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EFFECTS OF FIRE REGIME ON PLANT SPECIES RICHNESS AND COMPOSITION DIFFER AMONG FOREST, WOODLAND AND HEATH VEGETATION

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Nomenclature: Harden (1991) for species, Taws (1997) for plant communities

Running Head: Fire regimes in dry sclerophyll vegetation

1 ABSTRACT

2 *Question:* Do the effects of fire regimes on plant species richness and composition differ among
3 floristically similar vegetation types?

4 *Location:* Booderee National Park, south-eastern Australia.

5 *Methods:* We completed floristic surveys of 87 sites in Sydney Coastal dry sclerophyll vegetation,
6 where fire history records have been maintained for over 55 years. We tested for associations
7 between different aspects of the recent fire history and plant species richness and composition, and
8 whether these relationships were consistent among structurally defined forest, woodland and heath
9 vegetation types.

10 *Results:* The relationship between fire regime variables and plant species richness and composition
11 differed among vegetation types, despite the three vegetation types having similar species pools.
12 Fire frequency was positively related to species richness in woodland, negatively related to species
13 richness in heath, and unrelated to species richness in forest. These different relationships were
14 explained by differences in the associations between fire history and species traits among vegetation
15 types. The negative relationship between fire frequency and species richness in heath vegetation
16 was underpinned by reduced occurrence of resprouting species at high fire frequency sites (more
17 than four fires in 55 years). However, in forest and woodland vegetation, resprouting species were
18 not negatively associated with fire frequency.

19 *Conclusions:* We hypothesise that differing relationships among vegetation types were underpinned
20 by differences in fire behaviour, and/or biotic and abiotic conditions, leading to differences in plant
21 species mortality and post-fire recovery among vegetation types. Our findings suggest that even
22 when there is a high proportion of shared species between vegetation types, fires can have very
23 different effects on vegetation communities, depending on the structural vegetation type. Both
24 research and management of fire regimes may therefore benefit from considering vegetation types
25 as separate management units.

26

27 INTRODUCTION

28 The management of fire regimes is a significant challenge for biodiversity conservation in fire-
29 prone ecosystems (Bowman et al. 2009; Penman et al. 2011; Moritz et al. 2014). The structure,
30 composition and diversity of vegetation communities in these ecosystems reflects the long-term fire
31 regime (Pausas et al. 2004; Pausas & Keeley 2014). Species in these systems are often dependent on
32 some burning for their long-term persistence, and can be highly responsive to changes in the fire
33 regime (Buma et al. 2013). Contemporary fire regimes are often very different from the historical
34 regimes under which ecosystems have developed, but detailed knowledge of historical regimes,
35 including the frequency, variability, intensity, severity, extent, and seasonality of fires, is rarely
36 available (Russell-Smith et al. 2003; Miller et al. 2007; Bowman et al. 2011; O'Donnell et al.
37 2011). Conservation managers are therefore tasked with conserving fire-prone vegetation
38 communities without sufficient knowledge of the processes necessary to maintain them.

39 The dry sclerophyll vegetation complexes of south-eastern Australia are one example of a
40 fire-prone ecosystem that is highly responsive to fire regimes (Bradstock & Kenny 2003).
41 Differences in the seasonality, intensity and severity of fire have been associated with differences in
42 the diversity and dominance patterns of dry sclerophyll vegetation by affecting the ability of
43 different species to survive fire and/or re-establish after fire (Morrison & Renwick 2000; Morrison
44 2002; Ooi et al. 2006). One element of the fire regime that has repeatedly been found to be
45 important for the diversity and composition of dry sclerophyll vegetation is the length of inter-fire
46 intervals (Pausas et al. 2004). Repeated short inter-fire intervals (less than 5-7 years) can cause:
47 declines in species richness; local extinction of species that rely on seed for post-fire regeneration
48 (obligate seeders); and divergence in species composition towards herbaceous, fire-tolerant species
49 (Cary & Morrison 1995; Penman et al. 2008a; Penman et al. 2008b). Similarly, long periods of fire
50 exclusion can lead to low plant richness, diversity and evenness by either allowing mid-storey
51 shrubs to dominate and exclude understorey species (Keith & Bradstock 1994; Tozer & Bradstock
52 2003; Bargmann & Kirkpatrick 2015; Freestone et al. 2015), or by exhausting the seedbank of
53 short-lived species (Lamont et al. 1991). In contrast, variability in the length of inter-fire intervals
54 has been associated with greater richness and evenness in plant communities (Morrison et al. 1995).
55 Variation in inter-fire intervals can promote diversity by driving differences in propagule supply
56 among species over time, thereby preventing dominance by a single plant functional type (Keith &
57 Bradstock 1994). As the dry sclerophyll vegetation of south-eastern Australia includes some of the
58 most diverse vegetation communities in Australia, identifying appropriate fire management
59 practices to promote and maintain floristic diversity is a conservation priority (Bradstock & Kenny
60 2003; Keith 2004).

61 Knowledge of species responses to fire has led to the estimation of fire intervals tolerated by
62 different vegetation types. These are commonly known as tolerable intervals, and describe the
63 minimum and maximum inter-fire intervals that managers should aim to generate to prevent the
64 extinction of key plant functional types (Kenny et al. 2004). For example, based on the reproductive
65 and fire response traits of species occurring in dry sclerophyll vegetation of south-eastern Australia,
66 it has been recommended that managers aim for fire return intervals of between 7 and 30 years for
67 heaths and between 7 and 30-50 years for woodlands and forests (Bradstock & Kenny 2003; Kenny
68 et al. 2004). Fire management recommendations such as these, which are based on the vital
69 attributes (i.e. reproductive and fire-response traits) of individual species, are focused on extremes
70 of fire regimes, and the risk of too much or too little fire causing local extinctions of particular
71 species through death or recruitment failure (Kenny et al. 2004; Tulloch et al. 2016). Therefore,
72 while useful for identifying scenarios to avoid (e.g. return intervals of < 7 years), approaches based
73 on tolerable intervals provide little guidance for managers about the specific fire regimes that will
74 promote diverse vegetation communities (Duff et al. 2013).

75 Dry sclerophyll vegetation in south-eastern Australia typically occurs as a complex spatial
76 mosaic, comprised of structurally defined forest, woodland and heath vegetation types (Keith 2004).
77 While dry sclerophyll forests, woodlands and heaths differ in structure and dominant species, they
78 often have considerable overlap in the composition of their species pools (Keith 2004). This
79 similarity in species pools means that management guidelines derived from species fire-response
80 traits are often broadly similar among these vegetation types (Kenny et al. 2004). Yet, plant species
81 can respond differently to fire, depending on the environmental and competitive conditions they
82 experience (Tozer & Bradstock 2003; Gosper et al. 2010; Enright et al. 2014; Torres et al. 2017).
83 Therefore, because vegetation types differ in both abiotic (e.g. soil nutrients) and biotic conditions
84 (e.g. canopy shading) (Keith 2004; Keith & Tozer 2012), fire regimes likely to promote
85 biodiversity may differ among vegetation types. Therefore, an important question is whether fire
86 management goals should differ among dry sclerophyll forest, woodlands and heaths to ensure the
87 maintenance of floristic diversity.

88 In this study, we aimed to determine whether structurally defined vegetation types that have
89 a high level of floristic similarity should be considered as separate units for fire management and
90 research. We used a space-for-time approach, combining 55 years of fire history records with
91 floristic surveys of 87 sites to explore associations between fire history variables and plant
92 community attributes, addressing the question: Do associations between fire regime and plant
93 species richness and composition differ among dry sclerophyll forest, woodland and heath
94 vegetation types?

95

96 METHODS

97 *Study area*

98 We conducted this study in Booderee National Park (BNP), a ~ 6500 ha reserve located on a coastal
99 peninsula approximately 200 km south of Sydney in south-eastern Australia (35°10'S, 150°40'E,
100 Appendix S1). Booderee National Park is at the southern extent of the floristically diverse Sydney
101 Coastal Heath and Sydney Coastal Dry Sclerophyll Forest vegetation types, which occur in complex
102 spatial mosaics over sandstone. Woodlands occur in transitional areas between forests and heaths
103 (Taws 1997; Keith 2004), and the distribution of these vegetation types is driven primarily by
104 abiotic factors (Beadle 1954; Keith 2004; Keith & Tozer 2012). In this study, we focused on the
105 three most widespread vegetation formations in BNP ; forests (36.2 % of the park area), woodlands
106 (12.9 %), and heaths (15.3 %) (Taws 1997). For more detailed descriptions of vegetation types see
107 Appendix S1. While we acknowledge that vegetation structure will vary substantially within, as
108 well as among these vegetation types, our study focuses on broad structural vegetation types (i.e.
109 categories), rather than direct measures of vegetation structure for two reasons: (i) broad vegetation
110 type classifications are commonly used in conservation and land management planning, and so
111 differences in fire responses among these types have direct application value, and (ii) vegetation
112 structure is comprised of many different components which would make direct tests of interactions
113 between fire history and vegetation structure overly complex to implement and interpret.

114 *Fire in Booderee National Park*

115 Booderee National Park has a well-documented fire history and records of fire perimeters and cause
116 (wildfire or prescribed fire) have been maintained for fires occurring in the park since 1957 (for
117 details, see Appendix S2). From the 55 years of fire history data, we calculated time since fire and
118 the number of fires (fire frequency) for each of the 87 sites at which we conducted floristic surveys
119 (Table 1, Appendix S2). We were not able to include variables relating to the mean length or
120 variability of fire intervals in this study as many sites had burnt less than three times in the 55 year
121 record period. Instead, we recorded whether each site had experienced an inter-fire interval of less
122 than seven years or greater than 30 years (Table 1); outside the recommended tolerable fire intervals
123 for dry sclerophyll heaths and woodlands (Bradstock & Kenny 2003; Kenny et al. 2004). Among
124 the 87 sites surveyed in this study, most (79%) had burnt between one and three times in the period
125 1957-2012, few were long-unburnt at the time of survey (12% were > 20 years post-fire), and the
126 length of fire intervals was highly variable (Appendix S2, Fig. S2.3).

