

1 **The dynamic regeneration niche of a forest under a large,**
2 **infrequent disturbance regime**

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11 Decisions and the Long-term Ecological Research Network.

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17 **Running title:** dynamic forest regeneration

18

19 **Type of paper:** Biodiversity Research

20

21 **Word count** 4395

22

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24 **(A) ABSTRACT**

25

26 **Aim** Knowledge of how climate and fire regimes affect regeneration in foundation species is
27 critical to the conservation of entire ecosystems. Different stages of regeneration often require
28 different ecological conditions, but dynamic constraints on regeneration are poorly known for
29 species that regenerate only after infrequent wildfires. Focussing on a long-lived, foundation
30 tree species (*Eucalyptus regnans*), we tested the hypothesis that the relative importance of fire
31 regime variables (fire severity and time since previous fire) and environmental gradients on
32 post-fire regeneration would shift as seedlings developed.

33 **Location** Southeastern Australia

34 **Methods** Following a large (> 59 000 ha) summer wildfire in 2009, we sampled 131 sites (61
35 burnt) annually for four years (2009-2012), representing the range of environmental
36 conditions in which *E. regnans* occurs. We analysed the effect of fire severity, time since fire
37 and environmental variables on early regeneration processes critical for post-fire species
38 distributions: seedling establishment, seedling density and growth through different height
39 stages (10 cm, 25 cm, 50 cm and 200 cm).

40 **Results** The regeneration niche of *E. regnans* was defined by different factors at different
41 stages of development. Initially, seedlings established prolifically on burnt sites, regardless of
42 severity. Three years into the regeneration process, high severity fire became the dominant
43 driver of seedling persistence and growth over 25 cm. Growth over 50 cm was dependent on
44 environmental conditions relating to elevation and precipitation.

45 **Main conclusions** Our results describe how fire occurrence, fire severity and environmental
46 gradients affected seedling establishment, persistence and growth. The dynamic constraints
47 on regeneration likely reflect temporal changes in the biotic and abiotic environment and
48 variation in resource requirements during the early post-fire years. Our findings will enable

49 more accurate forecasts of species distributions to assist forest conservation in the face of
50 global changes in climate and fire regimes.

51

52 **Keywords**

53 Climate change; ecological disturbance; fire management; forest conservation; obligate
54 seeder; ontogenetic niche shifts

55

56 **(A) INTRODUCTION**

57

58 Climate and fire regimes shape the distribution of many plant species (Swab *et al.*, 2012;
59 Smith *et al.*, 2014) but climate change is driving fire regime shifts in many regions globally,
60 including ecosystems adapted to large, infrequent disturbances (Romme *et al.*, 2011; Stephens
61 *et al.*, 2013; Stephens *et al.*, 2014). Predicting the biogeographic effects of future climate and
62 fire regimes relies on a solid understanding of these processes in driving current species
63 distributions (Silvestrini *et al.*, 2011; King *et al.*, 2013; Aguirre-Gutiérrez *et al.*, 2015). For
64 ‘foundation’ or ‘keystone’ species that have a dominant structural and functional role, such
65 information is critical to the conservation of entire ecosystems (Bragg *et al.*, 2015; Yang *et*
66 *al.*, 2015).

67

68 Knowledge about regeneration is of particular importance to conservation biogeography
69 because it is a ‘make-or-break’ stage for plant species (Bell *et al.*, 2014). Regeneration plays a
70 critical role in defining species distributions (Bykova *et al.*, 2012; Swab *et al.*, 2012) and the
71 composition of ecological communities (Connell & Slatyer, 1977; Johnstone *et al.*, 2010;
72 Metz, 2012). Understanding the ecological drivers of regeneration is therefore essential for
73 describing ecosystem dynamics and forecasting global ecological change (Syphard *et al.*,
74 2013; Bowman *et al.*, 2014).

75

76 The regeneration niche defines the conditions required for viable seed production, dispersal,
77 seedling establishment and growth to maturity in plant populations (Grubb, 1977). The
78 phenomenon of ontogenetic niche shifts (Eriksson, 2002; Gabler & Siemann, 2013) arises
79 when the conditions required for successful regeneration shift as plants transition through
80 different phases of regeneration (Pérez-Ramos *et al.*, 2012; le Roux *et al.*, 2013; Bell *et al.*,
81 2014). In some species, regeneration is confined to distinct periods following infrequent,
82 unpredictable events. For example, some species depend on extreme climatic events for
83 successful regeneration (Holmgren *et al.*, 2006; Matías *et al.*, 2011), while others, including
84 many long-lived tree species, regenerate only after large, infrequent disturbances (Turner *et*
85 *al.*, 2003; Bowman *et al.*, 2014). The rarity of such events, and the impossibility of
86 experimentally manipulating severe fire in forest ecosystems, imposes a huge limitation to
87 understanding ecosystem dynamics for species that rely on infrequent disturbances for
88 regeneration (Driscoll *et al.*, 2010; Lindenmayer *et al.*, 2010; Lloret *et al.*, 2012).

