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46 *Combining optimisation and simulation modelling to measure the cumulative impacts of prescribed fire*
47 *and wildfire on vegetation species diversity*

48

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68 Prescribed fire

69 Simulation modelling

70 Species diversity

71 Wildfire

72

73

74 **Abstract**

75 1. Growth-stage optimisation (GSO) offers a new approach to biodiversity conservation in fire-prone
76 regions by estimating the optimal distribution of vegetation growth stages that maximise a species
77 diversity index. This optimal growth-stage structure provides managers an operational goal explicitly
78 linked to a positive conservation outcome but does not define the fire regime needed to achieve it.

79 2. We paired GSO with LANDIS II, a landscape succession and disturbance simulation model, to (i)
80 estimate the optimal growth-stage structure that maximised vegetation diversity in a south-east Australian
81 heathy woodland, (ii) define the fire regime needed to achieve it, and (iii) determine the cumulative effects
82 of different fire-regime scenarios on vegetation diversity over a 60-year period. Scenarios included 0, 2, 5
83 and 10% of the landscape burnt per year by prescribed fire only, or in combination with three alternative
84 wildfire regimes. Furthermore, we investigated the differences in the optimal growth-stage structure
85 relating to above-ground, soil seedbank, and total (above and soil seedbank) diversity data sets.

86 3. The growth-stage structure that maximised total vegetation diversity comprised approximately even
87 proportions of all stages. In contrast, separately analysed above-ground and soil seedbank data resulted in
88 a greater proportion of younger and older growth-stages, respectively.

89 4. Scenarios including 5% prescribed burning per year (with and without wildfire) resulted in diversity
90 values within 1.5% of the theoretical maximum value. Scenarios including 2% and 10% prescribed fire
91 resulted in diversity values 8 - 12% and 1.5 - 5% lower than the maximum, respectively. Scenarios without
92 prescribed fire caused diversity to fall 30 - 70%. Trends across the 60 years showed that wildfire depressed
93 diversity and subsequent prescribed fire drove recovery within 15 years. The largest threat to vegetation
94 diversity was the absence of fire.

95 5. *Synthesis and applications.* Combining growth-stage optimisation and simulation modelling is a
96 powerful way of defining a conservation-based fire management goal and identifying the prescribed fire
97 regime needed to achieve it. We demonstrated that vegetation diversity in heathy woodland was increased
98 by prescribed fire, with and without the cumulative effect of wildfire, and declined sharply when fire was

99 excluded. Our method provides a flexible platform for developing long-term fire management strategies
100 that seek to balance human safety and biodiversity conservation. Including both plants and animals in GSO
101 will help land managers meet the needs of multiple taxa.

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107 **Introduction**

108 Prescribed fire is an ecosystem management tool, predominantly used to reduce wildfire risk to human
109 life and assets in fire-prone regions (Moritz *et al.* 2014), but also to manage habitats for hunting in
110 regions of low wildfire risk (Harper *et al.* 2018). In addition to these traditional functions, prescribed fire
111 is increasingly used for broad-scale biodiversity conservation (Driscoll *et al.* 2010). Species often show
112 preferences for the habitat attributes of different vegetation growth stages (categorical groupings of time-
113 since-fire (TSF)) (Haslem *et al.* 2012), and, as a result, species diversity can be positively correlated with
114 growth-stage diversity (Fuhlendorf *et al.* 2006; Cohn *et al.* 2015). Consequently, land managers often
115 apply fire to increase growth-stage diversity, assuming this will have positive conservation outcomes
116 (Martin & Sapsis 1992; Parr & Andersen 2006). However, the link between growth-stage structure and
117 species diversity can be difficult to detect due to the influence of other fire-regime components and
118 external environmental factors (Driscoll *et al.* 2010), making it unclear how best to apply fire to benefit
119 multiple species.

120

121 Growth-stage optimisation (GSO) is a new method for incorporating biodiversity conservation into the
122 fire-management-planning-process. Numerical optimisation is applied to species' abundance estimates in
123 several pre-defined growth stages to determine the structure (proportions of each stage) that maximises
124 species diversity (Di Stefano *et al.* 2013). Although GSO provides a management goal explicitly linked to
125 a conservation outcome it does not define the fire regime needed to achieve this goal. To address this,
126 stochastic dynamic programming (Richards, Possingham & Tizard 1999) has been paired with GSO to
127 identify fire management actions consistent with the optimal growth-stage structure (Kelly *et al.* 2015).
128 Despite its utility, this method is not spatially explicit and therefore does not consider the complex spatial
129 fire and biodiversity relationships. Further, it does not track the temporal and spatial dynamics of growth-
130 stages and species diversity in response to alternative fire regimes.

