to survey beetles there was a risk that detectability might confound
133 occurrence patterns if detectability was also affected by time since fire (Guillera-Arroita,
134 2017; MacKenzie et al., 2002; Melbourne, 1999; Parmenter et al., 2011). We therefore also
135 investigated if detectability of trait groups changed with time since fire.

136

137

138 **Materials and Methods**

139 *Study region and survey design*

140 The study region on South Australia's Eyre Peninsula consists of mallee woodland dominated
141 by multi-stemmed *Eucalyptus* species and an understory of shrubs and spinifex (*Triodia*
142 *irritans*) (Driscoll & Henderson, 2008; Driscoll et al., 2012). Annual rainfall is within the
143 range 300-400mm. Parabolic and longitudinal sand dunes overlie a limestone-calcrete base
144 across a relatively flat landscape (Twidale & Campbell, 1985).

145 We sampled beetles from 23 transect and seven grid sites across four conservation reserves
146 (Fig. 1). Transect sites consisted of 11 pairs of 20 litre pitfall traps, each pair connected by a
147 20m drift fence. Trap pairs were spaced along the 400 m transect at 40 m intervals. Grid
148 sites included a 5 x 10 arrangement of individual 20 litre pitfall traps, each with a 10 m drift
149 fence, with traps spaced at 25 m intervals. Pitfalls were also used to trap vertebrates (Driscoll
150 & Henderson, 2008; Driscoll et al., 2012) but this is unlikely to have substantially influenced
151 the beetles in the dataset. Our observations were that beetles were often present in traps with
152 vertebrates suggesting limited predation, whereas spider remains were sometimes observed
153 when dasyurids (small predatory mammals) were trapped. The grids and transects were
154 placed in 15 areas that were burnt by different fires in five different locations (Appendix S1,
155 Fig. 1). Six transects were burnt during the study and therefore had two different times since
156 fire in the data (Appendix S1). Five of the grids straddled the edge of a burn for part or all of
157 the study, and when this was the case, each half was analysed as a separate site with different
158 times since fire (Appendix S1). The proximity of burnt halves to each other was
159 accommodated in analysis using random effects.

160 We surveyed beetles over four consecutive summers from December 2004–February 2005
161 (referred to as 2004) to December 2007–February 2008 (2007). In each summer, we
162 conducted three six-night sampling periods approximately monthly, except in the second
163 summer when we sampled in two periods (December and February). Sites were sampled for
164 an average of 15.4 (SD = 4.0) nights per year and we accommodated unequal sampling in the
165 analyses (see below). Data from February 2006 at Pinkawillinie were excluded from year
166 two due to a fire in December 2005 which changed the time since fire during the sampling
167 year. Post-fire data from Hincks in December 2006 were excluded because inflated capture
168 rates immediately after fire give a misleading impression of high abundance (Driscoll et al.,
169 2012). After the fire, which occurred a few days before trapping began, invertebrates were

170 very active across the ground, presumably as animals seek new shelter. The pitfalls may have
171 acted as an attractive shelter, leading to inflated counts. To avoid adding this additional
172 source of variation into the models, we excluded this month of data.

173 Beetles were identified to species or morphospecies level using a photographic guide to
174 common beetles that we prepared based on initial trapping, alongside a field-box of pinned
175 specimens. Species that were unambiguously identified were marked with a paint spot on the
176 ventral surface and released 5-10 m from the point of capture. Recaptured animals were
177 excluded from the data. Individuals that could not be identified in the field were assigned a
178 morpho-species name, and were preserved for later identification at the South Australian
179 Museum (Eric Matthews), or CSIRO Entomology (Tom Weir, Rolf Oberprieler). Beetles
180 below 6 mm in length could not be reliably collected from 20 litre pitfall traps in a time-
181 efficient manner and were excluded from analysis, and we excluded species with fewer than
182 five records as they were inadequate for analysis. We refer to species and morphospecies as
183 species throughout.

184

185 *Traits and generalised linear mixed models*

186 Four trait groups were used, flight (winged; not winged), size (big: range = 19-58mm, mean
187 = 32.2mm, SD = 11.4 mm; small: range = 6-15 mm, mean = 10.9 mm, SD = 2.9 mm), trophic
188 group (herbivore, carnivore, scavenger), and vegetation stratum position of adults (on ground,
189 above ground, below ground, concealed (under bark or rocks)) (Driscoll & Weir, 2005).

190 Trophic group was allocated based on expert knowledge (Tom Weir, CSIRO) of the family,
191 or where there were sub-family differences, the tribe level of classification was used.

192 Similarly, position was based on Tom Weir's expert opinion based on a lifetime studying
193 beetles. We acknowledge that our 'small' category does not include very small beetles

194 (<6mm), because these were not collected. Beetle sizes were based on measurement of one to
195 five pinned specimens from our study. The break between big and small beetles coincided
196 with the observed gap in lengths between 15 and 19 mm. These traits were selected because
197 they are expected to be influential (Fountain-Jones et al., 2015) and the information was
198 available.

199 To consider interactions between traits, factors representing all of the existing combinations
200 of two or more traits were created. This approach was taken to avoid complete separation
201 which occurred because some groups were empty. For example, there were no flying-
202 concealed species so the interaction of flight with trophic-group main effects would have
203 empty cells in the analysis. We created these trait-combination groups for all pairwise
204 interactions of traits (6 possible 2-way combinations of the four traits) and all three-way
205 interactions (4 combinations) (Appendix S2). The four trait combination, the four-trait
206 combination in interaction with year, and the interaction of size-position-trophic level with
207 year could not be modelled effectively due to data limitations. Another consequence of some
208 groups being empty for trait combinations was that most of the variation for one trait,
209 position for example, would be taken up in a flight-position combination, with no extra
210 variation to be explained by position in the trophic-position combination, leaving the model
211 rank deficient. It was not possible to estimate effects for rank-deficient models. Therefore,
212 we limited models to just a single "main" effect, where the "main" effect was one of the trait
213 groups, or one of the two-way, or three-way combinations. For example, we did not fit more
214 than one two-way interaction in a model. Because we defined trait combinations in this way,
215 we used categorical classification of all traits rather than continuous variables.

216 We analysed the trait groups using generalised linear mixed models with a binomial
217 distribution of errors and a logit-link function (Bolker et al., 2009) because these led to model
218 residuals that were not over-dispersed and our data were binomial samples. The response

219 variable was the number of weekly trap sessions in which a species was detected at a site
220 within year (the 'successes' in the binomial response), with the 'failures' in the binomial
221 response being the total number of weekly surveys in that year minus the number in which
222 the species was observed. This approach accounted for unequal sample effort among sites.

223 All models included three random effects: species-name, which accounted for clustering of
224 responses within species; burn, which accounted for sites that were spatially grouped within
225 the same fire event, and; site, which accounted for repeated measures of each site. Grids that
226 straddled the edge of a burn were given the same site name for this random effect, accounting
227 for their spatial proximity. The site random effect also accommodates any differences
228 between grid and transect trap arrangements. Phylogeny can impose non-random variation
229 among species, but can be accommodated by fitting higher taxonomic levels as random
230 effects in mixed models (Martinson & Raupp, 2013). However, when we fitted genus nested
231 in family as a random effect in the best model, no additional variation was accounted for
232 (variance Family = 0, genus/family = 8×10^{-9}) so this was omitted from analysis.

233 Our baseline model included location (a five-level factor), year (a four-level factor), and the
234 continuous variable time since fire (TSF), which was standardised and centred for analysis.
235 Exploratory data analysis revealed no convincing hump-shaped relationships between TSF
236 and beetle occurrence, so polynomial versions of TSF were not used (Smith et al., 2013). A
237 second model included an interaction between year and TSF. To evaluate trait effects, we
238 fitted each of the traits or trait-combinations in interaction with TSF, or in interaction with
239 TSF and year giving 28 additional models (Appendix S2).

240 The models were ranked using Akaike Information Criteria adjusted for small sample size
241 (AICc) (Burnham & Anderson, 2002). Where year interacted with trait groups, post-hoc

242 testing was used to compare among years within group using the least squares means
243 methods with Tukey adjustment of P values (Lenth, 2019).

244 Analyses were completed in R 3.5.0 (R Core Team, 2018) using libraries lme4 (mixed
245 models) (Bates et al., 2012); car (Anova function to provide P values for fixed effects in
246 models) (Fox & Weisberg, 2011); effects (obtaining predicted values) (Fox, 2003);
247 AICcmodavg (AICc calculation) (Mazerolle, 2012), and; emmeans (pairwise comparisons)
248 (Lenth, 2019).

249

250 *Probability of Detection*

251 Detectability rates for trait groups might vary with time since fire which could confound
252 interpretation of occurrence models. Data limitations prevented us from including
253 detectability in the occurrence models, so we examined detectability separately and
254 conducted a post-hoc examination of detectability and occurrence, with the latter analysed
255 using GLMM described above. When the response of detectability to time since fire was in
256 the same direction as occurrence, we inferred that the occurrence pattern could in part be
257 caused by variation in detectability.