127 *Plant surveys*

128 We surveyed the plant community at long-term monitoring sites which were established in 2003 to
129 assess biodiversity responses to fire (Lindenmayer et al. 2008a; Lindenmayer et al. 2008b;
130 Lindenmayer et al. 2016). These sites were selected in 2003 (prior to the 2003 wildfire) using a
131 stratified randomised approach. Polygons were generated to divide the park area into units that were
132 “homogenous” in both vegetation type and known fire history at the time of site selection (2003)
133 (Lindenmayer et al. 2008a). Sites (maximum of one per polygon) were then selected so that they
134 were stratified by vegetation type and time since fire, with the goal of distributing sites widely
135 throughout the park (see Lindenmayer et al. 2008b for details, and Appendix S1 for site locations).
136 The number of sites per vegetation type was selected to be roughly proportional to the area of that
137 type, and for our study we included data from the 87 study sites that were surveyed in 2012-2013,
138 and were located in our three vegetation types (forest = 40, woodland = 22 and heath = 25). Each
139 site comprised a 100 m transect which was located so that the full transect fell within the boundary
140 of the mapped polygon.

141 We conducted plant surveys once at each site between April 2012 and May 2013. Surveys
142 were conducted within two 20 x 20 m quadrats at each site, located between the 20 and 40 m, and
143 60 and 80 m marks of the transect (i.e. 20 m apart), one on each side of the transect. We completed
144 a timed 30 minute search in each quadrat (excluding breaks to identify plants), and identified each
145 vascular plant species present according to Harden (1991), then pooled these (presence/absence)
146 data at the site level for analysis. We used a 30 minute search time as earlier (pre-2012) surveys at
147 these sites had indicated that extending searches beyond this time yielded few additional species.

148 *Data analysis: Species richness*

149 We focused our analysis on plant species richness as maintaining plant species diversity has
150 been identified as a conservation priority for the dry sclerophyll vegetation of the Sydney Basin
151 region (Keith 1995; Tozer & Bradstock 2003; Keith 2004). We tested for associations between the
152 recent fire history and plant species richness using generalised linear models in R (version 3.2.3, R
153 Foundation for Statistical Computing, Vienna, Austria). To allow the effects of fire history to vary
154 among vegetation types, fire history variables were included as interactions with vegetation type in
155 the full model. Variation in fire history in space-for-time studies such as ours is unlikely to be
156 independent of underlying environmental variation because the occurrence of fire is influenced by
157 spatially co-varying factors such as site moisture, topography and the type, quantity and dryness of
158 fuels (i.e. living and dead vegetation) (Cheney et al. 2012). To reduce potential confounding of fire
159 effects with other spatially related environmental factors, we therefore included key topographic
160 variables as covariates in the models (aspect and elevation, Table 1). We did not allow any
161 interactions other than the two-way interactions between fire history and vegetation type, as

162 although other interactions are ecologically possible, they were not directly relevant to our study
163 questions, and we were unable to test more complex models with the available sample size.

164 We fit models using the “glm” function in R, using species richness as the response variable,
165 Poisson error distributions and a log-link function. The linear predictor for the full (maximal) model
166 was = veg + TSF + FF + shortI + longI + veg*TSF + veg*FF + veg*shortI + veg*longI + AspE +
167 AspN + Elev (see Table 1 for variable descriptions). We converted continuous predictor variables to
168 z-scores prior to analysis to allow direct comparison of regression coefficients. We did not include
169 the variable surface geology in the regression model due to a moderately strong association with
170 vegetation type (Generalised Variance Inflation Factor [GVIF] = 7.3, $GVIF^{(1/(2*df))} = 1.4$, Fox &
171 Monette 1992). All other pairwise correlations between predictor variables were less than 0.7
172 (Dormann et al. 2013). After checking the fit of the full models by inspecting residual plots (Zuur et
173 al. 2009), checking for over-dispersion, and testing for spatial autocorrelation in the residuals
174 (“correlog” function in the “ncf” package), we used Akaike’s Information Criterion corrected for
175 small sample sizes (AICc), to rank subsets of the full model (“dredge” function in “MuMIn”
176 package) (Burnham & Anderson 2002). To reduce the number of models being compared, we
177 retained the topographic environmental variables (aspect easting, aspect northing, and elevation) in
178 all models and restricted comparisons to among models with different subsets of fire history
179 variables and their interaction with vegetation type. We used the “confint” function to estimate 95%
180 confidence intervals for coefficients in the top-ranked model, and the “predict.glm” function (both
181 in the “R stats” package) for model predictions.

182 *Data analysis: Species traits*

183 To investigate whether differences in fire responses among vegetation types were associated
184 with plant species traits, we implemented a parametric approach to the fourth corner problem,
185 employing multivariate latent variable models (Warton et al. 2015) using the R package Boral (Hui
186 2016). We fit a separate model for each of two traits of interest: plant growth form when mature
187 (shrubs, trees, herbs [non-graminoid], ferns and graminoids) and dominant fire response (obligate
188 seeder, resprouter, or one of three intermediate levels, see Appendix S3). Trait data for each species
189 were collated from the Australian Fire Ecology Database, available from the TRY plant trait
190 database (Kattge et al. 2011). This model-based approach to ordination employs a hierarchical
191 multilevel approach to fit correlated response models that combine separate species occurrence
192 models with latent variables to account for residual variation. Species traits are incorporated into the
193 correlated response model as random effects. Where traits are associated with responses in the
194 correlated response model, this will be reflected in differences in the estimated model coefficients
195 among trait groups. We fit the model using the top-ranked model from the analysis of species

196 richness (linear predictor = veg + TSF + FF + shortI + veg*FF + veg*shortI + AspE + AspN +
197 Elev), using presence/absence data for all individual species occurring at five or more sites (n =
198 196), and a probit link function. As we were primarily interested in differences in fire responses
199 associated with species traits, we restricted the inclusion of traits to the interaction of the trait
200 random effects with the fire (TSF, FF, shortI) and fire \times vegetation type (veg*FF and veg*shortI)
201 terms in the model. All model parameters were assigned Cauchy priors with a centre of zero and
202 scale parameter 2.5 (Gelman et al. 2008). We also included two latent variables in the model to
203 parsimoniously model residual correlation among species (e.g. resulting from processes such as
204 spatial autocorrelation) (Hui 2016). We ran a single chain with 40,000 iterations with a burn in of
205 10,000 and a thinning factor of 30 (Robert & Casella 2004; Hui 2016).

206 *Data analysis: Species composition*

207 Tests of relationships between fire and species composition can be prone to confounding
208 effects as both the occurrence of species, and the occurrence of fire are likely to be associated with
209 underlying variation and co-variation in spatial (e.g. site proximity) and environmental factors (e.g.
210 topography). We therefore used redundancy analysis (RDA) to test for associations between
211 variation in fire history variables and multispecies occurrences, as these techniques can account for
212 potentially co-varying effects of space and environment (Legendre & Legendre 2012). We
213 conducted three separate analyses, analysing sites within each of the three vegetation types
214 separately. This approach allowed us to compare the fire history and environmental factors that
215 were important among the three vegetation types. To reduce spurious effects from rare species, we
216 included only those species that occurred at > 5% of sites.

217 We based all multivariate analyses on three groups of explanatory variables: fire history
218 variables (Table 1), environmental variables (Table 1), and spatial variables. Continuous fire and
219 environmental variables were standardised prior to analysis. Spatial variables were generated using
220 principal coordinates of neighbour matrix analysis (PCNM, “pcnm” function in the package
221 “vegan”) (Legendre & Legendre 2012). PCNM models the spatial structure among sites via
222 eigenvalue decomposition of a truncated matrix of geographic distances (Borcard & Legendre
223 2002). As this analysis relies on distances between sites, we ran a separate PCNM analysis,
224 generating a separate set of spatial variables for each of the vegetation types. The PCNM method
225 emphasises neighbouring sites, which is achieved by truncating all distances in the input distance
226 matrix above a nominated threshold to an arbitrary “large” value (4 times the threshold). For our
227 analyses, we employed a threshold distance equal to the minimum distance needed to keep all sites
228 connected in a network (3.5 km for forest, 2.7 km for woodland and 2.6 km for heath sites). PCNM
229 uses principal coordinate analysis to generate multiple linear spatial variables (eigenvectors) from

230 the truncated distance matrix, which can then be used to control for spatial autocorrelation. The first
231 PCNM vectors reflect variation at large-scales and later PCNM vectors reflect variation at smaller
232 spatial scales (Borcard & Legendre 2002). We used $\frac{1}{2}$ the number of created PCNM vectors (given
233 they possessed positive eigenvalues) as the spatial variables in our analysis (Borcard & Legendre
234 2002).

235 Implementation of the RDA involved three steps: variable selection, redundancy analysis,
236 and variance partitioning. For the variable selection step, we used forward selection with double
237 stopping criteria ($P < 0.05$ and adjusted $R^2 < \text{global } R^2$) (Blanchet et al. 2008) to select variables
238 from each of the three variable groups (fire history, environmental and spatial variables, see Table
239 1), that were significantly associated with variation in the site by species occurrence matrix. For the
240 redundancy analysis step, we used the selected variables as inputs for a canonical redundancy
241 analysis (function “rda” in package “vegan”), to test for associations between multivariate species
242 occurrence and fire frequency variables, after conditioning for environmental variables, and the
243 spatial structure of sites (Legendre & Legendre 2012). Significance testing of variable groups in the
244 redundancy analysis was performed via 999 permutations of the data, using the “anova” function in
245 the R “stats” package. Finally, for the partitioning step, we used partial RDAs (and adjusted R-
246 squared) to quantify the pure and shared contributions of fire history variables, environmental
247 variables, and spatial variables (PCNM eigenvectors), to variation in multivariate species
248 occurrence (function “varpart” in package “vegan”) (Peres-Neto et al. 2006).