131

132 Landscape-scale disturbance and succession-simulation models (Scheller *et al.* 2007; Gustafson &
133 Sturtevant 2013) offer an alternative approach to defining the fire regime needed to achieve a positive
134 biodiversity outcome. They can simulate fire-driven changes in growth-stage structure and vegetation
135 diversity across a landscape as they are not constrained by linear or non-linear spatial relationships.
136 Despite this capability, disturbance and succession simulation models have not yet been used to
137 determine the fire regime needed to achieve an optimal growth-stage structure or track temporal changes
138 in species diversity from alternate fire regimes.

139

140 Modelling conservation outcomes associated with prescribed fire regimes alone is likely to be inadequate,
141 as both prescribed fire and wildfire occur in managed landscapes. It is difficult, however, to quantify or
142 predict vegetation responses to the cumulative effects of deterministic prescribed fire and stochastic
143 wildfire (Bradstock, Williams & Gill 2002), thus modelling conservation outcomes from fire
144 management rarely accounts for both (Nitschke 2008). Landscape-scale disturbance and succession
145 simulation modelling provides an ideal platform for predicting the ecological consequences of alternative
146 management strategies, such as prescribed fire, while factoring in wildfire (Nitschke *et al.* 2017). By
147 integrating optimisation and simulation modelling managers can develop and compare management
148 scenarios to determine the strategy most likely to achieve conservation objectives.

149

150 In south-east Australia, GSO is incorporated into fire-management policy because it has a strong
151 theoretical basis, input data can be derived using a range of standard survey methods, and it
152 accommodates the needs of multiple species (McCarthy *et al.* 2014). To date, the application of GSO to
153 vegetation has focussed on above-ground diversity (Di Stefano *et al.* 2013) without including soil
154 seedbank diversity. In quasi-Mediterranean ecosystems, above-ground vegetation diversity may not be
155 representative of total vegetation diversity (Chick *et al.* 2018a); negative relationships between above-
156 ground diversity and TSF have been reported (Morrison & Cary 1995; Freestone, Wills & Read 2015),
157 while variable (Wills & Read 2007) or weak positive relationships (Chick *et al.* 2016) have been found
158 for soil seedbank diversity. This contrast highlights the importance of considering the soil seedbank
159 component when developing fire management conservation goals.

160

161 We paired GSO with a landscape-scale succession and disturbance simulation model to: 1. establish an
162 optimal growth-stage structure that maximises vegetation diversity (above-ground and soil seedbank) in a
163 heathy woodland in south-east Australia, 2. define the fire regime needed to achieve this optimal growth-
164 stage structure, and 3. determine the cumulative effects of alternate prescribed and wildfire regimes on
165 vegetation diversity over a 60-year period.

166

167 **Materials and Methods**

168 **Study area**

169 The study area is within the heathy woodlands of the Otway Ranges region 130 km south-west of
170 Melbourne, in Victoria, southeast Australia (Fig. 1) where the climate is a quasi-Mediterranean-type
171 (Dodson 2001), with warm, dry summers, and mild, wet winters. The vegetation is dry sclerophyll and
172 dominated by a short overstorey of brown stringybark *Eucalyptus baxteri* (Benth.) Maiden & Blakely ex
173 J.M.Black and a diverse heathy understorey comprising shrubs from the families: Fabaceae, Ericaceae,
174 Myrtaceae, Proteaceae, Thymelaeaceae, Xanthorrhoeaceae and Dilleniaceae. Three discrete heathy-
175 woodland distributions exist around the towns of Anglesea, Forrest, and Carlisle River (Fig. 1a).

176

177 Both wildfires and prescribed fires occur in the study area. Prescribed fires are generally smaller, patchier
178 and less intense than wildfires (McArthur 1966; Tolhurst 1999; Burrows & McCaw 2013). Unlike
179 wildfires, prescribed fires infrequently consume tree canopies and often leave patches of unburnt
180 vegetation in riparian areas (Hradsky *et al.* 2017, Fig. 2). In heathy woodland, wildfires occur every 20 to
181 100 years, typically in spring or summer (Murphy *et al.* 2013). The last major wildfires occurred in the
182 Anglesea region in 1983 and the Forrest and Carlisle River regions in 1939. Since 1983, prescribed fires
183 (individual burn blocks range in size from ~100 to ~1000 ha) have been applied in all three study regions
184 to satisfy fuel reduction and ecological goals (Department of Primary Industries 2013). This has resulted
185 in a heterogeneous fire history and a diversity of growth stages.