258

259 Because we use four years of data, we fitted extinction-colonisation models (MacKenzie et
260 al., 2003) with the colext function in the unmarked R package (Fiske et al., 2011). This model
261 estimates parameters for extinction, colonisation, detection, and occupancy. Our data set was
262 inadequate to examine covariates for all of these parameters. Our focus was on considering
263 the relationship of detectability with TSF and month, where month represented the three
264 sampling periods per year; December, January and February, the three summer months.

265 These two covariates were therefore only applied to the detection parameter to discover if
266 detection of each trait group (levels of combinations of traits identified in the best mixed
267 model) depended on time since fire or month. For each trait group, the response variable was
268 occurrence at each site in each of the trapping weeks in each year, where occurrence was
269 combined across the species that were in the trait group. We used the significance level of the
270 model parameter estimate ($P < 0.05$) as the limit to which relationships between the response
271 and TSF or month were plotted. For each response we also fitted a null model with no
272 predictor variables for comparison, using AIC, with models that included TSF and month as
273 predictors of detectability.

274

275 **Results**

276 We captured 10061 beetles from 161 species. Forty-six species had five or more records and
277 had all four traits known – these were used in the analysis (total of 9623 beetles, years 2004-7
278 had 2454, 1453, 2525, and 3191 individuals respectively) (Appendix S3). All 46 species
279 were identified to genus, but 13 of the species were not yet described and were given a
280 morphospecies number.

281

282 In the single best model to explain beetle occurrence, the three-way combination of size,
283 flight and trophic level interacted with time since fire and with year, but there was not a
284 significant three-way interaction of time-since-fire, year and size-flight-trophic level (Table
285 1, Appendix S4). In general there were strong negative effects of time since fire on
286 herbivores, with the exception of small flying herbivores that had a positive relationship with
287 time since fire (Fig. 2 a-d). Occurrence of big flying scavengers and small flightless
288 scavengers also increased with time since fire (Fig. 2 e, h). The remaining two scavenger
289 groups and carnivores showed weak declines with time since fire (Fig. 2 f, g, i, j).

290

291 The probability of occurrence of size-flight-trophic trait groups also varied among years, with
292 no systematic trends evident across trait groups (Appendix S5).

293

294 *Detection*

295 Detection declined significantly with time since fire for big flightless herbivores, small
296 flightless herbivores and small flightless carnivores (Fig. 3 c, d, j), the same trends observed
297 for occurrence (Fig. 2). Small flying scavengers, big flightless scavengers, and big flightless
298 carnivores had weak trends in detection with time since fire (Fig. 3 f, g, i) but these were
299 similar to their weak occurrence response to time-since-fire (Fig. 2). In contrast with trait
300 groups where detection could explain occurrence patterns, big and small flying herbivores,
301 big flying scavengers and small flightless scavengers had very weak effects of detection
302 covariates (Fig. 3 a, b, e, h) but relatively strong occurrence responses (Fig. 2). All but two
303 of the trait groups had a significant positive effect of month on detection, with detection
304 being highest in the last month of summer in all cases (Fig. 3).

305

306 **Discussion**

307 When we tested the importance of single traits, two-way combinations and three-way
308 combinations of traits, we found the three-way combination of traits best explained the
309 occurrence of beetles across a time-since-fire gradient. Thus relatively fine-grained resolution
310 of species characteristics are needed to describe beetle responses to fire. Needing multiple-
311 trait combinations to define fire responses places substantial constraints on how to further test
312 and refine generalisations about animal responses to fire. Beetles are particularly speciose
313 (Stork, 2018), but with our dataset of approximately 10,000 records, we had between one and
314 ten species in each trait group (Fig. 1) and could not examine more than three traits at once.

315 Very large data sets for taxonomic groups with many species will be needed to further test the
316 links between trait-group combinations and animal responses to fire, making arthropods
317 particularly useful in this respect (Brousseau et al., 2018; Fountain-Jones et al., 2015; Stork,
318 2018). Some of our trait groups had few species in them, so could represent the response of
319 individual species rather than the general response for beetles with those trait combinations,
320 emphasising the need for very large sample sizes for identifying general trends.

321

322 Trait combinations that included being flightless generally showed reduced detection
323 probability with time-since-fire, suggesting detection changes may reflect important
324 ecological processes. Reduced detection of flightless beetles as time since fire increases
325 probably reflects highest activity shortly after fire. For example, in Canada, highest activity
326 was observed after fire in the flightless beetle *Calosoma frigidum*, which may relate to
327 increased hunting opportunities for these large predators (Jacobs et al., 2011). Reduced
328 detection with increasing time since fire may also relate to movement behaviour in different
329 vegetation types. Movement can be physically impeded as time since fire and structural
330 complexity increase (Chown & Gaston, 2010; Goodwin & Fahrig, 2002); the vegetation
331 clutter hypothesis (Kaynas & Gurkan, 2008; Rainho et al., 2010). Leaf-litter and structural
332 complexity increase with time since fire in mallee (Haslem et al., 2011), which can inhibit
333 animal movement (Smith et al., 2016). There is also substantial turnover in plant species
334 (Gosper et al., 2012) and invertebrate composition (Teasdale et al., 2013) in the decades after
335 fire, which may alter non-consumptive effects on potential prey species (Buchanan et al.,
336 2017) and food availability (Smith, 2018), hence changing movement patterns and
337 detectability.

338

339 In addition to revealing ecological processes, detection differences across a time since
340 disturbance gradient has important implications for researchers studying disturbance. The
341 responses of big flying and big flightless herbivores provide a particularly stark warning.
342 Without considering detection, these groups have similar occurrence responses. However, the
343 response of big flightless herbivores could be entirely due to differences in detection, while
344 big flying herbivores have an actual change in occupancy. We reiterate that considering how
345 detection may confound observed disturbance effects is important for understanding how
346 species respond to disturbance (Driscoll et al., 2012; MacKenzie et al., 2003).

347

348 Four trait-combinations had occupancy responses to time since fire that were not confounded
349 by detection. The trait-combinations represented all three positive responses to time since fire
350 (small flying herbivores, big flying scavengers, small flightless scavengers) and one negative
351 response (big flying herbivores). Changes in occurrence could be directly related to changes
352 in resources. For example, most of the scavengers were Tenebrionids, consuming dead plant
353 material. The plant material in the litter layer changes with time since fire, with increasing
354 depth, more bark, sticks and fewer leaves (Haslem et al., 2011; Travers & Eldridge, 2012).
355 These changes in litter structure and composition may influence rates of population increase
356 among different trait groups of scavengers at different times since fire. This type of response
357 has been observed in other systems for an example of size effects in detritivores see:
358 (Buckingham et al., 2015), and for an example of detritivore traits responding to time since
359 disturbance see (Fountain-Jones et al., 2017)).

360

361 Occupancy can also be influenced by movement (Nathan et al., 2008; Pavlacky et al., 2012)
362 which is affected by size and flying ability (De Bie et al., 2012; Doherty & Driscoll, 2018),
363 and could interact with time since fire. For example, flying species can be most abundant

364 shortly after fire because they are rapid colonisers (Moretti et al., 2004; Podgaiski et al.,
365 2018; Ribera et al., 2001). However, flight also offers the choice to move to preferred habitat
366 (De Bie et al., 2012), and different species prefer different times-since-fire. The capacity of a
367 species to choose preferred habitat could depend on body size, because large species can
368 disperse larger distances than small species with the same mode of locomotion (Jenkins et al.,
369 2007). Conceivably, large flying beetles are able to choose their habitat at the scale of
370 multiple fires, over kilometres (Chiari et al., 2013; Rink & Sinsch, 2007). In our study, if
371 large beetles are flying to choose preferred habitat, the particular time since fire they choose
372 depends on trophic group, with scavengers preferring later times since fire, and herbivores
373 preferring short times since fire.

374

375 With multiple traits combining to determine how beetles respond to time since fire, our
376 results emphasise that it is probably too optimistic to expect that single ecological
377 mechanisms linked to individual traits will have very useful predictive power. For example,
378 it is possible to predict that species with better dispersal are likely to be faster colonisers and
379 therefore be more likely to use recently or frequently disturbed habitats (e.g. Pedley &
380 Dolman, 2014; Simons et al., 2016). However, our results suggest that single mechanisms
381 must be conditioned by competing mechanisms linked to other traits including trophic group,
382 which influences the resources that are attractive to the species, and size, which influences
383 the capacity of the animal to move to find preferred resources (Lazarina et al., 2016).

384

385 The ecosystem strata occupied by the adult (on, above, below ground, concealed places) was
386 not included in the best model. In contrast, strata, defined in the same way as we have used,
387 was important for predicting beetle responses to agricultural disturbance (Driscoll & Weir,
388 2005). There is inadequate knowledge about life histories of Australian beetles so it is

389 difficult to evaluate how the timing and places occupied by different life history stages of
390 each species might influence their fire response. For example if under-ground larvae are
391 present during a fire, they may ensure population persistence, regardless of the strata used by
392 the adults (Nunes et al., 2019). Further, the specific component of the strata that animals are
393 able to use can influence survival through fire, such as whether animals use the apical
394 meristem area of plants with tightly packed leaf bases, or other parts of plants that are
395 exposed to higher temperatures (Brennan et al., 2011).