249

250 RESULTS

251 *Species richness*

252 The most strongly supported model for species richness included fire frequency, time since fire and
253 the occurrence of short inter-fire intervals (< 7 years), but did not include the occurrence of long
254 fire intervals (> 30 years, Appendix S4). The two fire by vegetation type interactions included in the
255 top model indicate that associations between fire variables and species richness intervals differed
256 among vegetation types for both fire frequency and the occurrence of short intervals, but not for
257 time since fire. Species richness was positively associated with fire frequency in woodland,
258 negatively associated with fire frequency in heath, and not associated with fire frequency in forest
259 vegetation (Table 2, Fig. 1a). The occurrence of short fire intervals was associated with plant
260 species richness only in woodland vegetation, where sites which had been subject to short fire
261 intervals supported lower species richness than sites which had no short intervals (Table 2, Fig. 1c).
262 In contrast, the negative association between plant species richness and time since fire was

263 consistent among the three vegetation types, although this effect was not large and confidence
264 intervals were wide (Table 2, Fig. 1b). None of the topographic environmental variables were
265 strongly associated with site level species richness (Table 2).

266 *Species traits*

267 Fourth corner analysis of interactions between species traits and fire history variables
268 revealed that some, but not all fire associations were related to species trait groups. Within heath
269 vegetation, species that resprout after fire were negatively associated with fire frequency, while
270 obligate seeding species were not (Fig. 2a, see Appendix S5 for full model tables). This trend was
271 not apparent for forest or woodland sites. We found that all growth forms in heath were negatively
272 associated with fire frequency, while in forest vegetation, grasses and herbs were positively
273 associated with fire frequency (Fig. 2b). The association between species occurrences and time
274 since fire was also related to species traits groups, with obligate seeding species and shrub species
275 negatively associated, and ferns positively associated, with time since fire (Figs. 2c, d). We found
276 little association between short fire intervals and species traits, except for herbs, which were
277 negatively associated with the occurrence of short fire intervals in forest vegetation (Figs. 2e, f).

278 *Species composition*

279 The spatial, environmental and fire history variables associated with differences in species
280 composition of vegetation differed among vegetation types. For forest sites, the variable selection
281 procedure identified three spatial variables (PCNM 1, 2 and 3– all representing large-scale spatial
282 patterns), two environmental variables (elevation and surface geology), and three fire history
283 variables (fire frequency, time since fire, and the occurrence of long fire intervals) that were
284 significantly associated with differences in plant species composition. However, partial RDA
285 analysis revealed that after conditioning for the effects of spatial and environmental variables, fire
286 history variables were not associated with differences in species composition ($P = 0.512$, Appendix
287 S6). Variation partitioning showed that although 9.2% of variation in species composition was
288 associated with fire history variables, all of this this was shared with the spatial and environmental
289 components of the model (Fig. 3).

290 For woodland sites, the variable selection procedure identified one spatial variable (PCNM
291 1), two environmental variables (aspect northing and surface geology), and three fire history
292 variables (time since fire, fire frequency and the occurrence of short fire intervals) that were
293 significantly associated with differences in plant species composition. Partial RDA showed that
294 after conditioning for the effects of environmental and spatial variables, fire history variables were
295 still significantly associated with differences in species composition ($P = 0.003$, Appendix S6). Of

296 the 20.5% variation in species composition that could be explained through variance partitioning,
297 12.5% was associated with fire history variables, and 7.6 % was explained by fire history variables
298 alone (Fig. 3).

299 For heath sites, three spatial variables (PCNM 2 and 3 – large-scale variables, and PCNM 11
300 – a small-scale variable), and one fire history variable (time since fire) were selected as being
301 associated with plant species composition. No environmental variables were selected in the variable
302 selection component of the analysis. Partial RDA showed that time since fire was still associated
303 with differences in plant species composition after conditioning for spatial variables ($P = 0.028$,
304 Appendix S6). Variation in species composition that could be explained through variance
305 partitioning was attributed to spatial variables (10.2%), with only a small amount (2.5%) attributed
306 to fire history variables (Fig. 3).

307

308 DISCUSSION

309 Our study investigated whether associations between fire regime and plant species richness and
310 composition differed among dry sclerophyll forest, woodland and heath vegetation types. Despite
311 substantial overlap in the species pools of these vegetation types (see Appendix S2), we found that
312 relationships between fire regime variables and plant community measures differed markedly
313 among forest, woodland and heath vegetation. Our study suggests that fire management decisions,
314 even those within identified tolerable ranges (Bradstock & Kenny 2003; Kenny et al. 2004), could
315 have substantially different effects on plant communities, depending on the structural vegetation
316 type in question. We hypothesise that these differences in fire history associations occur due to
317 differences in abiotic and biotic conditions among vegetation types, and suggest that dry sclerophyll
318 forests, woodlands and heaths be considered as distinct units in future fire research and
319 management programs.

320 *Species richness and traits*

321 Total species richness was positively correlated with fire frequency in woodland sites, but
322 negatively correlated with fire frequency in heath sites and showed no association with fire
323 frequency in forest sites. Opposing relationships in heath and woodland vegetation are particularly
324 interesting given these vegetation types share a high proportion of species (72% of the 192 species
325 recorded in heath vegetation were also recorded at woodland sites and Jaccard similarity between
326 heath and woodland vegetation types was 0.7, Appendix S1). Therefore, the opposing effect of fire
327 frequency was unlikely to be due to differences in species composition (with different fire
328 responses) between heath and woodland vegetation, but rather species responding differently to the

329 occurrence of fire in different vegetation types. This idea was supported by the analysis of
330 associations between fire responses and trait groups, which revealed that in heath vegetation,
331 species that resprout after fire were negatively associated with fire frequency, while obligate
332 seeding species were not, a pattern that was not evident in forest or woodland vegetation types.
333 Differences among vegetation types were evident also for species growth form, where grasses and
334 herbs (many of which resprout after fire) were positively associated with fire frequency in forest
335 sites, but negatively associated with fire frequency in heath sites. We hypothesise that the different
336 fire frequency associations we observed in forest, woodland and heath vegetation occurred through
337 a combination of three interacting factors: (1) the fire regimes recorded in our study are
338 predominantly within tolerable ranges, and so direct extirpation of plant populations due to
339 inappropriate fire intervals was unlikely, (2) differences in vegetation structure can lead to
340 differences in fire properties (e.g. fire intensity) between vegetation types, leading to variation in
341 direct fire impacts on plants, and (3) vegetation responses to fire are mediated by biotic and abiotic
342 conditions in the post-fire environment, which differ among vegetation types.

343 Fire frequencies for 85 of our 87 study sites ranged from one to five fires in a 55-year period
344 (Fig. 1). This meant that both low fire frequency sites (one to two fires in 55 years, or fire return
345 intervals of approximately 25 – 30 years) and high fire frequency sites (four or five fires, or fire
346 return intervals of approximately 10-13 years) were, on average, within tolerable fire intervals for
347 dry sclerophyll vegetation types (Bradstock & Kenny 2003; Kenny et al. 2004). In contrast, many
348 other studies of the effects of fire frequency on dry sclerophyll vegetation have been in areas which
349 have experienced average fire intervals of less than five years (e.g. Morrison et al. 1995; Watson &
350 Wardell-Johnson 2004; Penman et al. 2008b), with some experiencing as many as three fires in
351 three years (Bradstock et al. 1997). Such fire frequencies are outside the biological limits of
352 persistence for many dry sclerophyll species (Bradstock & Kenny 2003), and under such conditions,
353 the same types of species would be expected to be lost from forest, woodland and heath
354 communities. In contrast, the fire frequencies (and corresponding intervals) recorded in our study
355 are unlikely to have led to the direct extirpation of species, and so the responses of the vegetation
356 community to fire frequency are likely to be mediated by both the properties of fires, as well as
357 post-fire conditions (Keith 1995), which will differ among vegetation types.

358 Differences in vegetation structure and biomass mean that the three vegetation types studied
359 will vary substantially in the quantity and spatial arrangement of fine fuels. Fine fuel is an important
360 driver of fire behaviour (Cheney et al. 2012). Therefore, variation in fire properties among
361 vegetation types (driven by differences in fuels) is one explanation for the different fire-history-
362 species richness associations we observed in different vegetation types. For example, we observed

363 that fire frequency was negatively associated with species richness in heath vegetation, particularly
364 for resprouting species. Heath vegetation has a high density of fine fuels compared with woodlands
365 and forests (Ingwersen 1977; Bradstock et al. 2012), meaning that fires in heath are likely to be, on
366 average, more intense than fires in woodlands and forests (Cheney et al. 2012). Resprouting species
367 rely on surviving fire for persistence, and in intense fires, fewer individuals are likely survive
368 (Noble 1984; Bradstock & Myerscough 1988). This means that fire-induced mortality rates of
369 resprouting species may have been higher in heath than other vegetation types, leading to the
370 negative association we observed between fire frequency and species richness for heath sites, but
371 not for sites in forest or woodland vegetation.

372 Differences in environmental and competitive conditions can also lead to differences in
373 plant responses to fire (Tozer & Bradstock 2003; Gosper et al. 2010; Torres et al. 2017). While
374 sharing many species, dry sclerophyll heaths, woodland and forests differ in both abiotic (e.g. soil
375 depth and nutrients), and biotic conditions (e.g. canopy shading) (Keith 2004; Keith & Tozer 2012),
376 and these differences could have led to the contrasting associations between fire frequency and
377 species richness that we observed. For example, species richness in heath was negatively associated
378 with fire frequency, and this negative association was related to reduced occurrences of resprouting
379 species, grasses and herbs under high fire frequencies. This relationship was not evident in
380 woodland and forest sites. Compared with woodlands and forests, heath vegetation is found in areas
381 of shallow soils and low productivity (Beadle 1954; Keith 2004). Under low productivity
382 conditions, regular fires can deplete the stored resources of resprouting species, leading to higher
383 rates of mortality, and a consequent dominance of obligate seeding species (Clarke & Knox 2002;
384 Clarke et al. 2005). The low productivity of heath sites may therefore have led to the negative
385 association between fire frequency and species richness that we observed in heath but not in forest
386 or woodland vegetation.