186

187 **Sampling design**

188 We used fire-history maps to stratify the landscape into four growth stages (Cheal 2010): 0-3 years since
189 fire (juvenile); 4–10 years (young); 11–34 years (mature); and >34 years (old). We established 71 sites
190 across the range of growth stages within each region (Table 1). Criteria for site selection were: (1) a
191 heathy-woodland patch ≥ 1 ha; and, (2) a slope of at least 5% with a ridge >50 m from the road and that
192 ran into a gully. To validate the mapped growth stage of each site, we aged at least 30 individual *Banksia*
193 *marginata* Cav. shrubs using growth whorls (Jenkins, Morrison & Auld 2005). Ten individuals were
194 sampled within a 20-m radius of the three sampling points established along transects (discussed below).

195

196 **Vegetation sampling and seed germination**

197 We established sampling transects extending between ~ 80 and 160 metres from ridge to lower-
198 slope/gully. At each site, we counted all above-ground shrub, sub-shrub, and herbaceous species in six 3
199 \times 3 m quadrats, two each at ridge, mid-slope (midway between ridge and gully) and lower-slope/gully

200 locations. At each topographic location, the two quadrats were established 10 metres apart along the
201 transect (Fig. 1b).

202

203 The soil seedbank was sampled by extracting soil cores (6 cm diameter, 5 cm depth) systematically at 13
204 positions within each quadrat (Fig. 1b), and then pooling samples within topographic locations, resulting
205 in three composite samples per site. Cores sampled the top 5 cm soil layer, as this is where most soil-
206 stored seeds are found (Carroll & Ashton 1965; Pywell, Putwain & Webb 1997; Ma, Zhou & Du 2011).
207 Surface litter was included in the soil core as it can be a source of fresh seed (Enright & Kintrup 2001).
208 The sampling intensity and volume of soil per site (78 cores; surface area: 0.220 m²; volume: 0.011 m³)
209 was consistent with similar studies (Enright & Kintrup 2001; Wills & Read 2007). Above-ground
210 sampling and core collection occurred in the austral autumn of 2014/15 (March-May) to capture seeds
211 released in spring and summer (Enright & Kintrup 2001). Soil seedbank germination and species
212 identification followed the methods of Chick *et al.* (2016).

213

214 **Growth-stage optimisation**

215 We calculated the growth-stage structure that maximised vegetation species diversity using the method
216 described in Di Stefano *et al.* (2013). We used the geometric mean of species' relative abundance (G) as a
217 diversity index because it represents abundance change more effectively than other diversity indices
218 (Buckland *et al.* 2011). Data for each species were pooled across each transect by summing abundance
219 values from ridge, mid-slope, and gully positions. This was done separately for above-ground and soil
220 seedbank data, and then for above-ground and soil seedbank data combined, resulting in three data
221 matrices. G cannot be calculated if abundance is zero (i.e. a species did not occur in a growth-stage)
222 (Buckland *et al.* 2011), so we replaced all zeros with 0.001.

223

224 Numerical optimisation in conjunction with a bootstrapping procedure was used to determine the
225 proportions of each growth-stage that maximised species diversity while representing uncertainty in the
226 raw data (Sitters *et al.* 2018). Abundance values from each species within each growth-stage were
227 resampled with replacement 1000 times. Each iteration was then passed to an optimisation function that
228 determined the set of growth-stage proportions that maximised species diversity. We then derived the
229 mean proportion and 95% lower and upper confidence limits associated with each growth stage from the
230 resulting distributions of values. We applied this procedure to the above-ground, soil seedbank, and
231 combined above-ground and soil seedbank data separately. For the combined analysis, each species'
232 above-ground and soil seedbank data were included as independent observations to ensure the optimal
233 growth structure reflected their requirements at different life-cycle stages. Optimisation was conducted in
234 the R statistical environment (R Core Team 2015) using the NLOPT_LD_MMA algorithm (Svanberg

235 2002) in the `nloptr` package (Johnson 2015), and subject to the constraint that the growth-stage
236 proportions sum to 1. Resampling was undertaken using the base package and `plyr` (Wickham 2011).

237

238 We decomposed the multi-species optimisation results to examine how individual species' abundances
239 differed between the present (2014/15) and optimal growth-stage structures. The value of G used in
240 growth-stage optimisation is derived from a species-specific abundance index that depends on growth-
241 stage proportions (Di Stefano *et al.* 2013; Swan *et al.* 2018). For each species, two index values were
242 calculated; one was associated with the optimal growth-stage structure, and the other was associated with
243 the present growth-stage structure. We used the two index values to calculate the proportional change in
244 abundance assuming a shift from the present structure to the optimal structure and used the estimated
245 change in abundance to predict the response of individual species to the optimal landscape.