396

397 While we are able to point towards a set of possible mechanisms that need to be examined in
398 further research, we do not expect the same mechanisms to necessarily apply across trait
399 groups or taxonomic groups. Pedley and Dolman (2014) found that small and flying Carabids
400 were most abundant after disturbance because they have high rates of population increase and
401 good dispersal, however, larger spider species were more common after disturbance because
402 open areas favour active hunting. It therefore seems likely that different mechanisms will
403 apply to different trait combinations in different taxonomic groups.

404

405 *Conclusions*

406 We found that detection varied with time since fire for over half of the trait combinations,
407 and this confounded occurrence. It is very useful to take detection into account when
408 comparing occupancy or abundance across habitats with contrasting structure or resources
409 (MacKenzie et al., 2002). If detection cannot be accounted for, then detection remains a
410 possible interpretation of occurrence or abundance differences across environmental
411 gradients, particularly for flightless species. However, detection is not just a nuisance
412 variable to be statistically removed, but raises new questions. For example, if low detection
413 reflects inactivity, does this also influence the species' functional role in the ecosystem?

414 Further, what drives inactivity, with possible mechanisms including non-consumptive effects
415 of predators (Buchanan et al., 2017; Hossie et al., 2017) or prey availability (Lai et al., 2017)?
416 If high detection is caused by increased movement linked to reduced food availability, does
417 abundance subsequently decline, and does increased movement have new impacts on prey
418 species (e.g. Christy et al., 2017)?

419

420 Trait groups have proven useful for describing how animals respond to fire in some study
421 systems. For example, animals that decline after fire include bees that nest above-ground
422 (Williams et al., 2010), mammals and reptiles that live in flammable vegetation (Kelly et al.,
423 2010), wood-feeding beetles (Moretti et al., 2010) and nectarivorous birds (Chalmandrier et
424 al., 2013). However, we found that a combination of three traits provided the best
425 explanation of how beetles respond to time since fire, where the effects of any one trait is
426 dependent on the interaction with two others. Large data sets and comparisons across
427 taxonomic groups are now needed to further address the challenge of building trait-based
428 predictions about animal responses to disturbance.

429

430 **Acknowledgements**

431 We thank the many volunteers who helped in the field and in the lab (listed in Driscoll &
432 Henderson, 2008; Driscoll et al., 2012). Entomological expertise was provided by Eric
433 Matthews, SA Museum and Tom Weir and Rolf Oberprieler, CSIRO. We thank Joe Tilley,
434 Meredith Henderson and the South Australian fire crew for help with setting up the study and
435 implementing experimental burns. Data collection was funded by the Department for
436 Environment and Heritage, South Australia, Flinders University, the Australia and Pacific
437 Science Foundation and the Australian Research Council LP0776604. ALS was supported
438 by Marie Skłodowska-Curie Individual Fellowship FIRESCAPE-746191 under the EU

439 H2020 Programme for Research and Innovation. Animals were handled under permit E194 of
440 the Flinders University Animal Welfare committee, and DEH SA permit to undertake
441 scientific research Q24788.

442

443 **Supporting Information**

444 Additional Supporting Information may be found in the online version of this article under
445 the DOI reference: (to be allocated)

446 **Appendix S1.** Time since fire for each site (t = transect, g = grid) and survey year.

447 **Appendix S2.** A table of models fitted.

448 **Appendix S3.** The number of positive records (No. non-zero), trait states and family of the
449 46 species used in the analyses.

450 **Appendix S4.** Models ranked by AICc fitting traits and combinations of traits to beetle
451 occurrence data

452 **Appendix S5.** Estimated occurrence and 95 % confidence intervals for each year for each
453 trait group in the three-way interaction between size, flight and trophic group.

454 **Appendix S6.** Null models and models fitting time since fire (tsf) and month as detection
455 covariates. (A) Models ranked by AIC within trait group; (B) Intercepts (Int) and standard
456 errors (SE).

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458

459 **Contributions of Authors**

460 DD conceived the project, analysed the data and led the write up with assistance from AS. All
461 authors took leadership roles in field data collection and beetle identification (DD 2005, IS
462 2006, AS 2007, SB 2008).

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751 fire? *Oikos*, **121**, 1516-1524.
- 752 Williams, N.M., Crone, E.E., Roulston, T.a.H., Minckley, R.L., Packer, L., & Potts, S.G.
753 (2010) Ecological and life-history traits predict bee species responses to
754 environmental disturbances. *Biological Conservation*, **143**, 2280-2291.
- 755
756

757 Table 1. Analysis of Deviance Table of the best model sfty (Type II Wald Chi-square tests).

758 Trait abbreviations when included in combinations as effects: flt: flight; pos: position; trop:

759 trophic group; y = year; TSF = time since fire.

760

Effect	Chisq	Df	Pr(>Chisq)
location	32.0	4	<0.0001
year	1.7	3	0.645
TSF	1.0	1	0.322
sizeflttrop	9.2	9	0.419
year:TSFscale	14.9	3	0.002
year:sizeflttrop	193.2	27	<0.0001
TSF:sizeflttrop	38.4	9	<0.0001
year:TSF:sizeflttrop	20.2	27	0.823

761

762

763

764 Figure 1. Location of 30 sites where beetles were sampled in four conservation reserves,
765 southern Australia. Exact fire dates for each site are in Appendix S1 including details of sites
766 burnt during the study. North is towards the top of the page in all panels.

767

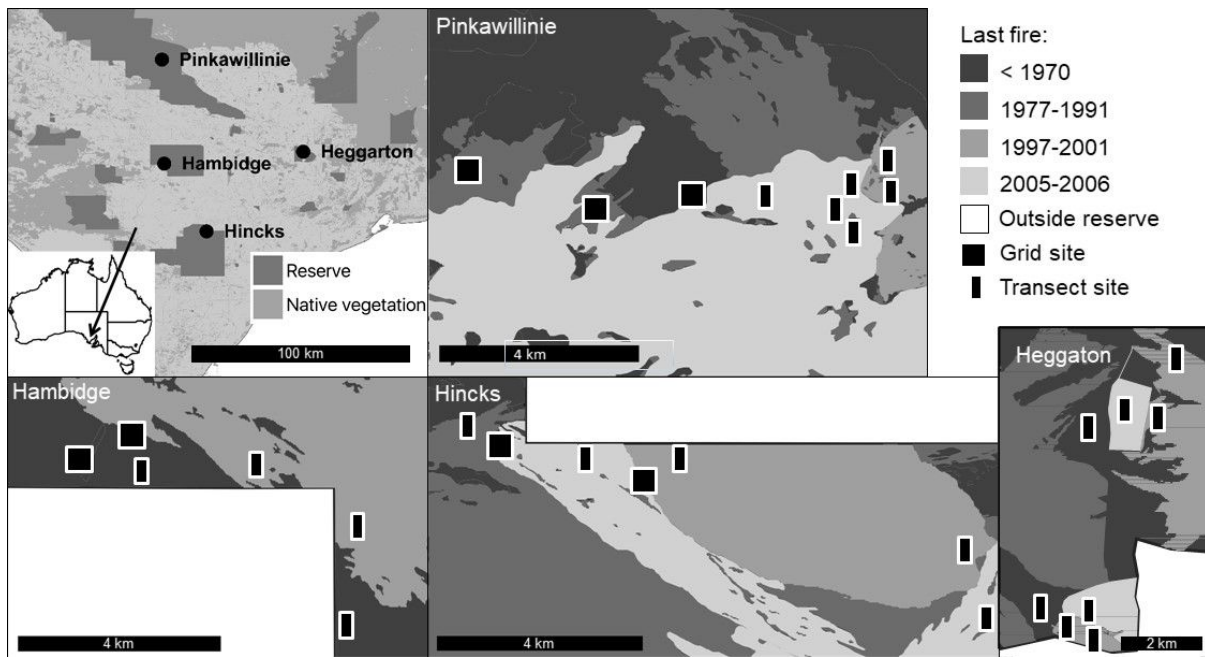
768 Figure 2. Predicted occurrence and 95 % confidence intervals across the range of observed
769 times since fire for each year for each trait group in the three-way interaction between size,
770 flight and trophic group. The number of species (no.sp.) and number of non-zero data points
771 (N) contributing to each trait group is indicated. a-d: herbivores; e-h: scavengers; i-j:
772 carnivores. Note that the maximum Y axis values vary among panels.

773

774 Figure 3. Predicted values illustrating the influence of time since fire and month of survey on
775 the probability of detection for size-flight-trophic trait groups. Month 1 = December, 2 =
776 January, 3 = February. P TSF = time since fire effect p value; P month = month effect p
777 value. The null model was the best model for big flying herbivores and big flying scavengers,
778 although delta AIC was < 1 (a, e, Appendix S6). The null model was worse than the model
779 with TSF and month in all other trait groups (delta AIC > 13 , Appendix S6). P = 0 indicates P
780 < 0.0001 .