387 Differences among vegetation types in the post-fire competitive environment could also
388 have contributed to the differences in fire-history-species richness associations we observed. In
389 Sydney coastal heaths, fire return intervals of 10-15 years (equivalent to high fire frequency in our
390 study) would be expected to lead to the dominance of a few tall, obligate seeding shrubs, such as
391 *Banksia ericifolia*, which can form dense thickets, out-competing, and reducing the diversity of
392 understorey species (Keith 1995; Keith & Tozer 2012), particularly slow-growing resprouting
393 species (Fig. 2a, Bond & Midgley 2001). In contrast to heaths, woodlands support an open canopy
394 of *Eucalyptus spp.* (Taws 1997) that survives, and resprouts after fire. Competition from overstorey
395 species could slow the growth of tall, obligate seeding shrubs in woodlands, and may even prevent
396 closed shrub thickets from forming altogether. In the absence of closed thickets, fire return intervals

397 of 10-15 years in woodlands could promote high plant diversity by maintaining midstorey and
398 canopy gaps (and hence ground-layer light) (Menges & Hawkes 1998), while also facilitating the
399 establishment and persistence of a diversity of obligate seeding shrubs, which tend to decline with
400 increasing time since fire (Fig. 2c ,d, Morrison et al. 1995; Tozer & Bradstock 2003; Freestone et al.
401 2015). In forest vegetation, fires often do not reach the canopy, and even if a fire is crowning,
402 canopy species in our study area can regrow rapidly from above-ground epicormic growth
403 (Ingwersen 1977). Fires will therefore often have limited effects on the growing conditions
404 experienced by understorey species in our forest study system, which may explain the limited
405 associations we found between fire history and the plant community in forest vegetation compared
406 with heaths and woodlands.

407 Although these different explanations would need more targeted, and ideally longitudinal,
408 studies to be verified (see examples from heaths: Keith & Bradstock 1994; Tozer & Bradstock
409 2003; Keith et al. 2007; Keith & Tozer 2012; Freestone et al. 2015), our results suggest that
410 different processes are driving fire responses of heath, woodland and forest vegetation. Fire
411 management regimes may therefore need to differ among vegetation types if the goal is to maintain
412 high levels floristic of diversity in dry sclerophyll vegetation.

413 *Species composition*

414 Vegetation composition was associated with fire history variables in woodland and heath
415 vegetation, but not in forests (Fig. 3). As for species richness, it is possible that the different
416 strength of fire associations among vegetation types occurred due to differences in fire intensity
417 and/or in the competitive environment post-fire. Fires that consume understorey and midstorey
418 strata but not the canopy will substantially modify the conditions experienced by understorey plants
419 in woodland and heath environments, which do not have a continuous canopy, but may have a
420 lesser effect on the understorey conditions in forests (Peterson & Reich 2008). Growing conditions
421 may therefore undergo more change following fire in heath and woodland than in forest
422 environments, leading to stronger associations with fire history variables (*sensu* Barton et al. 2014).
423 Alternatively, it is possible that the weak associations between fire variables and forest species
424 composition occurred because such effects were masked by high levels of spatial turnover in
425 species composition within this vegetation type (variance partitioning showed that much of the
426 explained variation in forest vegetation was shared between spatial and fire variables, Fig. 3).
427 Because spatial and temporal turnover in species composition is often driven by similar processes
428 (Soininen 2010), high levels of spatial turnover in species composition (as we observed here), have
429 the potential to mask relationships between species composition and spatially aggregated processes
430 (e.g. fire) in space-for time studies. Quantifying the level of spatial turnover in species composition

431 should therefore be an important step in studies using a space-for-time approach to study
432 community responses to disturbance.

433 *Conclusions*

434 Studies of fire regimes in dry sclerophyll vegetation are often focused on plant responses to extreme
435 regimes, and rarely compare plant community responses among different vegetation types. This is a
436 problem because the consequences of different management decisions within established tolerable
437 ranges remain poorly understood (Duff et al. 2013). Our findings indicate that fire regimes within
438 tolerable ranges may have quite variable effects among vegetation types due to differences in fire
439 behaviour, and biotic and abiotic conditions, even when these vegetation types are comprised of
440 highly overlapping species pools. Specifically, we found that the association between fire history
441 variables and plant species richness and composition differed among dry sclerophyll heath,
442 woodland and forest vegetation types, which differ in the density of fine fuels, abiotic conditions
443 and the cover of fire-tolerant canopy species. These different associations were underpinned by
444 differences in trait-fire history relationships among vegetation types. Our results suggest that future
445 studies of fire-prone ecosystems should acknowledge the probability of differences in fire responses
446 among vegetation types, even if they are floristically similar, and account for these in study design.
447 Further, the distinct differences in fire response that we found among vegetation types indicate that
448 consideration of different dry sclerophyll vegetation types as separate management units may be
449 needed to effectively conserve plant diversity in these fire-prone ecosystems.

450

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458

459 SUPPORTING INFORMATION

460 Additional Supporting Information may be found in the online version of this article:

461 **Appendix S1.** Descriptions of the vegetation types of Booderee National Park.

462 **Appendix S2.** Description of the fire history of Booderee National Park.

463 **Appendix S3.** Plant species and traits

464 **Appendix S4.** Model selection table for the species richness GLM.

465 **Appendix S5.** Results of BORAL analysis.

466 **Appendix S6.** Ordination plots for the canonical redundancy analysis.

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625

626

627 TABLES

628 **Table 1.** Explanatory variables used in analysis of associations between fire history variables and
 629 plant species richness and composition.

Variable	Code	Description	Range	Type	Source
Vegetation type					
Vegetation type	veg	Broad vegetation type. Classification based on height and cover of tallest strata.	Forest, Woodland, Heath	Factor (3 levels)	Taws (1997)
Fire history variables					
Fire frequency	FF	The number of fires recorded as occurring at a site between 1957 and 2012.	0 to 6 (Fig. S1)	Integer	BNP fire perimeter maps
Time since fire	TSF	Time in years since the most recent fire (as of 1.7.2012). If no fire recorded the maximum of 55 years was used. Natural log transformed.	3.5 to 55 (Fig. S1)	Continuous	BNP fire perimeter maps
Intervals < 7 years	shortl	0= no interval < 7 years 1= one or more intervals < 7 years	0 or 1 (Fig. S1)	Factor (2 levels)	BNP fire perimeter maps
Intervals >30 years	longl	0= no interval >30 years 1= one or more intervals >30 years	0 or 1 (Fig. S1)	Factor (2 levels)	BNP fire perimeter maps
Environmental variables					
Aspect Easting	AspE	Aspect was split into two linear components for inclusion in analysis. Easting component = sine of the prevailing aspect of the site.	-0.99 to 0.99	Continuous	BNP digital elevation model
Aspect Northing	AspN	Aspect was split into two linear components for inclusion in analysis. Easting component = cosine of the prevailing aspect of the site.	-0.99 to 0.99	Continuous	BNP digital elevation model
Elevation	Elev	Height above sea level (m)	3.2 to 127.7	Continuous	BNP digital elevation model
Surface Geology	Geol	Dominant lithology of parent material: Young sands: grey-brown sand over Permian bedrock Old Sands: leached quartz sand veneering feldspathic sand with podzolic soil profiles Clay-sands: Clay, peat and clayey sands Gravel/rocky: quartz gravel and/or quartz-pebbly sandstone	Young sand, Old sand, Clay, Gravel	Factor (4 levels)	Abell (1992)
Spatial Variables					
Site Location	LatLong	Site latitude and longitude		Decimal degrees	Measured with handheld GPS

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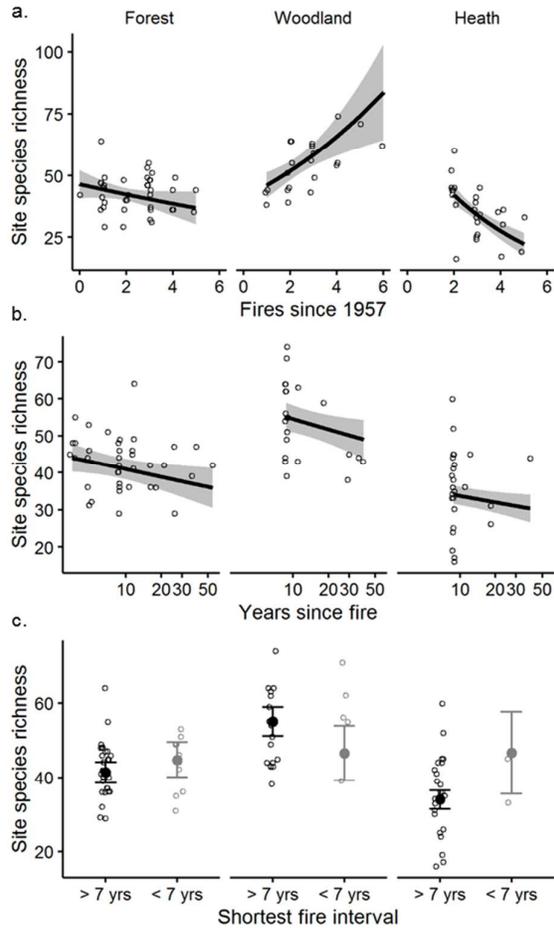
631

632 **Table 2.** Results of the generalised linear model testing the association between fire regime
 633 variables and site species richness (i.e. the total number of species detected within the two 400 m²
 634 quadrats at each site) across the 87 survey sites. Standardised regression coefficients and estimated
 635 95% confidence intervals are shown for the top-ranked model (by AICc, see Appendix S4 for model
 636 selection table). Note that the reference level for vegetation type, and vegetation type × fire
 637 interactions (against which other types are compared) is Forest.