246 To assess the sensitivity of the maximum species diversity value to sub-optimal growth-stage structures
247 we compared the optimal structure generated at each iteration of the resampling process to a randomly
248 generated alternative structure. The difference between the optimal and alternative structures was
249 calculated as $\sum |o_i - a_i|/n$, where o_i represents the proportion of the optimal structure in growth-stage i ,
250 a_i represents the proportion of the alternative structure in the same growth stage, and n is the number of
251 growth stages sampled. The resulting index reflects the mean absolute difference between the optimal and
252 alternative proportions. Next, we used a regression model to determine the strength and magnitude of the
253 relationship between index values (x-axis) and the proportional reduction in species diversity (y-axis).
254 Increasingly rapid and predictable declines in y with x represent increasing sensitivity of modelled species
255 diversity values to departures from the optimal growth-stage structure. Regressions were run in R using
256 the package 'lm' (Mazerolle 2011).

257

258 **Simulation model scenarios**

259 LANDIS-II is a simulation model with flexible temporal and spatial resolution that is designed to
260 simulate vegetation community succession with the incorporation of disturbances such as fire (Scheller *et al.*
261 *et al.* 2007). We used LANDIS-II to simulate 60 years of alternative fire regime components (type
262 (prescribed or wildfire), size, and frequency) and link their cumulative effects to species diversity using
263 growth-stage optimisation. This simulation period was chosen as it reflects current management planning
264 in this region (~40 - 50 years) (Department of Environment and Primary Industries 2014). We simulated
265 prescribed burning of 0, 2, 5, and 10% of the study area per annum without wildfire, with a single
266 wildfire at either year 5 or 25, and with two wildfires at years 20 and 30, resulting in $n = 16$ scenarios.
267 The 2 and 5% scenarios represent the range of plausible operational practice, while the 0 and 10%
268 scenarios represent ecological and management extremes. A ten-year inter-fire interval was chosen for
269 the double wildfire scenario as it is shorter than the recommended tolerable fire interval for heathy

270 woodland (12 - 45 years; Cheal 2010), representing a potentially ecologically stressful scenario with
271 repeated impact across the extent of the landscape, rather than the smaller scale impacts of prescribed
272 fire. Anglesea is separated from Forest and Carlisle River by 80 km (Fig. 1a), so we split the study area
273 into two regions and ran ten replicates of each scenario separately for each region, combining the results
274 for subsequent analyses. The methods used to parameterise LANDIS-II are described in Appendix S1 in
275 the supporting information.

276

277 **Simulated scenario analyses**

278 We tracked species diversity through each scenario and represented change as a proportional reduction in
279 the geometric mean relative to the optimal value. At each of the 60 time-steps a growth-stage structure
280 was calculated from a LANDIS-II time-since-fire raster output, while mean species diversity values and
281 their 95% upper and lower confidence limits were generated using the bootstrapping procedure described
282 above. Analyses were undertaken using the combined (above-ground and soil seedbank) vegetation data
283 and undertaken in R v.3.1.1 (R Core Team 2015) using the packages raster (Hijmans & van Etten 2012),
284 car (Fox & Weisberg 2011) and plyr (Wickham 2011). Graphs were produced using the package ggplot2
285 (Wickham 2016).

286

287 **Results**

288 We identified 102 native plant species in total; no weed species were present. All 102 species were
289 detected above-ground (mean number per site \pm SE = 21.5 ± 0.6 , range = 11-34), and 92 species were
290 represented in the soil seedbank (16.1 ± 0.6 , 6-27). *Banksia* whorl counts were significantly correlated
291 with GIS fire history mapping ($r = 0.85$, $P < 0.001$), indicating this method was a useful validation tool.
292 However, this correlation was stronger within the range of 2–20 years, after which the *Banksia* whorls
293 under estimated mapped TSF.

294

295 **Growth-stage optimisation**

296 The above-ground optimal growth-stage structure favoured the two younger stages, with minimal
297 coverage of the oldest growth stage (15%) (Fig. 2a). Conversely, when GSO was applied to the soil
298 seedbank, coverage of the oldest growth-stage was around 50%, while coverage of the youngest growth-
299 stage was close to zero (Fig. 2b). The optimal growth-stage structure associated with the combined
300 species pool comprised approximately even coverage of younger and older growth stages (Fig. 2c).

301

302 A shift from the present to the optimal growth-stage structure resulted in pronounced abundance changes
303 above-ground. More shrub (e.g. four *Acacia* species and a *Dillwynia* species), sub-shrub (e.g. an *Epacris*,
304 *Pimelia* and *Isopogon* species) and herbaceous species (e.g. a *Viola* and *Xanthosia* species) increased
305 their abundance by $\geq 10\%$ than decreased it by $\geq 10\%$. In the soil seedbank, a shift to the optimal growth-
306 stage structure favoured most shrub, sub-shrub, and herbaceous species (See Appendix S2 in Supporting
307 Information).

308

309 The species diversity index was moderately sensitive to departures from the optimal growth-stage
310 structure. Diversity declined slowly as the departure index increased to around 0.1. The r^2 value was high
311 (0.93), indicating a consistent and predictable trend. A departure from the optimal growth-stage structure
312 of 0.2 resulted in a 20% decline in species diversity, suggesting large departures from the optimal
313 structure may result in significant declines in species diversity (Fig. 3).