781

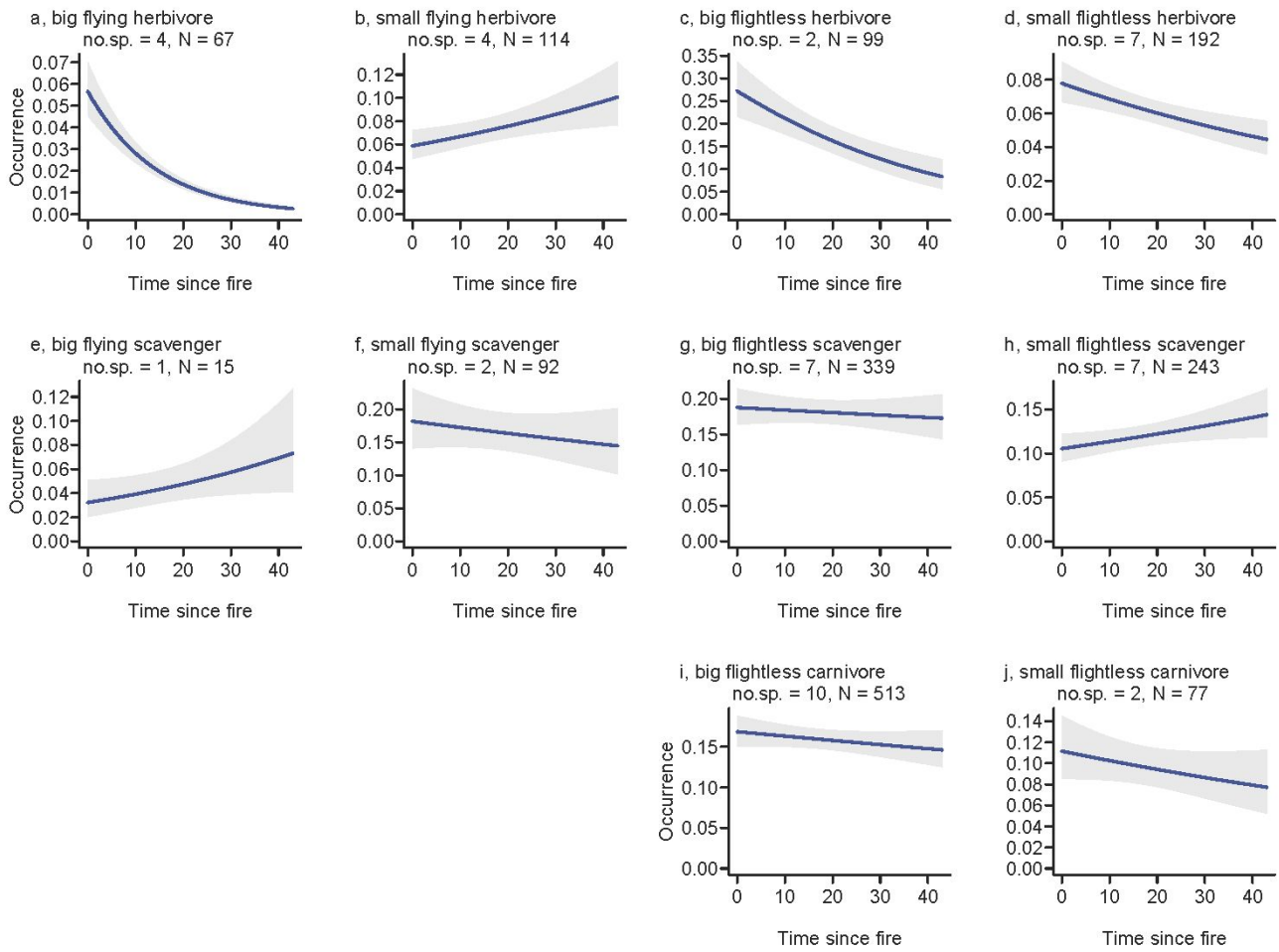
782 Figure 1.



785 Figure 2.

786

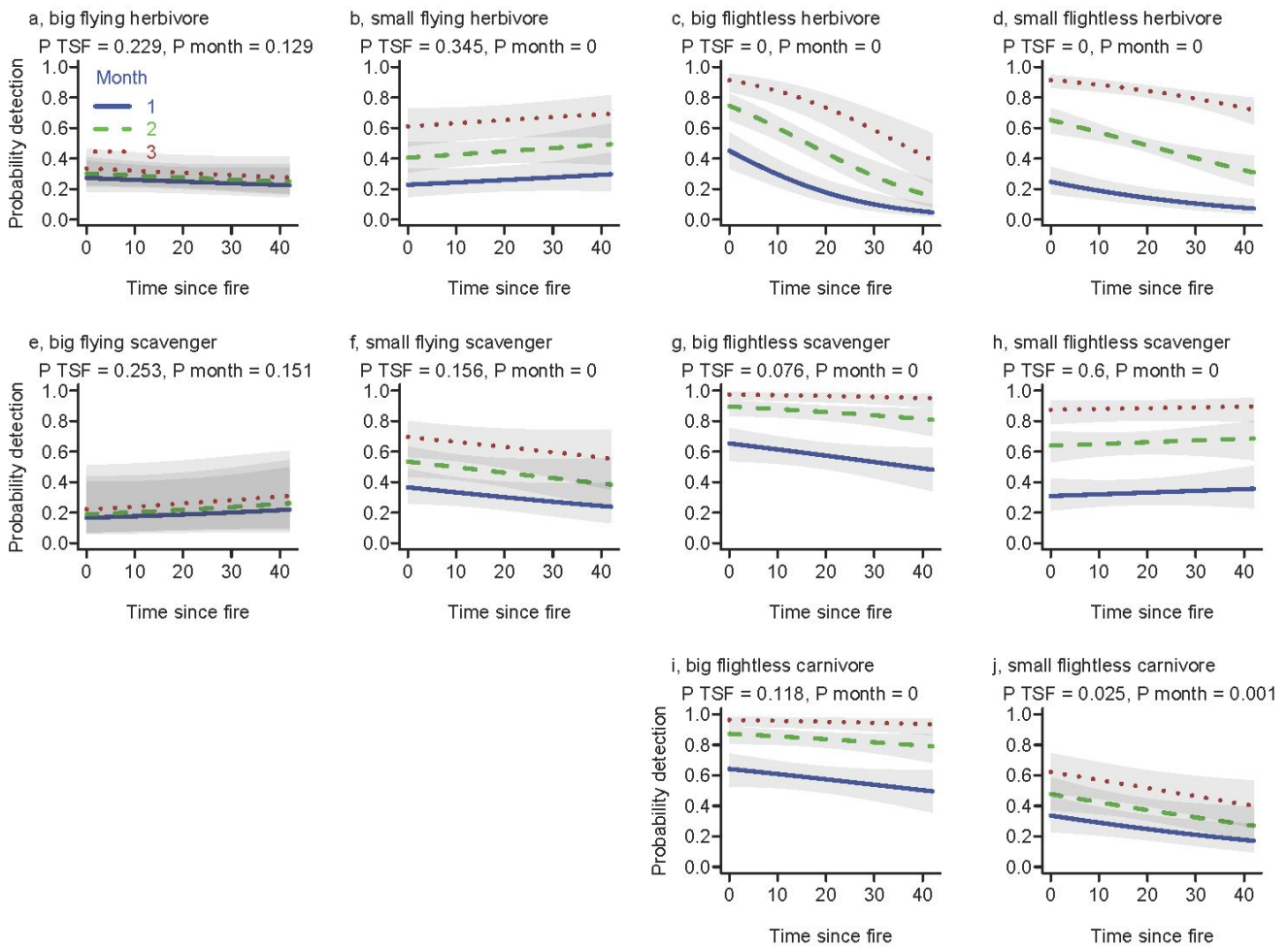
787



788

789 Figure 3.

790



1 Appendix S1. Time since fire for each site (t = transect, g = grid) and survey year. Burn No. is the label assigned to individual fires; some fires
 2 spanned more than one site, and labels refer to the most recent fire in which a site occurs. Some sites were burnt during the study so were
 3 sampled in two different fires. Dash indicates that the site was not surveyed in that year. Four sites with unknown most recent fire had not been
 4 burnt within the 30 years preceding the study at least, and were allocated the same age as the oldest known time since fire at other sites (39),
 5 justified by similar tree size (Lazzari et al. 2015). Grid sites with a lower case a or b indicate that each half (25 traps in 1ha) had a different time
 6 since fire. Grid I6 was burnt during the study so is listed as I6 when entirely within burn number 4, and I6a and I6b after half of that grid was
 7 burnt by fire 5. Grid site A6 was not burnt during the study (despite attempted planned burns). Grid site P6 was entirely burnt in an unplanned
 8 fire, so was replaced with P9a and P9b at the edge of the unplanned burn in 2006.