89

90 The lack of knowledge about regeneration following infrequent disturbances means that the
91 principle of ontogenetic niche shifts has not yet been integrated into a theoretical framework
92 for plant regeneration after fire. The regeneration niche of fire-dependent species is often
93 defined statically. For example, some plant species and communities are reported to require
94 fires of a particular severity or intensity for initial establishment (Knox & Clarke, 2006;
95 Vivian *et al.*, 2008). Yet there is potential for variation in fire regimes (i.e. the frequency,
96 intensity and timing of fires, Gill, 1975) to play a key role in driving regeneration niche shifts
97 (Johnstone & Chapin, 2006; Staver *et al.*, 2012). For example, fire intensity can drive changes
98 in nutrient availability and competition in the post-fire environment (Wan *et al.*, 2001;
99 Hollingsworth *et al.*, 2013). The effects of these changes have only been examined over
100 limited time scales (e.g. Morrison, 2002) or through simple comparisons of the presence or

101 absence of fire (e.g. Zimmermann *et al.*, 2008). Knowledge of the relationship between fire
102 regimes and plant regeneration therefore lacks the temporal component that may be critical in
103 driving the distribution of species.

104

105 We conducted a landscape-scale study of regeneration in a long-lived, foundation tree species,
106 allowing us to integrate the principles of ontogenetic niche shifts with the principles of post-
107 fire regeneration. We investigated effects of fire regime characteristics and the environment
108 on early post-fire regeneration in *Eucalyptus regnans* F. Muell, an obligate seeder that is
109 killed by severe fire and regenerates only from seed. It is the world's tallest flowering plant,
110 growing to over 100 m tall and living for up to 500 years (Wood *et al.*, 2010). *Eucalyptus*
111 *regnans* is the dominant structural component in the wet montane forests of south-eastern
112 Australia (Lindenmayer *et al.*, 2014) making it an exemplar for testing hypotheses about the
113 effects of climate and fire regimes on regeneration in long-lived, foundation species.

114

115 Beginning two months after the 'Black Saturday' wildfires in 2009, we studied distinct phases
116 of the early regeneration niche (first four years) from initial establishment through different
117 stages of growth. Annually, over four years, we surveyed 131 sites (61 burnt) in *E. regnans*
118 forest (Table 1), spanning environmental gradients (elevation, temperature, precipitation, soil
119 moisture and slope) and fire regime variables (fire severity and time since previous fire). This
120 is an important study given that fires capable of initiating regeneration in *E. regnans* occur
121 infrequently (75-150 yr, McCarthy *et al.*, 1999) and fires of such large spatial scale (> 59 000
122 ha) have not occurred in these forests since 1939. The spatial extent of the Black Saturday
123 fires allowed us to sample widely across the landscape, representing the range of
124 environmental conditions in which *E. regnans* occurs. We tested the hypothesis that the
125 importance of fire regimes and environmental gradients would shift during early seedling
126 development, reflecting temporal changes in the biotic and abiotic environment and variation

127 in resource requirements. Knowledge about the effects of climate and fire regimes on the
128 regeneration niche is fundamental to forecasting future distributions of long-lived, foundation
129 species and conserving the ecosystems in which they play a critical role.

130

131 **(A) METHODS**

132

133 *(B) Study region and seedling surveys*

134 Our study region was the Central Highlands of Victoria, south-eastern Australia (Fig. S1)
135 where *Eucalyptus regnans* (Mountain Ash) forest covers approximately 162 000 ha. Wildfire
136 is the most common natural disturbance in the region and the majority of fire events occur in
137 late summer to early autumn (Mackey *et al.*, 2002). Fire intensity in *E. regnans* forest can be
138 extreme (35 000 - 100 000 kWm⁻¹) and such fires usually kill trees resulting in stand-
139 replacement from seedlings (Gill & Catling, 2002). The mean fire return interval in *E.*
140 *regnans* forest is 75-150 years for tree-killing fires and 37-75 yr for all fires (McCarthy *et al.*,
141 1999). Approximately 79 % of the study region was burnt by wildfire in 1939 and major
142 wildfires also occurred in 1983 (Fig. S1). The February 2009 fires burnt approximately 59
143 000 ha of *E. regnans* forest in the region.