314 **Simulation modelling**

315 Applying prescribed fire to 5% of the study area annually, with or without wildfire, resulted in fire
316 regimes that generated species diversity values within 1.5% of the theoretical maximum after 60 years
317 (Fig. 4 e, i, m, q). Other prescribed fire scenarios generated a variety of growth-stage structures, but in all
318 cases vegetation diversity was, on average, within 12% of the theoretical maximum. Scenarios that
319 included 2% prescribed burning (Fig. 4 d, h, l, p) generated growth-stage structures and species diversity
320 values that were further from the optimal state compared to scenarios that included 10% prescribed
321 burning (Fig. 4 f, j, n, r).

322

323 Trends in species diversity under the prescribed fire scenarios (2, 5 and 10% burnt/year) were similar
324 (within one standard error) over the 60-year period (Fig. 5 a); species diversity increased sharply within
325 the first 12 years and remained close to optimal in the absence of wildfire. Wildfire decreased species
326 diversity by 50%, after which 15 years of prescribed fire returned diversity to pre-wildfire levels (Fig 5 b,
327 c). The no prescribed fire scenario resulted in an 75% decline in species diversity (Fig 5 a), unless one or
328 two wildfires occurred, when species diversity dropped by 60-70% and 40%, respectively (Fig 5 b, c, d).
329 A long period without any fire (prescribed or wildfire) resulted in a sudden drop in diversity as a large
330 proportion of the landscape transitioned to a more homogenous growth-stage structure. This is a function
331 of using a categorical representation (growth stage) of a continuous variable (TSF).

332 **Discussion**

333 Prescribed fire is increasingly used to manage fuel and conserve biodiversity in fire-prone landscapes. We
334 present a methodology that links fire regime scenarios to biodiversity outcomes by pairing growth-stage
335 optimisation with spatially and temporally explicit landscape simulation modelling. Our approach

336 enabled us to (1) define a theoretically optimal growth-stage structure (2) assess the response of
337 biodiversity to different fire-regime scenarios and (3) track the response of biodiversity over time. We
338 show that the absence of fire is a threat to vegetation diversity, and that scenarios including 5%
339 prescribed burning per year, with and without wildfire, were best. We found that using above-ground or
340 soil seedbank data alone could result in poor conservation outcomes as these components of plant
341 diversity responded differently to fire regimes.

342

343 Our simulations suggest that species diversity remained stable when burning occurred within appropriate
344 intervals. Empirical research in similar ecosystems has shown above-ground diversity to be highest
345 shortly after fire and decrease over time as short-lived species senesce (Specht & Specht 1989; Enright,
346 Miller & Crawford 1994; Freestone, Wills & Read 2015). Conversely, seedbank diversity typically
347 increases with time since fire (TSF) as the recovering above-ground vegetation reaches maturity and
348 releases propagules (Milberg 1995; Chick *et al.* 2016). Our data reflected similar patterns and resulted in
349 optimal growth-stage structures that differed between above-ground and soil seedbank data sets,
350 highlighting the problem associated with using either dataset alone. Previous growth-stage optimisation
351 using above-ground vegetation data (Di Stefano *et al.* 2013) likely misrepresented the optimal growth-
352 stage structure, as species loss above-ground does not necessarily reflect a loss from the community.
353 Combining above-ground and soil seedbank data resulted in a flat optimal growth-stage structure, with
354 similar proportions of the landscape in each of the four stages. This suggests a high degree of
355 generalisation (i.e., most species occupy multiple growth-stages, either above-ground or as soil-stored
356 seed), which in turn suggests that species diversity is likely to be insensitive to small departures from the
357 optimal growth-stage structure. Indeed, our sensitivity analysis showed that departures from the optimal
358 structure below about 0.1 (a 10% total difference in growth stage proportions) reduced species diversity
359 by < 5%. This implies that conservation objectives can be achieved with a degree of flexibility in fire
360 management practice.

361

362 Scenarios that included a single wildfire resulted in sharp declines in modelled diversity that rapidly
363 increased again if prescribed fire resumed. The cumulative effects of a single wildfire and prescribed fire
364 appear to be antagonistic under the 2 and 10% scenarios with increased losses in diversity ranging from
365 9.4-11.6% and 3.8-4.6% respectively. Under the double burn scenario, the effects were synergistic for the
366 2% scenario, with an 8.2% diversity decline, but remained antagonistic for the 10% scenario, with a 5%
367 diversity decline. These results highlight that the growth-stage structure created by prescribed burning
368 can influence how wildfire shapes vegetation diversity. Following wildfire, the resumption of prescribed
369 fires improved post-wildfire recovery as it increased heterogeneity in growth-stage structure. Our findings
370 support the theory that pyrodiversity promotes biodiversity at the landscape scale (Martin & Sapsis 1992)
371 However, for some animal groups, diversity is promoted in landscapes dominated by mid-aged and older

372 vegetation growth stages (Watson *et al.* 2012; Nimmo *et al.* 2013), highlighting the need to consider
373 multiple taxa when developing fire-management strategies.