9

Site	Location	Burn No.	Time Since fire				Date of most Recent fire	Date of fire during study	Fire type during study	Latitude	Longitude
			2004	2005	2006	2007					
A1 (t)	Hambidge	1	4	5	6	7	11/01/2000		-33.4382	135.8696	
A2 (t)	Hambidge	1	4	5	6	7	11/01/2000		-33.4251	135.8479	
A3 (t)	Hambidge	2	39	40	41	42	29/10/1965		-33.4593	135.8676	
A4 (t)	Hambidge	2	39	40	41	42	29/10/1965		-33.4261	135.8236	
A5a (g)	Hambidge	2	39	40	41	42	29/10/1965		-33.4187	135.8202	
A5b (g)	Hambidge	1	4	5	6	7	11/01/2000		-33.4187	135.8202	
A6 (g)	Hambidge	2	39	40	41	42	29/10/1965		-33.4242	135.8098	
I1 (t)	Hincks	3	5	6	7	8	4/01/1999		-33.7633	136.0797	
I2 (t)	Hincks	3	5	6	-	-	4/01/1999		-33.7897	136.1405	
I3 (t)	Hincks	4, 5	27	28	0	1	31/12/1977	10/04/2006	planned	-33.7632	136.0593
I4 (t)	Hincks	4, 6	27	28	0	1	31/12/1977	30/11/2006	unplanned	-33.8093	136.1451
I5a (g)	Hincks	4, 5	27	28	0	1	31/12/1977	10/04/2006	planned	-33.7707	136.0706
I5b (g)	Hincks	3	5	6	7	8	4/01/1999		-33.7707	136.0706	
I6 (g)	Hincks	4	27	28	-	-	31/12/1977		-33.7599	136.0395	
I6a (g)	Hincks	5	-	-	0	1	31/12/1977		-33.7599	136.0395	
I6b (g)	Hincks	4	-	-	29	30	31/12/1977		-33.7599	136.0395	

I7 (t)	Hincks	3	-	-	7	8	31/12/1977			-33.7548	136.0343
N1 (t)	Heggarton N	7	7	8	9	10	24/11/1997			-33.3659	136.5425
N2 (t)	Heggarton N	7	7	8	-	-	24/11/1997			-33.3539	136.5463
N3 (t)	Heggarton N	8	39	40	41	42	unknown			-33.3685	136.5271
N4 (t)	Heggarton N	8, 9	39	40	0	1	unknown	26/04/2006	planned	-33.3646	136.5349
P1 (t)	Pinkawillinie	10	3	4	5	6	22/10/2001			-32.9001	135.8779
P2 (t)	Pinkawillinie	10	3	4	5	6	22/10/2001			-32.9057	135.8785
P3 (t)	Pinkawillinie	11, 12	18	19	1	2	22/10/2001	27/12/2005	unplanned	-32.91	135.867
P4 (t)	Pinkawillinie	11, 12	18	19	1	2	20/11/1986	27/12/2005	unplanned	-32.9142	135.8709
P5a (g)	Pinkawillinie	11, 12	18	19	1	2	20/11/1986	27/12/2005	unplanned	-32.91	135.8157
P5b (g)	Pinkawillinie	10	3	4	5	6	22/10/2001			-32.91	135.8157
P6 (g)	Pinkawillinie	11	18	19	-	-	20/11/1986			-32.902	135.789
P7 (t)	Pinkawillinie	11	-	-	20	21	20/11/1986			-32.9048	135.8703
P8 (t)	Pinkawillinie	11	-	-	20	21	20/11/1986			-32.9071	135.8522
P9a (g)	Pinkawillinie	12	-	-	1	2	20/11/1986	27/12/2005	unplanned	-32.9064	135.8365
P9b (g)	Pinkawillinie	11	-	-	20	21	20/11/1986			-32.9064	135.8365
S1 (t)	Heggarton S	13	4	5	-	-	24/01/2001			-33.4114	136.5227
S2 (t)	Heggarton S	13	4	5	6	7	24/01/2001			-33.4134	136.5285
S3 (t)	Heggarton S	14	39	40	41	42	unknown			-33.4067	136.5172
S4 (t)	Heggarton S	14, 15	39	40	0	1	unknown	26/04/2006	planned	-33.408	136.5274

10

11

Reference

12

Lazzari, J., Yoon, H.-J., Keith, D.A. & Driscoll, D.A. (2015) Local environmental covariates are important for predicting fire history from tree

13

stem diameters. *Journal of Wildland Fire*, **24**, 871-882.

14

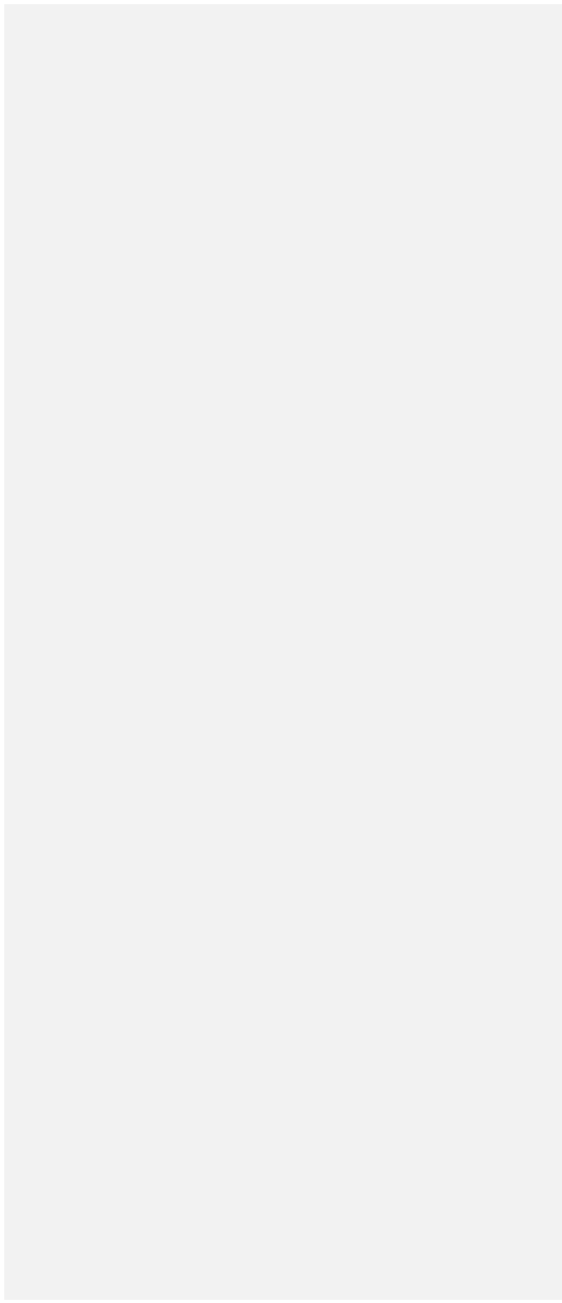
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Effects	null	null.year	s	f	p	t	sy	fy	py	ty	sf	sp	st	fp	ft	pt	sfy	spy	sty	fpf	fty	pty	sfp	sft	spt	fpt	sfpf	sfty	spty	fpty
year:TSF:trophic									1																					
sizeflt											1						1													
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For Review Only

Effects	null	null.year	s	f	p	t	sy	fy	py	ty	sf	sp	st	fp	ft	pt	sfy	spy	sty	fpv	fty	pty	sfp	sft	spt	fpt	sfpv	sfty	spty	fpty
sizefltpos																						1				1				
sizeflttrop																							1				1			
sizepostrop																								1				1		
fltpostrop																									1				1	
year:sizefltpos																										1				
year:sizeflttrop																											1			
year:sizepostrop																												1		
year:fltpostrop																													1	
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Appendix S3. The number of positive records (No. non-zero), trait states and family of the 46 species used in the analyses.

Species	No. non-zero	Size	Flying	Position	Tropic	Family
<i>Julodimorpha bakewelli</i>	15	big	flying	above	herbivore	Buprestidae
<i>Themognatha yarrelli</i>	20	big	flying	above	herbivore	Buprestidae
<i>Adotela apicalis</i>	41	big	not flying	on	carnivore	Carabidae
<i>Adotela frenchi</i>	6	big	not flying	on	carnivore	Carabidae
<i>Broschini sp1</i>	11	small	not flying	on	carnivore	Carabidae
<i>Carenum elegans</i>	108	big	not flying	below	carnivore	Carabidae
<i>Conopterum gagatinum</i>	50	big	not flying	below	carnivore	Carabidae
<i>Epilectus fortis</i>	14	big	not flying	below	carnivore	Carabidae
<i>Euryscaphus obesus</i>	71	big	not flying	below	carnivore	Carabidae
<i>Gnathoxys sp</i>	66	small	not flying	below	carnivore	Carabidae
<i>Neocarenum blackburni</i>	6	big	not flying	below	carnivore	Carabidae
<i>Neocarenum elongatum</i>	65	big	not flying	below	carnivore	Carabidae
<i>Philoscaphus costalis</i>	105	big	not flying	above	carnivore	Carabidae
<i>Scaraphites lenaeus</i>	47	big	not flying	below	carnivore	Carabidae
<i>Elaptus sp</i>	17	big	flying	above	herbivore	Cerambycidae
<i>Microtragus mormon</i>	79	small	not flying	above	herbivore	Cerambycidae
<i>Acantholophus franklinensis</i>	73	big	not flying	above	herbivore	Curculionidae
<i>Catasarcus armatus</i>	12	small	not flying	above	herbivore	Curculionidae
<i>Oophthalmus sp</i>	42	small	not flying	above	herbivore	Curculionidae
<i>Polyphrades fortis</i>	12	small	not flying	above	herbivore	Curculionidae
<i>Polyphrades sp</i>	18	small	not flying	above	herbivore	Curculionidae
<i>Talaurinus sp1</i>	19	small	not flying	on	herbivore	Curculionidae
<i>Talaurinus sp2</i>	26	big	not flying	on	herbivore	Curculionidae
<i>Talaurinus sp3</i>	10	small	not flying	on	herbivore	Curculionidae
<i>Byrrhomorpha basicollis</i>	17	small	flying	above	herbivore	Scarabaeidae
<i>Heteronyx sp</i>	65	small	flying	above	herbivore	Scarabaeidae