Variable	Coefficient	(95% CI)
Intercept	3.72	(3.65, 3.79)
Time since fire (ln transformed)	-0.043	(-0.082, -0.003)
Fire Frequency (FF)	-0.056	(-0.122, 0.010)
Short interval (Shortl)	0.08	(-0.056, 0.216)
Vegetation type (veg) – woodland	0.282	(0.181, 0.383)
– heath	-0.122	(-0.224, -0.019)
FF x veg – woodland	0.198	(0.105, 0.292)
– heath	-0.197	(-0.316, -0.078)
Shortl x veg – woodland	-0.248	(-0.472, -0.026)
– heath	0.236	(-0.055, 0.518)
Aspect easting	-0.007	(-0.042, 0.028)
Aspect northing	-0.014	(-0.049, 0.022)
Elevation	0.019	(-0.021, 0.058)

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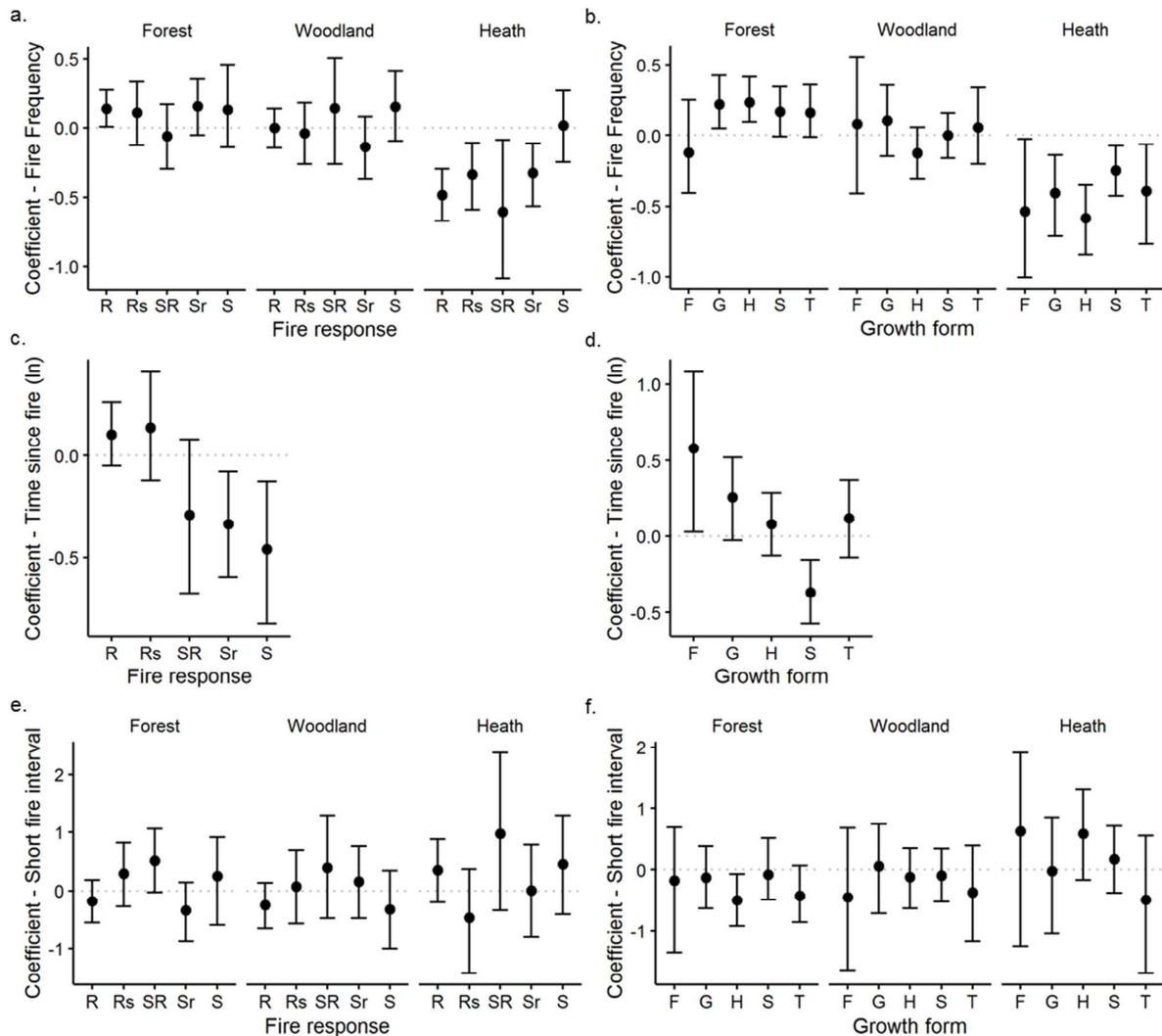
639 FIGURES



640

641 **Figure 1.** Relationship between (a) fire frequency, (b) time since fire, and (c) the length of the
 642 shortest fire interval and site species richness (total number of species detected within the two 400
 643 m² quadrats at each site) within different vegetation types in Booderee National Park. Predicted
 644 values from the top-ranked GLM and 95% confidence intervals, as well as raw values (open circles,
 645 n = 87) are shown. Variables not depicted in the plot that were included in the top-ranked model
 646 (see Table 2, Appendix S4) were held at the median for that vegetation type for predictions (mode
 647 for categorical variables).

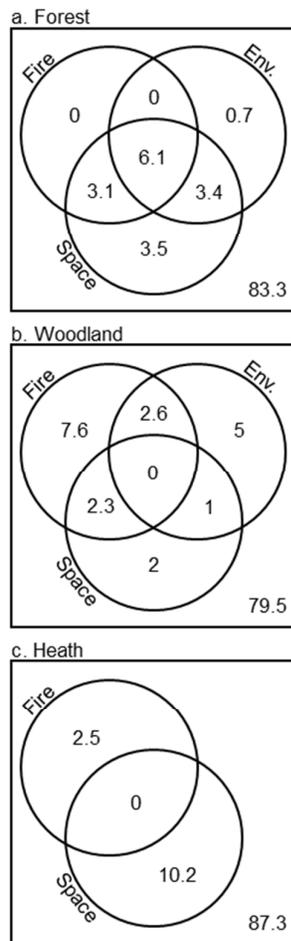
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650 **Figure 2.** Results of BORAL analysis testing association between fire regime and the occurrence of
 651 plant species belonging to different trait groups. Panels a,c and e represent estimated trait group
 652 coefficients (and 95% credible intervals) for species fire response (R = resprouter, Rs = resprouter
 653 with some seeding capacity, SR = both reseeds and resprouts, Sr = seeder with some capacity for
 654 resprouting, S = obligate seeder). Panels b, d and f represent estimated trait group coefficients (and
 655 95% credible intervals) for species growth form (F = ferns, G = graminoids, H = herbs [excluding
 656 graminoids], S = shrubs, T = trees). Where the 95% credible intervals of estimated model
 657 coefficients do not overlap zero, this indicates that there is an association between that trait group
 658 and species' relationships with fire history variables.

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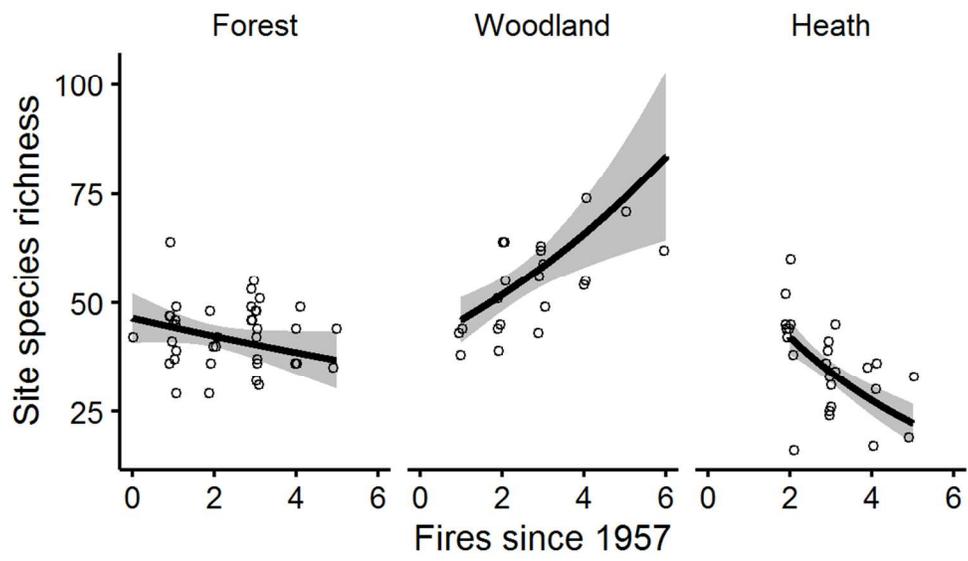