374

375 Managing for vegetation may not result in appropriate management strategies for other taxa (Driscoll *et*
376 *al.* 2010). For example, GSO predicted that shifting from the present to the optimal growth stage structure
377 would increase the abundance of shrub species that can dominate the top understory layer (~0.75 - 3 m),
378 but lead to declines in dominant ground cover shrubs (20 – 75cm). Within the Anglesea region, bush rats
379 *Rattus fuscipes*, superb fairy wrens *Malurus cyaneus*, crescent honeyeaters *Phylidonyris pyrrhopterus*,
380 brown-headed honey eaters *Melithreptus brevirostris*, and golden whistlers *Pachycephala pectoralis*
381 responded positively to vegetation structure between 50 – 200 cm, while southern brown bandicoots
382 *Isodon obesulus* responded positively to vegetation structure between 20 – 50 cm (Sitters *et al.* 2015;
383 Swan *et al.* 2015). This suggests that managing for vegetation diversity could benefit bush rats and the
384 five bird species but reduce the preferred habitat of southern brown bandicoots. However, growth stage
385 optimisations run for birds in our study area (See Appendix S3 in Supporting Information – for survey
386 methods see Sitters *et al.* (2014)), and for birds and mammals in other heathy woodland ecosystems (Di
387 Stefano *et al.* 2013; Hale *et al.* 2016) show diversity maximised when mature or old growth-stages
388 dominate the landscape. These results differ from our combined vegetation analysis and highlight the
389 need for managers to include both vegetation and fauna in growth-stage optimisation to adequately
390 manage for multiple taxa.

391

392 Our double-wildfire scenario was intended to be ecologically stressful, as the 10-year inter-fire interval
393 fell below the minimum specified for heathy-woodland (12 years; Cheal 2010). Nevertheless, in the
394 presence of prescribed fire, vegetation diversity increased rapidly after the second wildfire, recovering to
395 near maximum levels under the 5% prescribed fire scenario. This result was unexpected, as short inter-
396 fire intervals can have negative effects on vegetation communities (Morrison & Cary 1995; Fairman *et al.*
397 2017). Our results were potentially influenced by how we linked GSO to LANDIS-II. We used a coarse
398 filter approach due to the complexity imposed on the simulation modelling by the high species diversity
399 and lack of knowledge of species autecology. We did not include the responses of the key indicator
400 species used in the LANDIS-II modelling as they are proxies for different communities and not species
401 diversity. Instead we used the spatial patterns of wildfire generated from the LANDIS-II simulations,
402 which were strongly influenced by the species composition and age structure of the underlying
403 vegetation, to investigate growth-stage patterns and their associated species diversity. We assumed
404 diversity (G) was drawn from a consistent species pool, tolerable fire intervals that constrained prescribed
405 fire in the modelling are robust for all species in the pool, and that species could disperse to all suitable
406 locations within the landscape. It is possible that species diversity occurring post wildfire was

407 overestimated as we did not account for metapopulation dynamics or individual species' responses to
408 frequent fire. Further study is required to explore the response of individual species to changing fire
409 regimes in this system and to test the robustness of the integrated modelling approach using a bottom-up,
410 species-specific framework.

411

412 Current fire management policy in Victoria, Australia (DELWP 2015), and worldwide (Husari &
413 McKelvey 1996; Bridgett *et al.* 2003; Pastor *et al.* 2009), aims to use fire strategically to protect both
414 human and ecological communities. However, as the protection of human life, property and assets is
415 prioritised (DSE 2012), prescribed burning is often focused around human settlements. For example, in
416 the Otway Ranges there has been a recent focus on strategic burning around townships. Over time, this
417 strategy could lead to a spatially skewed growth-stage structure, with younger stages occurring closer to
418 towns, and older vegetation dominating other parts of the landscape. Our findings show that vegetation
419 diversity is increased when fires promote heterogeneity in growth stages, as different stages are needed
420 for the persistence of different species. Consequently, fire management strategies that cause younger and
421 older growth-stages to occur in different places may result in the loss of some species from some parts of
422 the landscape. Incorporating the spatial asymmetry of prescribed fire programs into fire regime
423 modelling, and representing the implications for vegetation diversity spatially, will be an important next
424 step for conserving biodiversity in fire-prone landscapes.