<i>Maechidius crenaticollis</i>	17	small	flying	above	herbivore	Scarabaeidae
<i>Metallesthes metallescens</i>	15	big	flying	above	herbivore	Scarabaeidae
<i>Semanopterus angustatus</i>	15	small	flying	below	herbivore	Scarabaeidae
<i>Adelium lindense</i>	35	small	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Agasthenes westwoodi</i>	40	big	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Blaps polychresta</i>	11	big	not flying	on	scavenger	Tenebrionidae
<i>Celibe australis</i>	48	small	not flying	on	scavenger	Tenebrionidae
<i>Chalcopteroides sp1</i>	15	big	flying	on	scavenger	Tenebrionidae
<i>Helea haagi</i>	69	small	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Helea intermedia</i>	25	big	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Helea monilifera</i>	113	big	not flying	above	scavenger	Tenebrionidae
<i>Helea sp</i>	26	small	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Hypaulax orcus</i>	36	big	not flying	on	scavenger	Tenebrionidae
<i>Isopteron brevis</i>	30	small	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Metistete ebenina</i>	73	small	flying	on	scavenger	Tenebrionidae
<i>Metistete sp</i>	19	small	flying	on	scavenger	Tenebrionidae
<i>Nyctozoilus sp</i>	32	big	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Saragus frenchi</i>	10	small	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Saragus pascoei</i>	82	big	not flying	concealed places/nocturnal	scavenger	Tenebrionidae
<i>Omorgus elderi</i>	25	small	not flying	on	scavenger	Trogidae

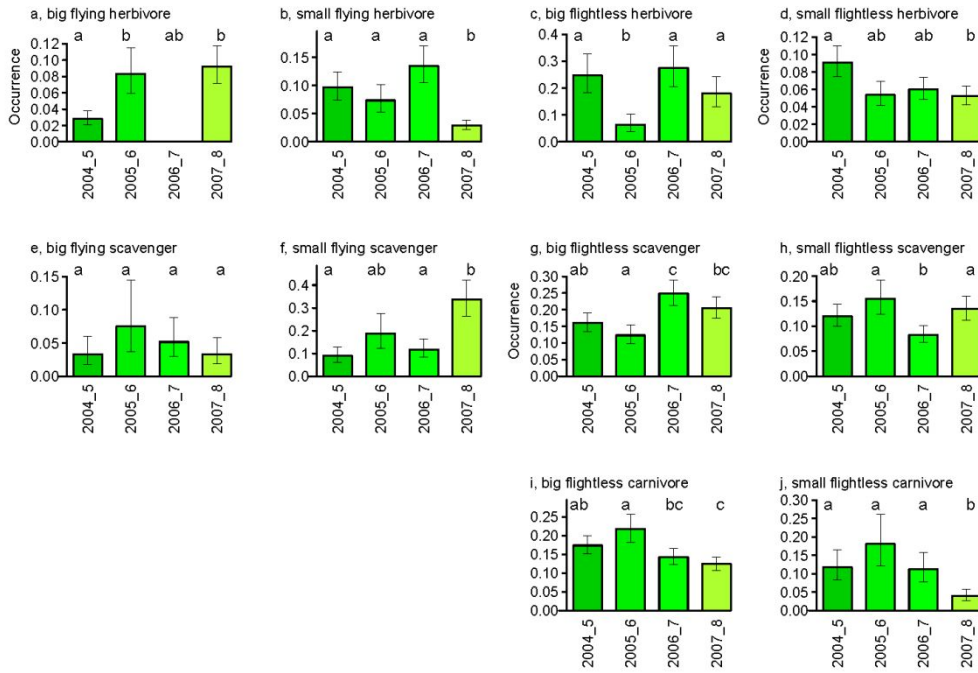
Appendix S4. (A) Models ranked by AICc fitting traits and combinations of traits to beetle occurrence data. The best fitting model has the lowest AICc and highest weight (see Burnham and Anderson [2002 #10187] for formulas for AICc and Weights). Model names in the Model column equate with the column names in Appendix S2.

Commented [DD1]: update refs

A.

Model	LogLik	df	AICc	deltaAICc	Weights
sfty	-3709	87	7513	0	1
sfp	-3668	111	7551	38	0
sty	-3740	55	7591	78	0
fty	-3754	47	7603	90	0
fpty	-3662	95	7612	99	0
spy	-3740	71	7625	112	0
fpy	-3751	63	7629	116	0
ty	-3785	31	7632	119	0
pty	-3739	79	7638	125	0
py	-3790	39	7658	145	0
sfp	-3794	36	7660	147	0
sft	-3802	30	7665	152	0
sfy	-3795	39	7668	155	0
fpt	-3802	32	7669	156	0
ft	-3818	20	7676	163	0
fy	-3815	23	7677	164	0
fp	-3815	24	7678	165	0
null.year	-3826	15	7681	168	0
st	-3820	22	7684	171	0
spt	-3802	40	7684	171	0
pt	-3814	28	7684	172	0
sy	-3820	23	7686	174	0
s	-3830	14	7688	175	0
t	-3828	16	7688	176	0
sf	-3826	18	7689	176	0
f	-3831	14	7690	178	0
null	-3833	12	7691	178	0
sp	-3821	26	7694	182	0
p	-3829	18	7695	182	0

Appendix S5. Estimated occurrence and 95 % confidence intervals for each year for each trait group in the three-way interaction between size, flight and trophic group. Different letters within panels indicate significant differences at the 0.05 level. a-d: herbivores; e-h: scavengers; i-j: carnivores. Note that the maximum Y axis values vary among panels.