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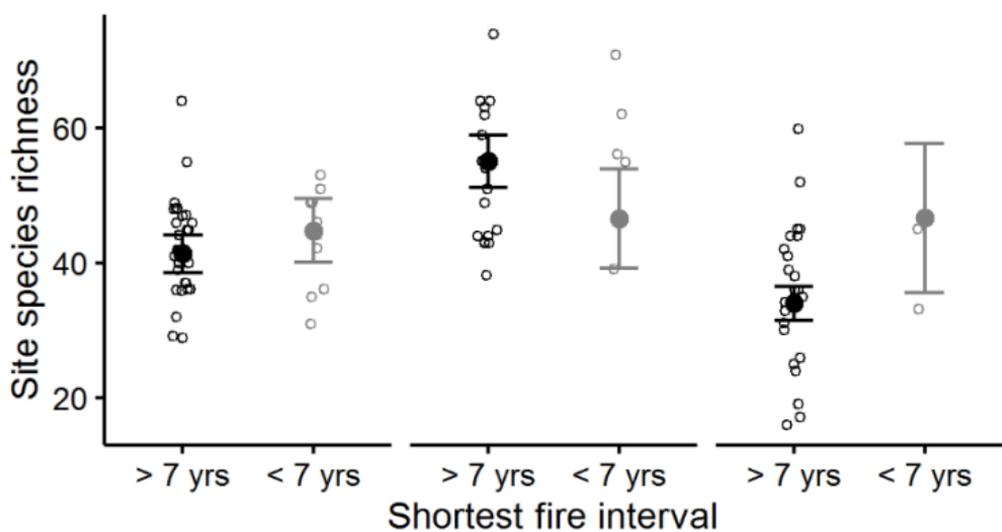
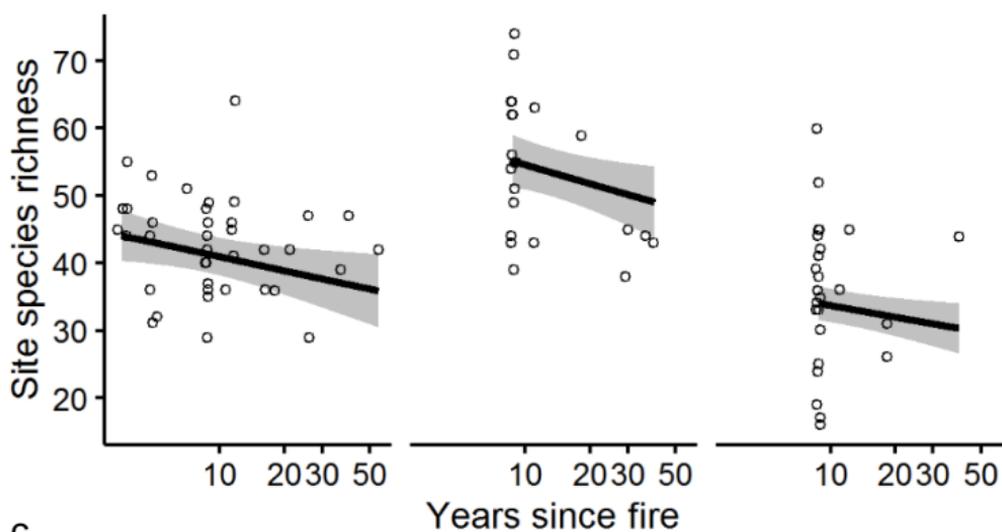
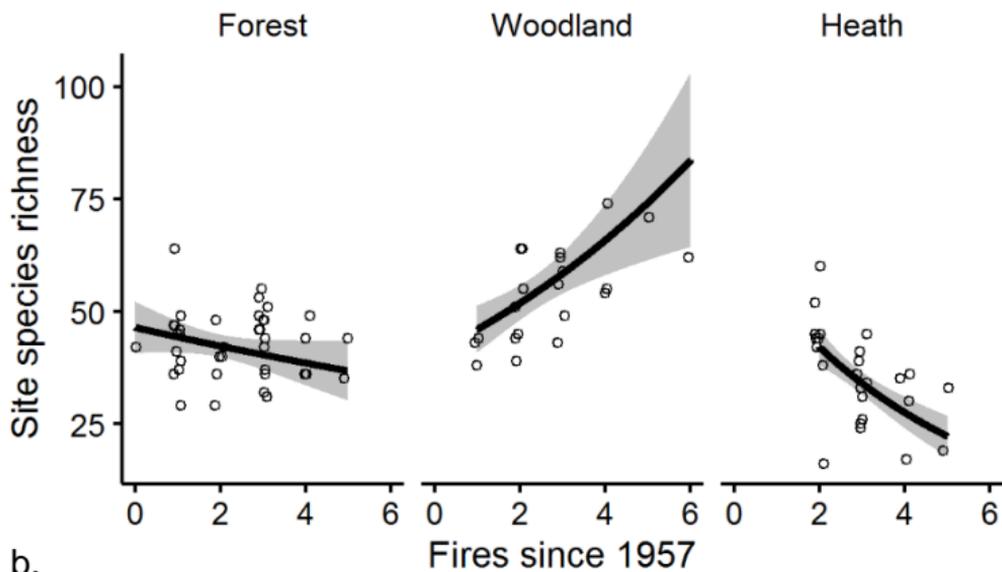
661 **Figure 3.** Results of variance partitioning based on the RDA adjusted R^2 , for (a) forest (n=40), (b)
 662 woodland (n=22) and (c) heath (n=25) vegetation, showing the percentage of variation in species
 663 composition explained by fire history, environmental (Env.), spatial and shared components.

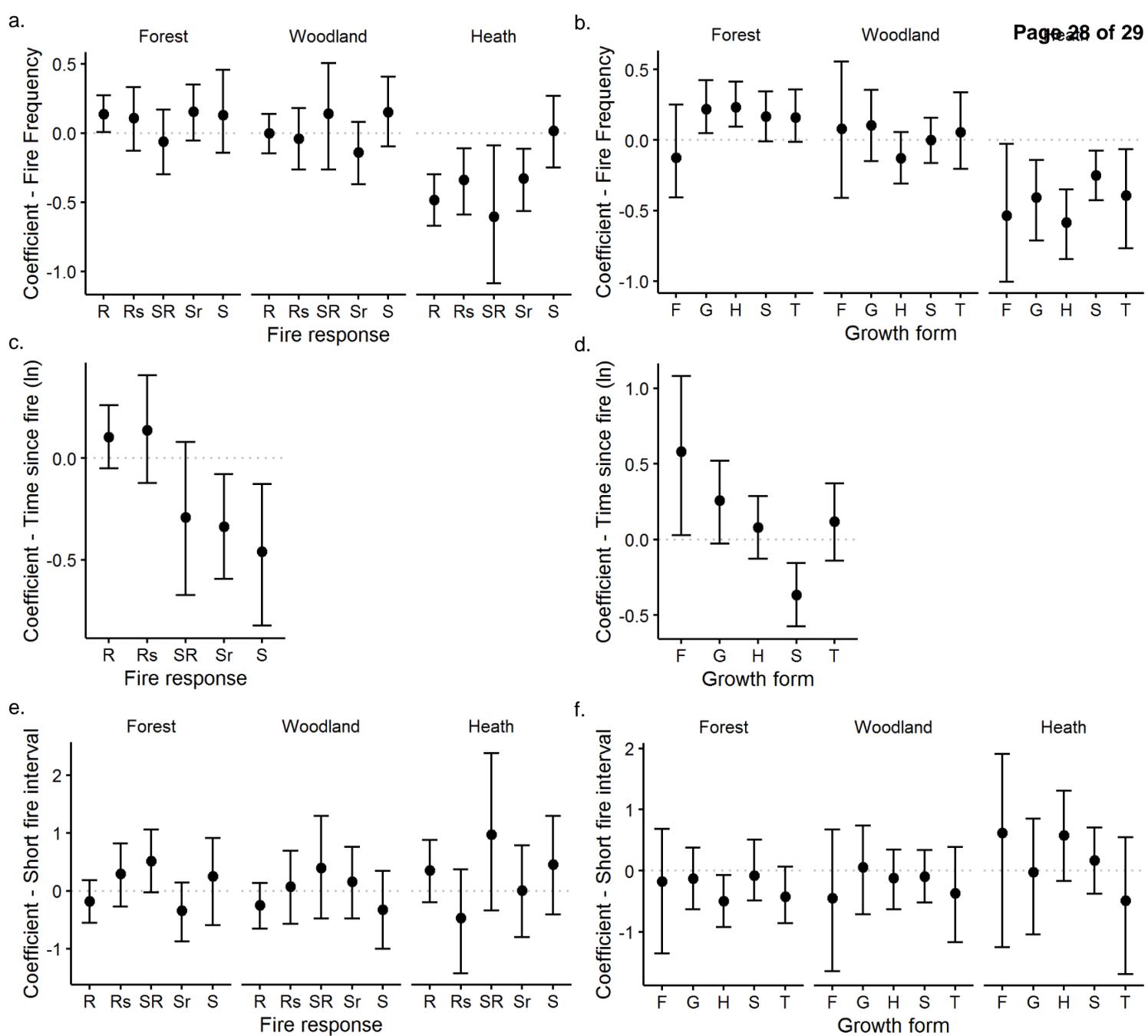
60 word summary

We investigated associations between fire history and plant species richness and composition in three structurally defined vegetation types. Fire frequency was positively associated with species richness in woodland, negatively associated in heath, and unrelated to species richness in forest. These different associations are likely unpinned by variation in fire behaviour, abiotic conditions and biotic interactions among forests, woodlands and heaths.



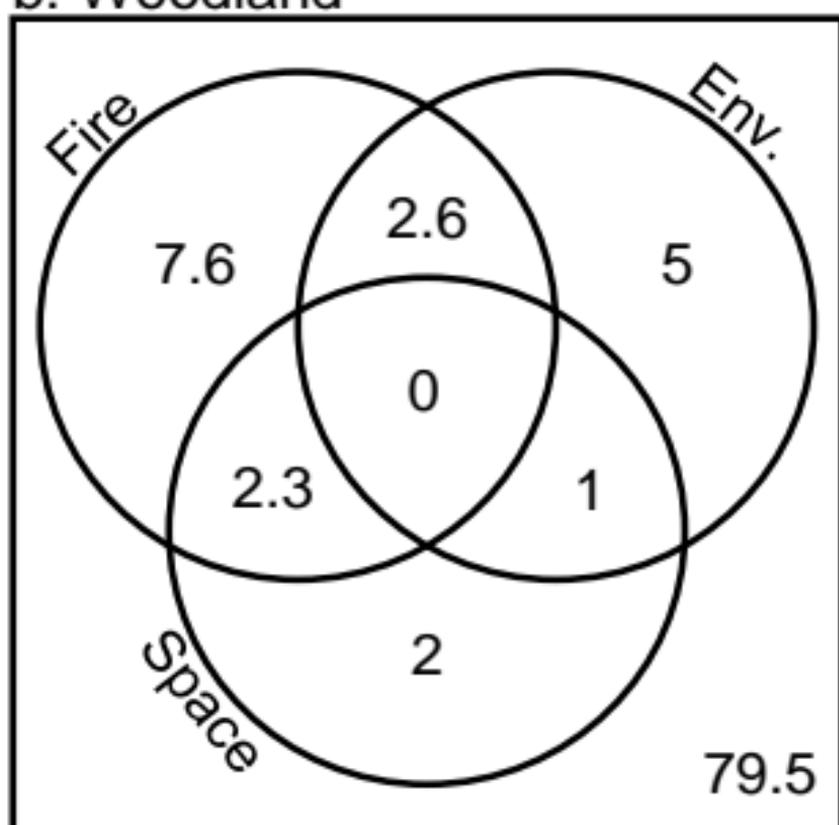
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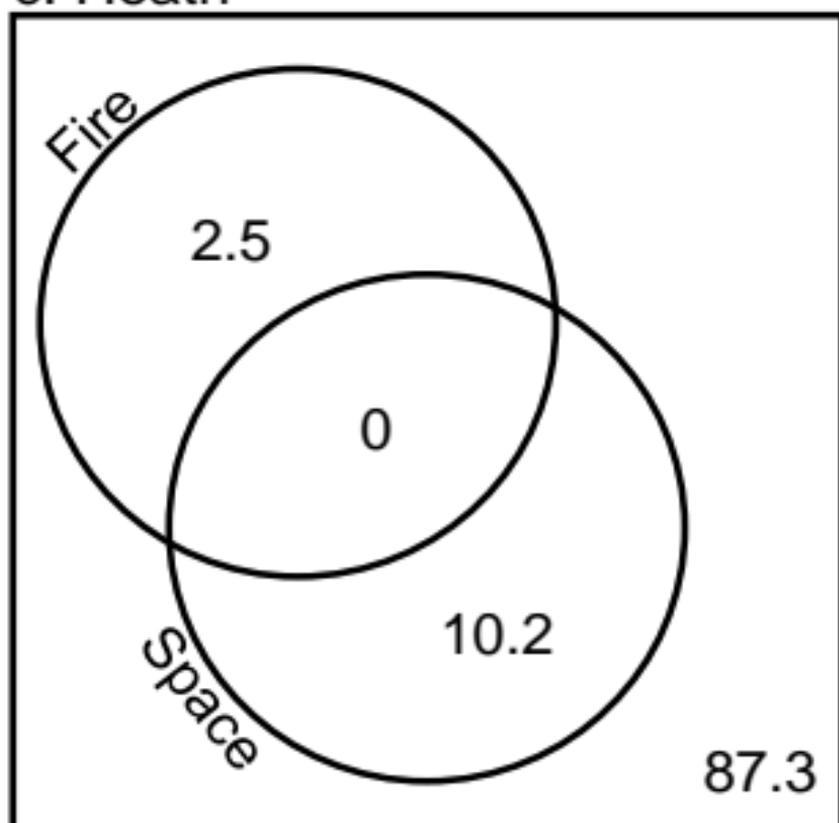