425

426 **Conclusions**

427 Using prescribed fire to create diverse vegetation communities is common practice throughout fire-prone
428 regions, but it is often unclear how fire should be applied to achieve this end. Linking fire simulation
429 modelling and growth-stage optimisation enables managers to predict the biodiversity outcomes
430 associated with alternative burning practices, including regimes that include prescribed fire and wildfire.
431 Specifically, our findings guide the management of vegetation diversity in heathy woodlands. More
432 generally we provide a framework to promote biodiversity in fire-managed ecosystems worldwide.
433 Including both vegetation and animals in future analyses is desirable, as broad-scale biodiversity
434 strategies should benefit multiple taxa.

435

436

437 **Authors' contributions**

438 MC, CN, HS, AY, and JD conceived the ideas and designed the methodology; MC collected the data; CN
439 and MC parameterised the LANDIS-II model for the region; HS and MC developed the R script; MC, HS
440 and JD analysed the data; MC led the writing of the manuscript. All authors contributed critically to the
441 drafts and gave final approval for publication.

442

443 Data available via the Dryad Digital Repository <https://doi:10.5061/dryad.6s2b0p9> (Chick *et al.* 2018b).

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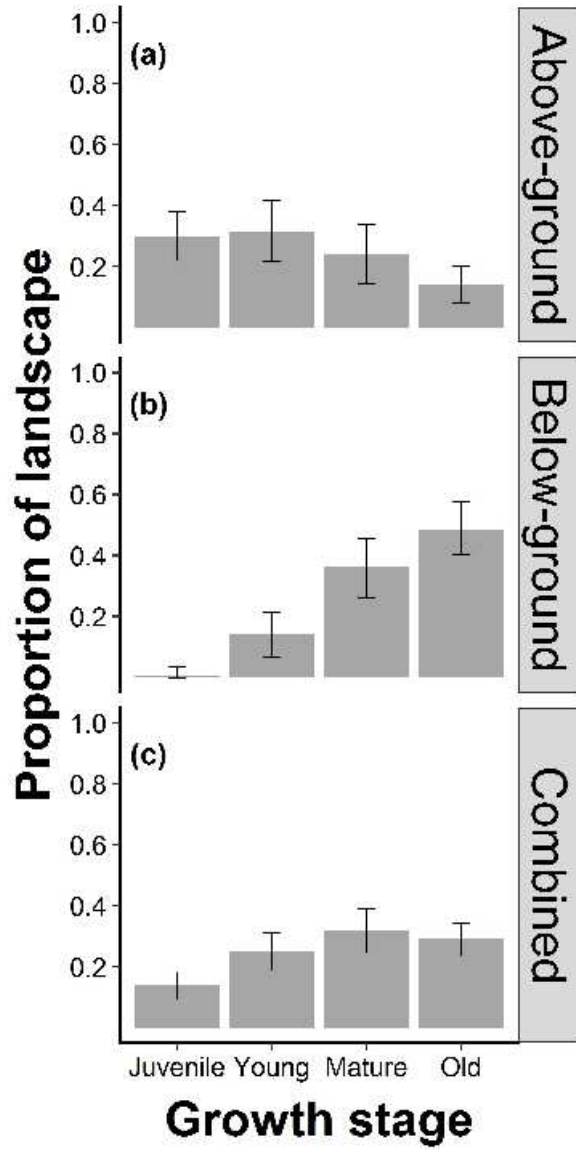
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Table 1: Growth stages sampled in the three regions

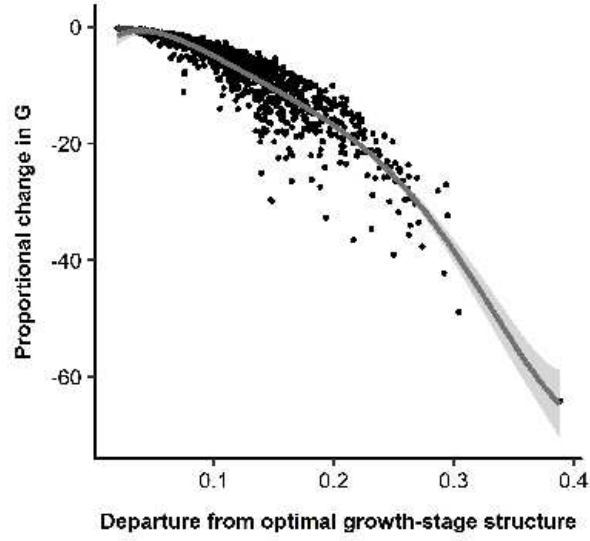
	Anglesea	Forrest	Carlisle River
Size (ha) of Healthy-Woodland distribution	6187	1500	11509
Sites (growth stage, n)			
Juvenile (0 - 3 yrs)	3	2	4
Young (3 - 10 yrs)	8	7	2
Mature (11- 34 yrs)	18	8	7
Old (> 34 yrs)	0	6	6
Growth stage total (n)	29	23	19
Average inter-fire interval	19.1(± 1.5) SE	30.4 (± 1.6) SE	32.1 (± 2.7) SE