144

145 Following the 2009 wildfires, we surveyed 131 one-hectare sites (61 burnt, Fig. S1) where *E.*
146 *regnans* is the dominant overstorey species (Lindenmayer *et al.*, 2000). Our sites were a
147 subset of those established in 1997 for a long-term forest ecology and monitoring project
148 (Lindenmayer *et al.*, 2003) that included only sites dominated by *E. regnans* (Lindenmayer *et*
149 *al.*, 2000). Research on high-severity fire in forest ecosystems depends on infrequent,
150 stochastic events and achieving a balanced design is often impossible given the lack control
151 over the placement of fire ‘treatments’ (Driscoll *et al.*, 2010). A key strength of our study was
152 the ability to examine the effects of this rare disturbance event using our controlled,

153 landscape-scale sampling approach (Lindenmayer *et al.*, 2010; Romme *et al.*, 2011). Several
154 decades are likely to pass before a similar study can be conducted again in this system.

155

156 We grouped sites into three forest age categories based on stand age before the 2009 fires
157 (Lindenmayer *et al.*, 2000) (Table 1). Forest age, representing the time since previous fire, is
158 relevant to our study because it is the key variable determining reproductive potential in
159 obligate seeders. *Eucalyptus regnans* trees begin producing seed at 15-20 years of age (Gill,
160 1975) and may live for 350 to 500 years (Wood *et al.*, 2010). The short lived canopy-stored
161 seed bank in *E. regnans* (2-3 yr, Ashton, 1975c) is likely the primary source of seed for
162 regeneration given limited seed dispersal distances (65 m, Cunningham, 1957) (although fire
163 might increase long distance dispersal, Nathan *et al.*, 2008). Some multi-aged sites were
164 classified according to the predominant age class. ‘Old-growth’ sites (N = 22 total, 13 burnt)
165 were established following fires that occurred between the early 1700s and 1908. In the ‘70
166 year-old’ category (N = 83 total, 37 burnt), 95 % of sites were established after extensive fires
167 in 1939, with the remainder established after fires in 1926 and 1932. Some ‘young’ forest
168 sites (N = 26 total, 11 burnt) were established following clearcut and slash burn logging or
169 post-fire salvage logging between 1974 and 1983 (12 sites), 1955 (1 site), 1990 (1 site) and
170 1998 (1 site). The remaining 11 young sites established naturally following wildfires in 1983.
171 Although it was not possible to separate the effects of fire and mechanical disturbance in the
172 small number of young forest sites, we did not find strong effects of forest age on
173 regeneration (see Results) so this feature will not affect our conclusions.

174

175 We conducted surveys between April and November 2009 to assess fire severity (variation in
176 vegetation consumption during the 2009 fires) and grouped sites into three burn categories
177 (Table 1): unburnt (N = 70); moderate severity (N = 40) where the majority of the understorey

178 and midstorey was scorched but the overstorey remained unburnt; and high severity (N = 21)
179 where the understorey, midstorey and overstorey had been scorched or completely consumed.
180

181 We conducted seedling surveys annually for four years (15 Apr-25 Nov 2009; 11 Mar-15
182 Sept 2010; 7 Feb-10 May 2011; 5 Mar-31 Jul 2012) after the main *E. regnans* growing season
183 (midsummer, Ashton, 1975b). Three 1 x 1 m plots were established at each of the 131 sites,
184 spaced 40 m apart along a central transect and we recorded the presence, density and height
185 (in categories: 0-10, 11-25, 26-50, 51-200, 201-500 cm) of all *E. regnans* seedlings (defined
186 as individuals up to 3 m in their first four years, Ashton, 1975a). The plots, set along a GPS-
187 marked transect, were permanently marked with flags so the precise survey area was
188 consistent across years. Five high severity sites (two old-growth, three 70 year-old) were
189 established in 2010, thus not surveyed in 2009. Four young forest sites (one moderate
190 severity, three high severity) were established in 2011, thus not surveyed in 2009 and 2010. In
191 2010, 51 sites were not surveyed due to logistical constraints but these were all unburnt sites
192 where *E. regnans* seedlings were rare (Smith *et al.*, 2014). Of these sites, 90% (46/51) had no
193 change in seedling density between 2009 and 2011 and in 96 % of these cases zero seedlings
194 were recorded. For sites with no change over this period, we used the seedling density value
195 from 2009 and 2011 for the 2010 record. For the five sites where seedling density changed
196 between 2009 and 2011, we omitted the 2010 record from the analysis.