b. Woodland



c. Heath



Appendix S3. Plant species list for the 87 surveyed sites, including species traits, and the number of sites each species was detected in. Singletons have not been listed. Plant trait data were collated from the Australian Fire Ecology Database developed by Ross Bradstock, and available from the TRY plant trait database (Kattge et al. 2011). Codes for fire response traits are R (resprouter), R s (resprouter with some seeding capacity), S R (both reseeds and resprouts), S r (seeder with some capacity for resprouting), S (obligate seeder). The growth form group herb/shrub was re-coded as shrub, and the group shrub/tree was re-coded as tree for traits analysis. For species that were not included in the fire response database, the species was assigned the trait of other species in the same genus (if the trait was consistent within the genus). Species where the trait was unknown were not included in the analysis of fire response trait groups.

Species	Number of sites recorded at				Traits	
	Forest (of 40)	Woodland (of 22)	Heath (of 25)	Total (of 87)	Fire response	Growth form
Total species recorded (excl singletons)	210 (167)	231 (204)	192 (171)	376 (283)		
<i>Pteridium esculentum</i>	40	18	5	63	R	fern
<i>Entolasia marginata</i>	30	17	8	55	R	graminoid
<i>Lomandra longifolia</i>	40	13	1	54	R	herb
<i>Dianella caerulea</i>	33	15	2	50	S R	herb
<i>Imperata cylindrica</i> var. <i>major</i>	38	8	3	49	R	graminoid
<i>Hibbertia scandens</i>	38	5	5	48	R s	herb
<i>Lepidosperma concavum</i>	21	19	6	46	R	graminoid
<i>Gonocarpus teucrioides</i>	29	14	2	45	S r	herb
<i>Monotoca elliptica</i>	37	3	3	43	R s	shrub/tree
<i>Acacia longifolia</i>	24	10	8	42	S r	shrub
<i>Banksia serrata</i>	23	16	2	41	R	shrub/tree
<i>Banksia ericifolia</i>		15	25	40	S	shrub
<i>Leucopogon lanceolatus</i>	24	12	3	39	S	shrub
<i>Microlaena stipoides</i> var. <i>stipoides</i>	35	4		39	R	graminoid
<i>Corymbia gummifera</i>	13	20	5	38	R	tree
<i>Acacia suaveolens</i>	7	20	11	38	S r	shrub
<i>Xanthorrhoea resinifera</i>	3	16	19	38	R	shrub
<i>Entolasia stricta</i>	21	6	9	36	R	graminoid
<i>Glycine clandestina</i>	36			36	R s	herb
<i>Desmodium varians</i>	35	1		36	R	herb
<i>Hibbertia linearis</i>	23	11	1	35	S r	shrub
<i>Elaeocarpus reticulatus</i>	19	13	3	35	R s	tree
<i>Eucalyptus pilularis</i>	29	6		35	R	tree
<i>Billardiera scandens</i>	21	7	6	34	S R	shrub
<i>Persoonia linearis</i>	14	12	6	32	R	shrub/tree
<i>Hakea teretifolia</i>		11	20	31	S r	shrub
<i>Smilax glycyphylla</i>	16	13	1	30	R	herb/shrub
<i>Marsdenia rostrata</i>	28	2		30	R	herb
<i>Schelhammera undulata</i>	27	2		29	R	herb
<i>Themeda australis</i>	24	2	2	28	R	graminoid
<i>Bossiaea ensata</i>	9	17	2	28	R s	shrub
<i>Eustrephus latifolius</i>	27			27	R s	shrub
<i>Empodisma minus</i>		7	20	27	R	herb
<i>Bauera rubioides</i>		11	16	27	R s	shrub
<i>Actinotus minor</i>		14	13	27	S r	herb
<i>Banksia integrifolia</i>	24	1	1	26	R	tree
<i>Xanthosia pilosa</i>	5	15	6	26	S r	shrub
<i>Hardenbergia violacea</i>	16	10		26	R s	herb
<i>Epacris microphylla</i> var. <i>microphylla</i>		8	18	26	S r	shrub
<i>Oplismenus aemulus</i>	25			25	R	graminoid
<i>Darwinia leptantha</i>		8	17	25	S	shrub
<i>Lambertia formosa</i>		16	9	25	R	shrub
<i>Gahnia clarkei</i>	3	9	12	24	R	graminoid
<i>Dichondra repens</i>	24			24	S r	herb
<i>Poa labillardierei</i>	18	6		24	R	graminoid
<i>Leptocarpus tenax</i>		5	19	24	R	herb
<i>Isopogon anemonifolius</i>		13	11	24	R s	shrub
<i>Parsonsia straminea</i>	18	4	1	23	R	herb
<i>Bossiaea heterophylla</i>	5	16	2	23	R s	shrub

<i>Pultenaea rosmarinifolia</i>	3	14	6	23	S	shrub
<i>Dampiera stricta</i>	2	13	8	23	R	shrub
<i>Galium propinquum</i>	22		1	23	R	herb
<i>Acianthus</i> sp.	19	4		23	R	herb
<i>Acacia ulicifolia</i>	10	13		23	S r	shrub
<i>Banksia paludosa</i>		13	10	23	R	shrub
<i>Helichrysum elatum</i>	20		2	22	S	shrub
<i>Persoonia levis</i>		15	7	22	R	shrub
<i>Poranthera microphylla</i>	19	1	1	21	S	herb
<i>Leucopogon ericoides</i>	3	15	3	21	S r	shrub
<i>Lomandra glauca</i>	3	15	3	21	R	herb
<i>Caustis recurvata</i>	1	15	5	21	S r	graminoid
<i>Glycine tabacina</i>	21			21	R	herb
<i>Baumea acuta</i>		11	10	21	R	graminoid
<i>Petrophile sessilis</i>		12	9	21	S r	shrub
<i>Leptospermum polygalifolium</i>	1	10	9	20	R s	shrub
<i>Lagenifera stipitata</i>	19		1	20	R s	herb
<i>Breynia oblongifolia</i>	20			20	R s	shrub
<i>Corybas</i> sp.	19	1		20	R	herb
<i>Cissus hypoglauca</i>	15	2	2	19	R	shrub
<i>Chrysanthemoides monilifera</i>	19			19	S R	shrub
<i>Clematis aristata</i>	19			19	R s	herb
<i>Leptospermum juniperinum</i>		4	15	19	R s	shrub
<i>Eucalyptus botryoides</i>	16	1	1	18	R	tree
<i>Viola hederacea</i>	15	2	1	18	S r	herb
<i>Patersonia sericea</i>	4	11	3	18	R	herb
<i>Selaginella uliginosa</i>	2	12	4	18	R	fern
<i>Stephania japonica</i> var. <i>discolor</i>	18			18	R	herb
<i>Notelaea ovata</i>	16	2		18	R	shrub/tree
<i>Lepyrodia scariosa</i>		11	7	18	R	herb
<i>Lindsaea linearis</i>		14	4	18	R	fern
<i>Leptomeria acida</i>	2	11	4	17	S r	shrub
<i>Styphelia triflora</i>	1	12	4	17	S	shrub
<i>Lomandra filiformis</i> subsp. <i>filiformis</i>	9	8		17	R	herb
<i>Sprengelia incarnata</i>			17	17	S r	shrub
<i>Epacris obtusifolia</i>		1	16	17	S r	shrub
<i>Gleichenia dicarpa</i>		4	13	17	R	fern
<i>Casuarina glauca</i>	13	2	1	16	R	tree
<i>Woollisia pungens</i>	3	12	1	16	S r	shrub
<i>Geranium homeanum</i>	15	1		16	S R	herb
<i>Acacia longissima</i>	14	2		16	S	shrub
<i>Leptospermum trinervium</i>		12	4	16	R	shrub
<i>Synoum glandulosum</i>	13	1	1	15	R	tree
<i>Opercularia aspera</i>	6	8	1	15	S r	shrub
<i>Pittosporum undulatum</i>	14		1	15	S r	shrub/tree
<i>Ricinocarpos pinifolius</i>	3	12		15	R s	shrub
<i>Lepidosperma forsythii</i>		1	14	15	R	graminoid
<i>Viminaria juncea</i>		3	12	15	S	shrub
<i>Dillwynia floribunda</i> var. <i>floribunda</i>		6	9	15	S	shrub
<i>Pterostylis</i> sp.	13		1	14	R	herb
<i>Acacia implexa</i>	14			14	S r	shrub/tree
<i>Desmodium rhytidophyllum</i>	14			14	R s	herb/shrub
<i>Veronica calycina</i>	13	1		14	S R	herb
<i>Melaleuca squarrosa</i>			14	14	R s	shrub/tree
<i>Hypolaena fastigiata</i>		11	3	14	R	herb
<i>Eucalyptus sclerophylla</i>		12	2	14	R	tree
<i>Leptospermum laevigatum</i>	6	3	4	13	S r	shrub/tree
<i>Cassytha glabella</i>	1	6	6	13	S	herb
<i>Epacris pulchella</i>	1	9	3	13	S	shrub
<i>Cyperus gracilis</i>	12	1		13	R	graminoid
<i>Allocasuarina distyla</i>		2	11	13	S r	shrub/tree
<i>Leptospermum epacridoideum</i>		3	10	13	R s	shrub
<i>Hibbertia riparia</i>		4	9	13	R	shrub