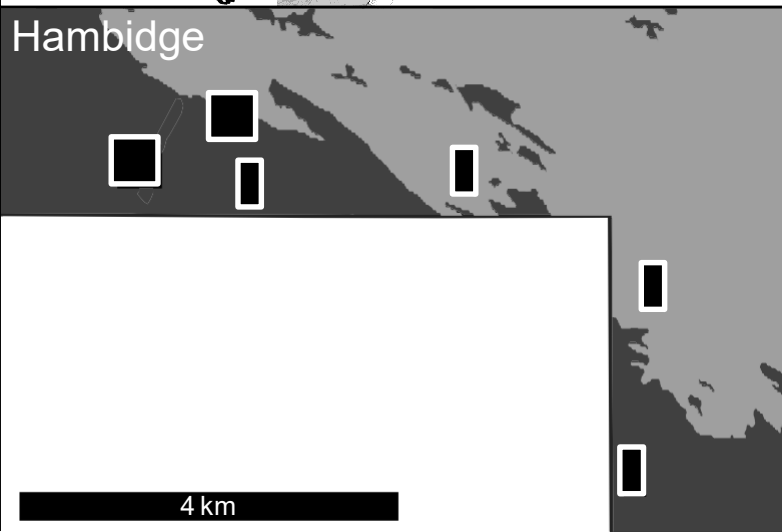
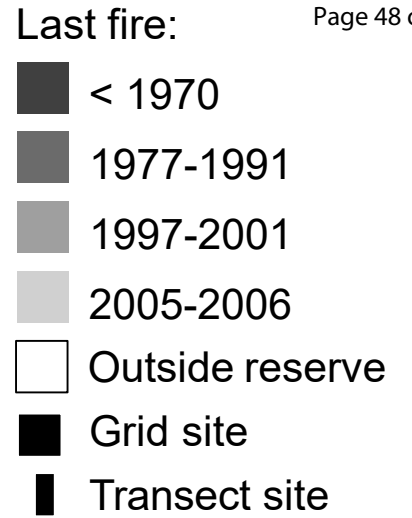
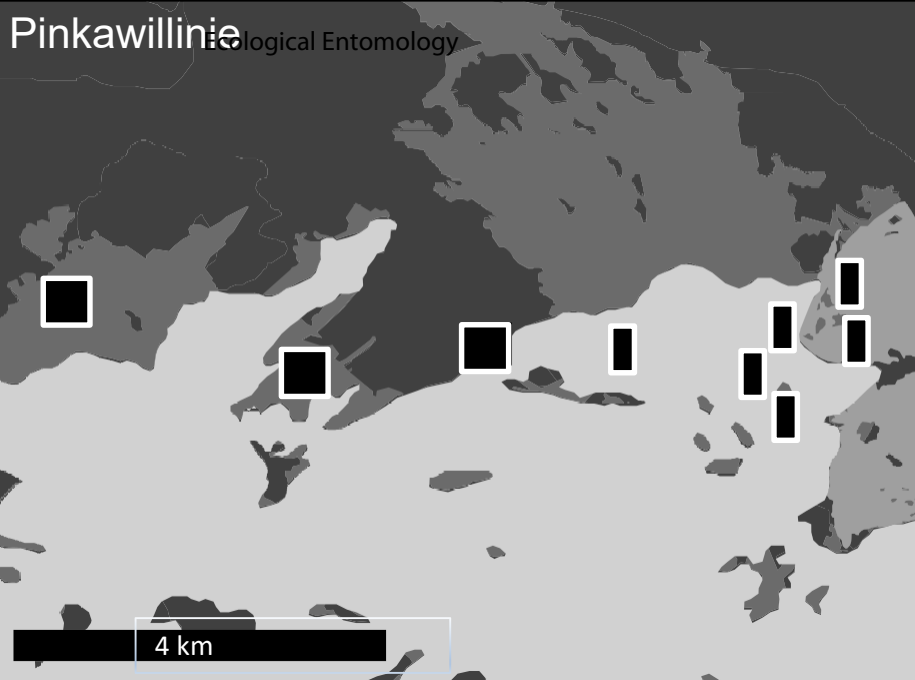
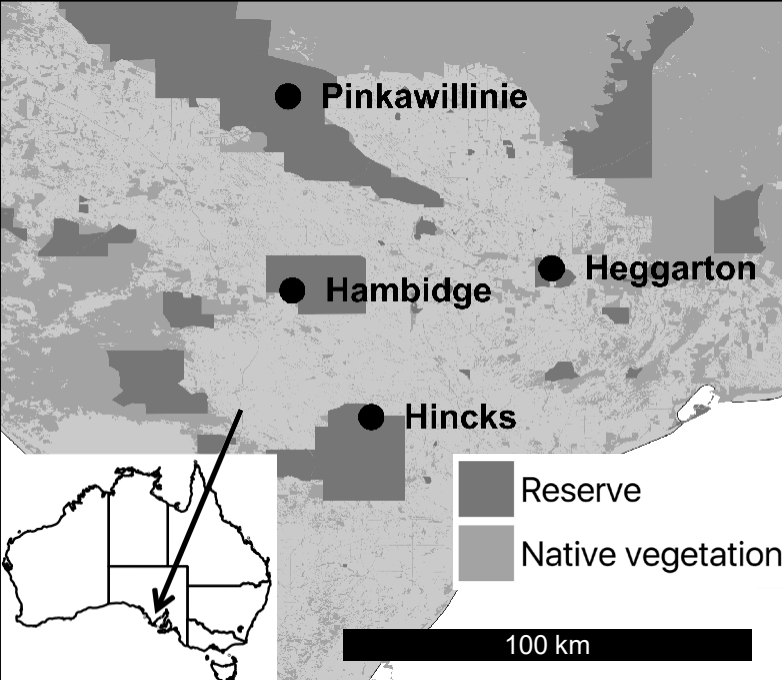
Appendix S6. Null models and models fitting time since fire (tsf) and month as detection covariates. A: Models ranked by AIC within trait group (negLogLike = negative log likelihood), nPars = number of parameters in the model, n = number of sites, AIC = Akaike Information Criterion, delta = change in AIC from the best model, AICwt = model weight. B: Intercepts (Int) and standard errors (SE) for colonisation (col), extinction (ext), initial occupancy (psi) and detection (p), and effects of month (p (month)) and time since fire (p (tsf)) on detection.

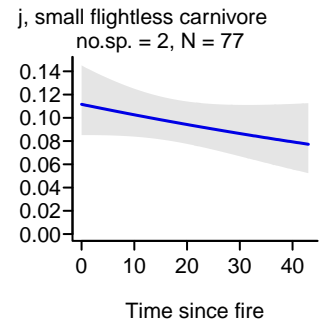
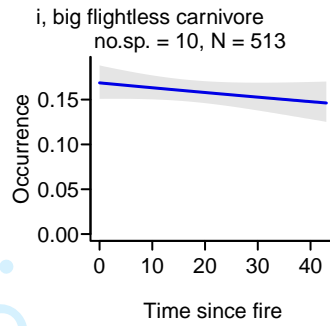
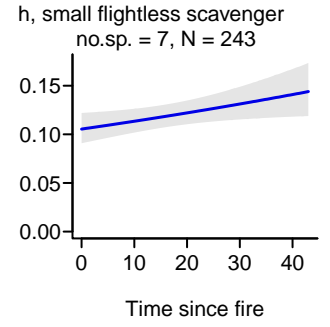
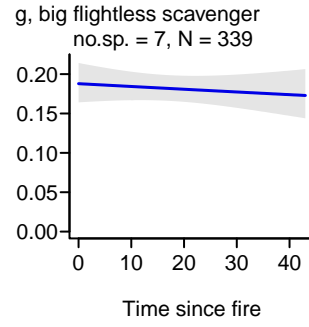
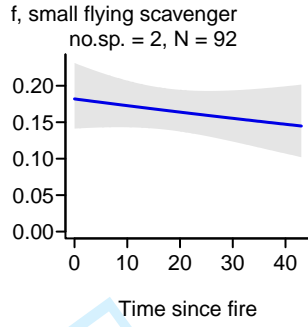
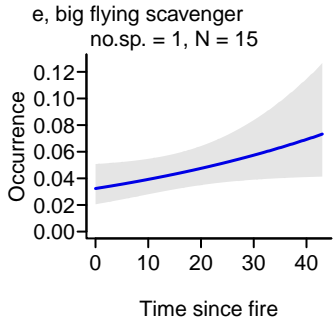
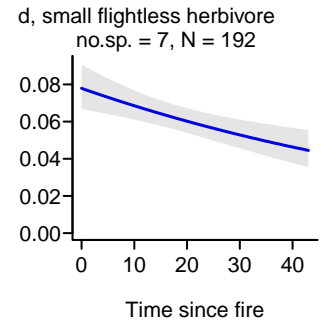
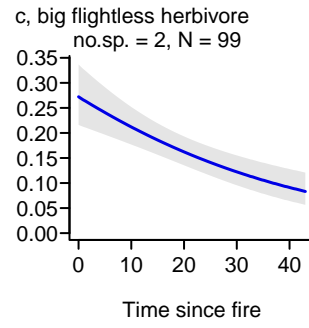
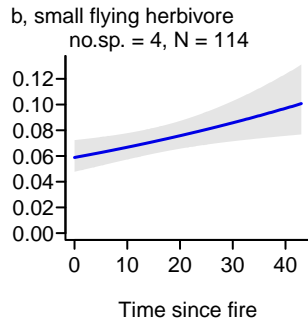
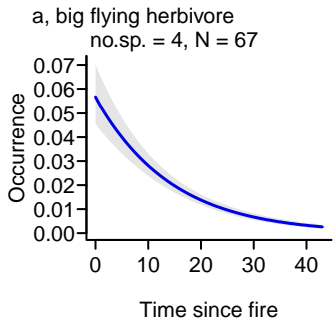
A.

Trait Group	formula	negLogLike	nPars	n	AIC	delta	AICwt
b f herbivore	~1 ~ 1 ~ 1 ~ 1	159	4	35	325.35	0.00	0.51
b f herbivore	~1 ~ 1 ~ 1 ~ tsf + month	157	6	35	325.45	0.10	0.49
b f scavenger	~1 ~ 1 ~ 1 ~ 1	69	4	35	146.24	0.00	0.60
b f scavenger	~1 ~ 1 ~ 1 ~ tsf + month	68	6	35	147.01	0.77	0.40
b nf carnivore	~1 ~ 1 ~ 1 ~ tsf + month	149	6	35	310.35	0.00	1.00
b nf carnivore	~1 ~ 1 ~ 1 ~ 1	174	4	35	356.30	45.95	0.00
b nf herbivore	~1 ~ 1 ~ 1 ~ tsf + month	166	6	35	344.21	0.00	1.00
b nf herbivore	~1 ~ 1 ~ 1 ~ 1	206	4	35	420.09	75.89	0.00
b nf scavenger	~1 ~ 1 ~ 1 ~ tsf + month	140	6	35	292.71	0.00	1.00
b nf scavenger	~1 ~ 1 ~ 1 ~ 1	169	4	35	345.98	53.26	0.00
s f herbivore	~1 ~ 1 ~ 1 ~ tsf + month	200	6	35	412.46	0.00	1.00
s f herbivore	~1 ~ 1 ~ 1 ~ 1	217	4	35	441.91	29.45	0.00
s f scavenger	~1 ~ 1 ~ 1 ~ tsf + month	200	6	35	412.15	0.00	1.00
s f scavenger	~1 ~ 1 ~ 1 ~ 1	210	4	35	428.80	16.65	0.00
s nf carnivore	~1 ~ 1 ~ 1 ~ tsf + month	182	6	35	376.92	0.00	1.00
s nf carnivore	~1 ~ 1 ~ 1 ~ 1	191	4	35	390.54	13.62	0.00
s nf herbivore	~1 ~ 1 ~ 1 ~ tsf + month	167	6	35	345.66	0.00	1.00
s nf herbivore	~1 ~ 1 ~ 1 ~ 1	228	4	35	463.61	117.95	0.00
s nf scavenger	~1 ~ 1 ~ 1 ~ tsf + month	192	6	35	395.01	0.00	1.00
s nf scavenger	~1 ~ 1 ~ 1 ~ 1	223	4	35	454.75	59.74	0.00