197
198 We used spatial modelling software to derive values for environmental variables for each site
199 that were important for first-year seedling emergence in *E. regnans* (Smith *et al.*, 2014). We
200 used fixed values to model relative environmental variation among sites but also interpreted
201 our findings in the context of annual variation in precipitation during the study (Fig. S2).
202 Elevation (327-1054 m above sea level) was derived from a 20 m resolution digital elevation
203 model (DEM, see Fig. S1) in ANUDEM (Hutchinson, 2011). Annual mean temperature (8-

204 12°C) and precipitation (1293-1776 mm/yr) were estimated from monthly mean climate
205 surfaces from 1921-1995 for each cell in the DEM using the BIOCLIM module in
206 ANUCLIM (Xu & Hutchinson, 2011). Slope (1-31° of inclination) was derived from
207 neighbouring cell geometry in the DEM (M. Hutchinson, unpublished software). Topographic
208 wetness index (TWI, -4.34-6.95) was calculated as a measure of available soil moisture
209 ($\log(\text{specific catchment/slope})$) (Beven & Kirkby, 1979).

210
211 There were correlations among the environmental variables (Smith *et al.*, 2014), so we
212 analysed them as two independent principal components (PC). Principal component 1 (56%
213 variance explained) accounted for relationships among elevation (loading = -0.58),
214 temperature (0.58) and precipitation (-0.56), and PC2 (27% variance explained) accounted for
215 the relationship between soil moisture (0.69) and slope (-0.72). To investigate
216 multicollinearity, we conducted linear regression of each principal component separately on
217 burn category, forest age and burn category + forest age. We did this for the 131 sites used to
218 analyse the probability of seedling occurrence and for the subset of sites used in the seedling
219 density (N = 64) and height analyses (N = 42). The adjusted R^2 values for these models were
220 low (PC1 < 0.084, PC2 < 0.005) indicating that our environmental and fire related variables
221 were not confounded. We assessed spatial autocorrelation in the residuals of our models after
222 analysis (see below).

223

224 (B) Analysis

225 We analysed the regeneration niche of *E. regnans* using six response variables: probability of
226 seedling occurrence, seedling density and the probability of growing through four different
227 height categories: 10, 25, 50 and 200 cm. We analysed height data only from burnt sites
228 (moderate and high severity) because seedlings were virtually absent on unburnt sites, and
229 only from 2010-2012 because, in 2009, 99 % of seedlings were < 10 cm. Few unburnt sites

230 were included in the density analysis (see below), thus the unburnt sites were predominantly
231 used to investigate probability of seedling occurrence. Site-within-year was the observational
232 unit for the probability of occurrence and density analyses, with data from the three plots at
233 each site pooled. This scale is appropriate for our landscape-scale focus (Dale & Fortin,
234 2014). Individual seedling was the observational unit for the height analyses.

235

236 For the probability of seedling occurrence, we fitted binomial generalised linear mixed-effects
237 models (GLMM) using the lme4 library (Bates *et al.*, 2013) in R 3.0 (R Core Team, 2013).

238 For seedling density, there was a high proportion of zeros in our data (70%), so we modelled
239 density conditional on presence (Smith *et al.*, 2014). To do this, we fitted a truncated negative
240 binomial GLMM to analyse only the positive values in the data, using the glmmADMB
241 library (Skaug *et al.*, 2013) in R. This accounted for overdispersion, previously identified in a
242 subset of the data (Smith *et al.*, 2014). For seedling height, we used binomial GLMMs to
243 analyse four separate cumulative logits: height >10, >25, >50 and >200 cm. This allowed us
244 to examine factors affecting the probability of growth at different stages of development. Our
245 approach was similar to cumulative ordinal logistic regression (Agresti, 2010) but we
246 analysed each height variable separately because the proportionality assumption was not met.