Drosera peltata		6	7	13	R s	herb
Austrostipa pubescens	2	8	2	12	R	graminoid
Eurychorda complanata			12	12	R s	herb
Lepidosperma filiforme		1	11	12	R s	graminoid
Mirbelia rubiifolia		2	10	12	S r	shrub
Hakea dactyloides		8	4	12	S	shrub
Baumea juncea	5	3	3	11	R	graminoid
Petrophile pulchella	1	6	4	11	S r	shrub
Ficinia nodosa	11			11	R	graminoid
Correa reflexa var. reflexa	6	5		11	R s	shrub/tree
Pultenaea daphnoides		7	4	11	S	shrub
Boronia pinnata		8	3	11	S R	shrub
Pimelea linifolia		8	3	11	S R	shrub
Hibbertia empetrifolia	3	6	1	10	R	shrub
Asteraceae sp.	10			10	Unknown	herb
Boronia barkeriana			10	10	R	shrub
Dillwynia retorta		3	7	10	S	shrub
Persoonia mollis subsp. caleyi		8	2	10	S	shrub
Echinopogon ovatus	9			9	S R	graminoid
Senecio minimus	9			9	S r	herb
Hydrocotyle bonariensis	9			9	R	herb
Pratia purpurascens	8	1		9	R	herb
Hibbertia dentata	7	2		9	R	herb
Acacia terminalis	5	4		9	S r	shrub/tree
Actinotus helianthi	3	6		9	S	herb/shrub
Callistemon citrinus			9	9	R	shrub
Drosera spathulata		1	8	9	R s	herb
Burchardia umbellata		1	8	9	R	herb
Gymnoschoenus sphaerocephalus		1	8	9	R	graminoid
Mitrasacme polymorpha		4	5	9	S r	herb
Cryptostylis erecta		4	5	9	R	herb
Solanum stelligerum	8			8	S	herb
Acianthus fornicatus	7	1		8	R	herb
Marsdenia suaveolens	6	2		8	R	herb
Dillwynia glaberrima	1	7		8	S R	shrub
Ceratopetalum gummiferum	1	7		8	R	shrub
Leptospermum squarrosum			8	8	S r	shrub
Kunzea capitata		2	6	8	R s	shrub
Xanthosia tridentata		3	5	8	S r	herb/shrub
Comesperma volubile	5	1	1	7	S R	herb
Platysace lanceolata	4	2	1	7	R s	shrub
Leucopogon juniperinus	3	2	2	7	S r	shrub
Scaevola ramosissima	2	3	2	7	R	herb
Caustis flexuosa	1	3	3	7	R s	graminoid
Hydrocotyle peduncularis	6		1	7	R	herb
Oxalis sp.	7			7	R s	herb
Notelaea longifolia forma longifolia	5	2		7	R	shrub/tree
Lomandra multiflora subsp. multiflora	2	5		7	R	herb
Eucalyptus sieberi	1	6		7	R	tree
Sphaerolobium vimineum		1	6	7	S r	shrub
Juncus usitatus		1	6	7	R	graminoid
Melaleuca thymifolia		1	6	7	R	shrub
Lomandra obliqua		5	2	7	R s	herb
Telopea speciosissima		5	2	7	R	shrub
Caustis pentandra		6	1	7	R s	graminoid
Cassytha pubescens	2	3	1	6	S	herb
Monotoca scoparia	1	4	1	6	R s	shrub
Syncarpia glomulifera	5		1	6	R	tree
Oxalis perennans	6			6	R s	herb
Desmodium brachypodum	6			6	R	herb/shrub
Oplismenus imbecillis	6			6	R	graminoid
Lomandra gracilis	4	2		6	R	herb
Leucopogon esquamatus			6	6	S	shrub

Leptospermum rotundifolium			6	6	R s	shrub
Leptospermum continentale		1	5	6	R s	shrub
Chordifex fastigiatus		1	5	6	R	herb
Comesperma ericinum		2	4	6	S r	herb
Eucalyptus burgessiana		2	4	6	R	tree
Conospermum ericifolium		4	2	6	S	shrub
Hibbertia diffusa		6		6	S R	shrub
Tetratheca thymifolia		6		6	S r	shrub
Hovea linearis		6		6	R s	shrub
Lycopodium deuterodensum	1	3	1	5	R	fern
Commelina cyanea	5			5	S R	herb
Solanum pungetium	5			5	S	herb
Zoysia macrantha	5			5	Unknown	graminoid
Astroloma pinifolium	3	2		5	S	shrub
Gompholobium latifolium	1	4		5	S r	shrub
Drosera binata		1	4	5	R	herb
Xyris gracilis ssp. gracilis		1	4	5	R	herb
Allocasuarina littoralis		3	2	5	R s	tree
Lomandra cylindrica		3	2	5	R	herb
Hakea sericea		5		5	S	shrub
Banksia spinulosa		5		5	R	shrub
Galium gaudichaudii	4			4	S r	herb
Kennedia rubicunda	4			4	S r	herb
Solanum nigrum	4			4	S	herb
Astroloma humifusum	4			4	R	shrub
Leucopogon parviflorus	4			4	R	shrub/tree
Livistona australis	4			4	R	tree
Pterostylis nutans	4			4	R	herb
Zieria smithii	3	1		4	S r	shrub
Patersonia glabrata	3	1		4	R	herb
Gompholobium grandiflorum	1	3		4	R s	shrub
Baeckea linifolia			4	4	R	shrub
Baumea rubiginosa			4	4	R	graminoid
Lycopodium laterale			4	4	R	fern
Dodonaea triquetra		2	2	4	S	shrub
Darwinia camptostylis		2	2	4	R	shrub
Lepidosperma urophorum		2	2	4	R	graminoid
Hybanthus vernonii subsp. scaber		3	1	4	S R	herb
Tetraria capillaris		3	1	4	R	graminoid
Eriostemon buxifolius subsp. buxifolius		3	1	4	Unknown	shrub
Grevillea macleayana		4		4	S	shrub
Pultenaea villifera		4		4	S	shrub
Lomatia ilicifolia		4		4	R	shrub
Baloskion tetraphyllum	1	1	1	3	S	herb
Solanum prinophyllum	3			3	S	herb
Trema aspera	3			3	S	tree
Sarcopetalum harveyanum	3			3	R	herb/shrub
Oxalis articulata	3			3	R s	herb
Phyllanthus hirtellus	2	1		3	R s	shrub
Caladenia carnea	2	1		3	R	herb
Gastrodia sesamoides	2	1		3	R	herb
Xanthorrhoea australis	2	1		3	R	shrub
Hibbertia aspera	1	2		3	S R	shrub
Platylobium formosum	1	2		3	R s	shrub
Caladenia catenata	1	2		3	R	herb
Dampiera purpurea	1	2		3	R	shrub
Goodenia stelligera			3	3	R s	herb
Thysanotus juncifolius			3	3	R s	herb
Gahnia sieberiana			3	3	R	graminoid
Baumea nuda			3	3	R	graminoid
Melaleuca sieberi			3	3	R	shrub/tree
Xyris operculata			3	3	R	herb
Hibbertia fasciculata		1	2	3	S r	shrub

Schoenus lepidosperma subsp. pachylepis		1	2	3	R	graminoid
Thelionema umbellatum		1	2	3	R	herb
Acacia elongata		2	1	3	S r	tree
Isopogon anethifolius		2	1	3	R s	shrub
Lasiopetalum ferrugineum var. ferrugineum		2	1	3	R s	shrub
Styphelia tubiflora		3		3	S r	shrub
Goodenia heterophylla subsp. eglandulosa		3		3	R	herb
Restio tetraphyllus subsp. meostachyus	1		1	2	S R	herb
Epacris sp.	1		1	2	S	shrub
Poa annua	1		1	2	S	graminoid
Melaleuca linariifolia	1		1	2	R s	tree
Calochilus paludosus	1		1	2	R	herb
Lepidosperma longitudinale	1		1	2	R	graminoid
Hibbertia obtusifolia	2			2	S R	shrub
Opercularia diphylla	2			2	S r	shrub
Pandorea pandorana	2			2	S R	herb
Wahlenbergia communis	2			2	S r	herb
Anagallis arvensis	2			2	S	herb
Cassinia aculeata	2			2	S	shrub
Conyza bonariensis	2			2	S	herb
Acmena smithii	2			2	R	shrub/tree
Cynodon dactylon	2			2	R	graminoid
Glochidion ferdinandi	2			2	R	shrub/tree
Smilax australis	2			2	R	herb/shrub
Austrostipa mollis	1	1		2	R s	graminoid
Eragrostis brownii	1	1		2	R	graminoid
Dillwynia sericea			2	2	S r	shrub
Schoenus apogon			2	2	R s	graminoid
Xanthorrhoea minor subsp. lutea			2	2	R	shrub
Hybanthus vernonii subsp. vernonii		1	1	2	S R	herb
Cassytha sp.		1	1	2	S	herb
Leucopogon microphyllus		1	1	2	S	shrub
Baeckea imbricata		1	1	2	R	shrub
Lepyrodia muelleri		1	1	2	R	herb
Opercularia hispida		2		2	S r	shrub
Phebalium squamulosum		2		2	S R	shrub
Philothea buxifolius		2		2	S r	shrub
Pultenaea blakelyi		2		2	S	shrub
Pultenaea villosa		2		2	S	shrub
Dendrobium speciosum		2		2	R	herb
Lepidosperma laterale		2		2	R	graminoid
Schizaea dichotoma		2		2	R	fern
Schoenus ericetorum		2		2	R	graminoid
Baeckea virgata		2		2	Unknown	shrub
Pultenaea paleacea		2		2	S	shrub

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