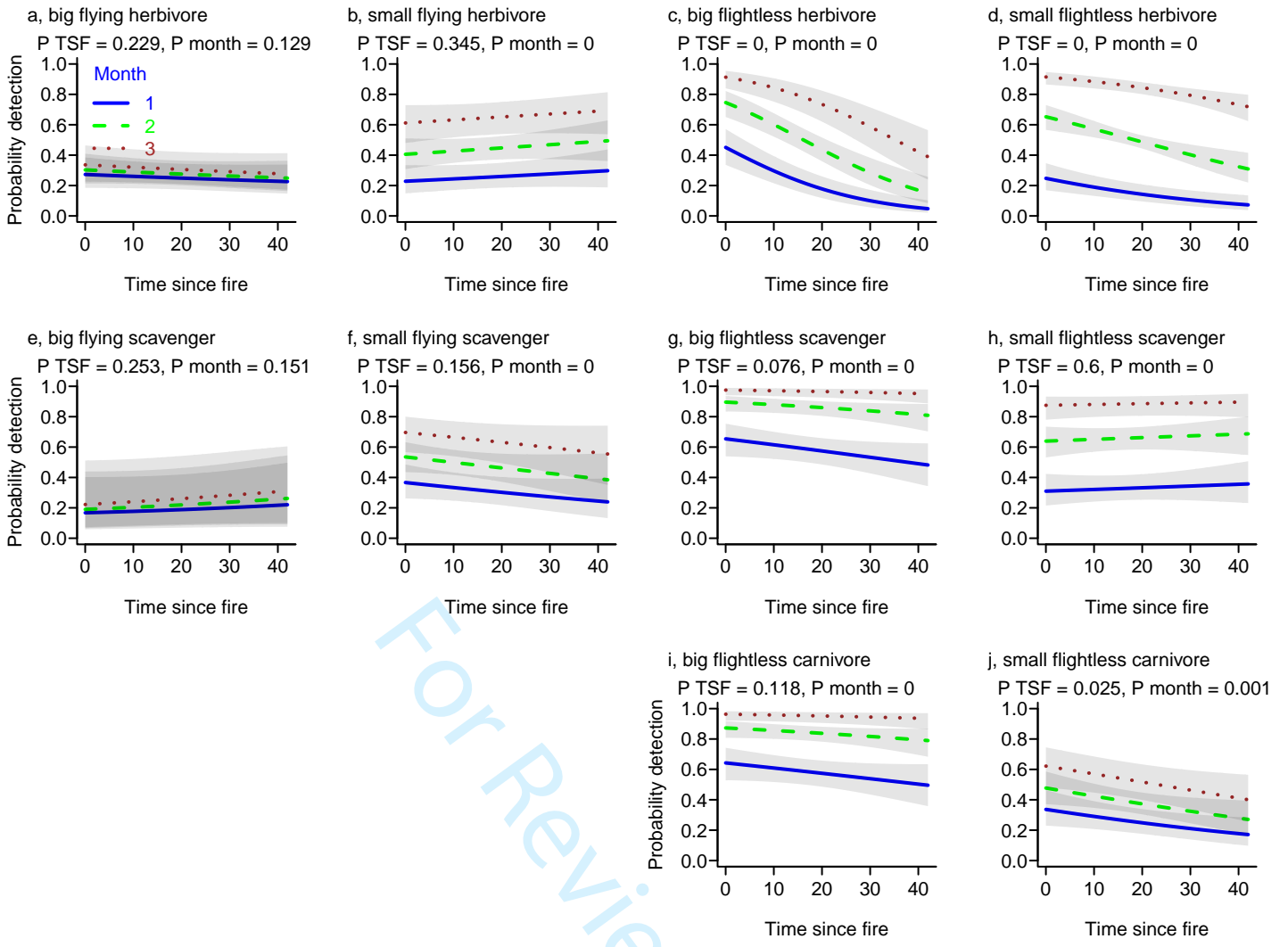
B.

Trait Group	formula	SEcol		SEext		SEp		p (month)	SEp (month)	p(tsf)	SEp (tsf)	psi (Int)	SEpsi (Int)
		col(Int)	(Int)	ext(Int)	(Int)	p(Int)	(Int)						
b f herbivore	~1 ~ 1 ~ 1 ~ 1	8.09	24.88	-0.59	0.71	-0.97	0.21	NA	NA	NA	NA	0.17	0.60
b f herbivore	~1 ~ 1 ~ 1 ~ tsf + month	6.66	11.81	-0.46	0.62	-1.50	0.41	0.29	0.19	-0.21	0.17	0.07	0.56
b f scavenger	~1 ~ 1 ~ 1 ~ 1	-1.01	0.67	0.10	1.05	-1.30	0.56	NA	NA	NA	NA	-1.87	0.90
b f scavenger	~1 ~ 1 ~ 1 ~ tsf + month	-0.82	0.76	0.38	0.88	-2.35	0.84	0.51	0.36	0.37	0.32	-1.98	0.86
b nf carnivore	~1 ~ 1 ~ 1 ~ tsf + month	0.62	105.01	-11.77	41.19	-0.99	0.36	1.34	0.22	-0.22	0.14	10.69	37.22
b nf carnivore	~1 ~ 1 ~ 1 ~ 1	0.72	96.47	-11.20	32.71	1.25	0.13	NA	NA	NA	NA	10.56	34.83
b nf herbivore	~1 ~ 1 ~ 1 ~ tsf + month	-8.29	33.58	-2.98	0.66	-2.55	0.40	1.27	0.20	-1.02	0.17	2.63	0.72
b nf herbivore	~1 ~ 1 ~ 1 ~ 1	-1.18	0.70	-2.21	0.63	0.16	0.15	NA	NA	NA	NA	1.51	0.52
b nf scavenger	~1 ~ 1 ~ 1 ~ tsf + month	0.62	106.89	-12.05	48.11	-1.15	0.38	1.51	0.24	-0.26	0.15	10.70	37.39
b nf scavenger	~1 ~ 1 ~ 1 ~ 1	0.81	97.63	-11.32	35.33	1.33	0.14	NA	NA	NA	NA	10.68	36.99
s f herbivore	~1 ~ 1 ~ 1 ~ tsf + month	7.69	33.59	-1.31	0.55	-1.92	0.35	0.84	0.17	0.13	0.14	8.00	34.31
s f herbivore	~1 ~ 1 ~ 1 ~ 1	4.90	139.00	-12.24	NA	-0.53	0.11	NA	NA	NA	NA	10.58	58.48
s f scavenger	~1 ~ 1 ~ 1 ~ tsf + month	8.60	32.03	-1.47	0.62	-1.47	0.35	0.69	0.17	-0.22	0.16	0.50	0.47
s f scavenger	~1 ~ 1 ~ 1 ~ 1	6.57	21.04	-1.33	0.58	-0.13	0.16	NA	NA	NA	NA	0.55	0.48
s nf carnivore	~1 ~ 1 ~ 1 ~ tsf + month	-6.40	10.19	-1.93	0.47	-1.61	0.37	0.59	0.17	-0.33	0.15	2.48	0.84
s nf carnivore	~1 ~ 1 ~ 1 ~ 1	-8.17	29.23	-1.91	0.48	-0.51	0.15	NA	NA	NA	NA	2.73	1.11
s nf herbivore	~1 ~ 1 ~ 1 ~ tsf + month	1.05	26.64	-6.60	NA	-3.41	0.39	1.74	0.17	-0.52	0.14	8.99	16.23
s nf herbivore	~1 ~ 1 ~ 1 ~ 1	1.03	NA	-9.03	NA	-0.08	0.11	NA	NA	NA	NA	9.96	26.12
s nf scavenger	~1 ~ 1 ~ 1 ~ tsf + month	0.03	0.81	-2.67	0.56	-2.09	0.36	1.37	0.20	0.08	0.15	2.63	0.95
s nf scavenger	~1 ~ 1 ~ 1 ~ 1	-1.89	4.65	-3.32	1.00	0.28	0.13	NA	NA	NA	NA	8.81	18.83





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Highlights.

Interactions among body size, trophic level and dispersal traits predict beetle detectability and occurrence responses to fire

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The three-way combination of size, flight and trophic level best explained beetle responses to time since fire, suggesting that generalisation using main effects of traits risks oversimplifying animal responses to fire.

The relationship of detectability with time since fire was similar to the occurrence relationship in the majority of response variables, so taking detectability into account is critical to correctly interpret occupancy data.

Three-way trait combinations that differ by just one trait, particularly dispersal ability, can result in either negligible effects of disturbance on detectability, or strong effects that influence observed occurrence.