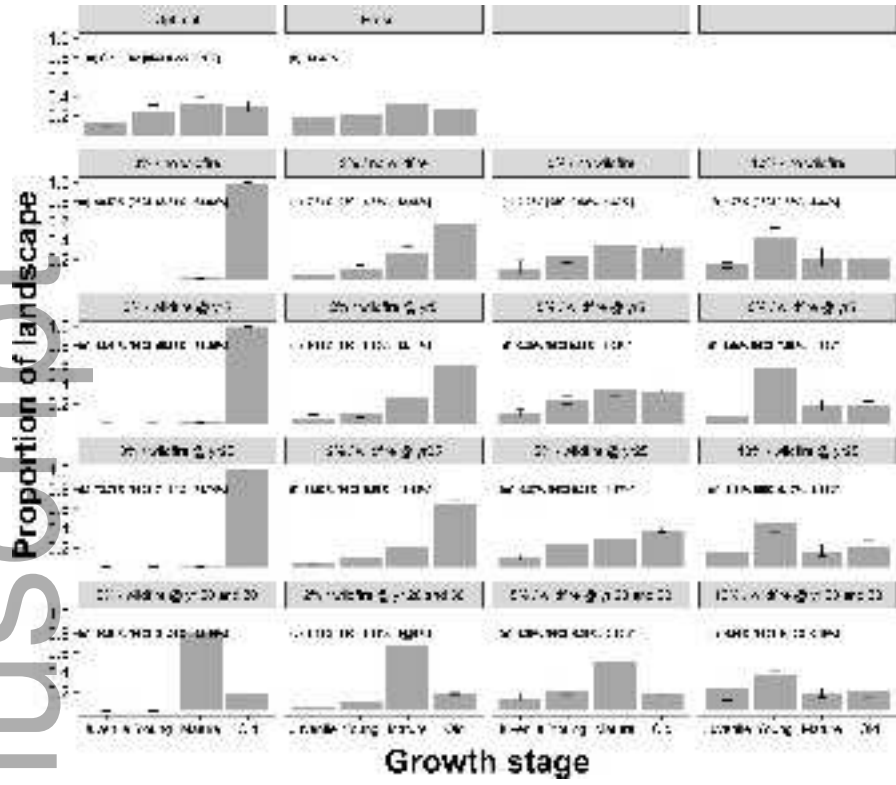
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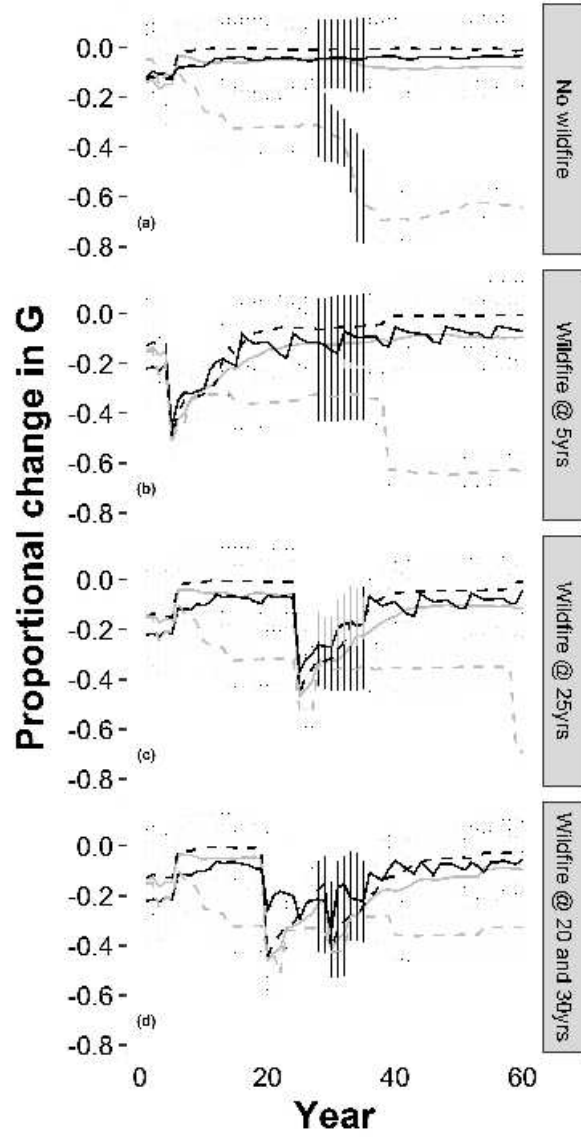
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