247

248 For each response, we fitted a global model with five main effects (time since fire + burn
249 category + forest age + PC1 + PC2) and four interactions between time since fire and all other
250 terms. Site was fitted as a random effect in all models to account for repeated sampling. In all
251 models, time since fire was treated as ratio variable (0, 1, 2, 3) (Howitt & Cramer, 2011) as
252 seedlings experience exponential declines over time (West *et al.*, 2009), corresponding to
253 linear on the link (log) scale. There were no patterns (e.g. quadratic) in plots of final model
254 residuals and time since fire, supporting the treatment of time as a ratio variable. We did not
255 fit an interaction between burn category and forest age as this overparameterised our models

256 given the limited number of sites when these categories were combined. To find a
257 parsimonious model or set of models, we used a modified ‘all subsets’ model selection
258 procedure, appropriate when all terms have potential importance (Stephens *et al.*, 2007;
259 Doherty *et al.*, 2012). We included time in all models because we were interested in temporal
260 changes and fitted all plausible combinations of the other terms using the MuMIn library
261 (Bartoń, 2013) in R. This produced 81 candidate models for each response variable. We
262 ranked models using the Bayesian Information Criterion (BIC) ($-2 \ln \text{likelihood} + (\ln \text{number}$
263 $\text{of sites}) (\text{number of fitted parameters})$) (Jones, 2011). We considered all models that differed
264 in BIC from the top-ranked model (ΔBIC) by ≤ 2 to have support from the data (Hegyi &
265 Garamszegi, 2011). We did not conduct model averaging because it biases parameter
266 estimates, particularly when interactions are present (Freckleton, 2011; Hegyi & Garamszegi,
267 2011), but made inference from all models with a $\Delta\text{BIC} \leq 2$ (Table 2; see Table S1 for all
268 models with $\Delta\text{BIC} \leq 4$; see Table S2 and Fig. S3 for estimates of models with $\Delta\text{BIC} \leq 2$). For
269 factorial variables, we estimated the difference and 95 % confidence interval between each
270 pair of levels (e.g. moderate vs. high severity fire) within the parameter (Fisher’s Least
271 Significant Difference). Differences were considered significant when confidence intervals
272 did not include zero on the log scale.

273

274 To determine if there was spatial autocorrelation in the residuals of our models, we produced
275 variograms using the geoR package (Ribeiro Jr & Diggle, 2001) in R for each year separately.
276 We visually assessed autocorrelation at three spatial scales. For each scale, we divided the
277 data into 10 evenly-distributed spatial distance classes where the first class began at the
278 minimum distance between sites. We generated three sets of distance classes representing
279 three spatial scales by modifying the maximum distance class using the first quartile, third
280 quartile and maximum distance between sites. There was no strong or consistent evidence of a

281 sill that would indicate spatial autocorrelation in the model residuals (Liebhold & Sharov,
282 1998) (Fig. S4).

283

284 **(A) RESULTS**

285

286 In the first year after fire, there was a high probability of seedling occurrence on sites burnt at
287 moderate and high severity (Table 2, Fig. 1a). By the third year, the probability of seedling
288 occurrence had declined on moderately burnt sites but remained high on severely burnt sites
289 (Fig. 1a). Seedling density on burnt sites was initially high, followed by marked declines over
290 the four years (Fig. 1b). Density was higher on burnt than unburnt sites in all years, regardless
291 of severity (Fig. 1b). By 2012, despite strong and significant differences in seedling
292 occurrence between moderately and severely burnt sites (Fig. 1a), there was a mean of only
293 one seedling per site (3 m^2) on burnt sites where they were present (Fig. 1b). Seedling density
294 increased with increasing elevation and precipitation and with decreasing temperature (Table
295 2, Fig. 1c). Seedling density also increased with increasing soil moisture availability and
296 decreasing slope (Table 2, Fig. 1d). The second-ranked model for seedling density indicated
297 that the number of seedlings returned to the same level as unburnt sites within three years
298 after fire (Table S2, Fig. S3a).

299

300 The probability of seedling growth over 10 cm was high on all burnt sites (Fig. 2a) and not
301 strongly influenced by fire regime or environmental variables (Table 2). In 2010, growth over
302 10 cm was higher at low elevations (second-ranked model, Table 2, Fig. S3b), probably
303 reflecting heavy snowfall suppressing growth at high elevations in 2010 (Fig. S2). In all
304 survey years, the probability of growing over 25 cm was greater on severely burnt compared
305 to moderately burnt sites (Table 2, Fig. 2b). Growth over 50 and 200 cm was also promoted
306 by high severity fire (Fig. 2c, e) and by increasing elevation and precipitation and decreasing

307 temperature (PC1, Fig. 2d,f). Growth over 50 and 200 cm was more likely on flat terrain with
308 high soil moisture availability (Table 2, Fig. S2c,d). Forest age did not affect any of the six
309 response variables (Table 2).

310

311 **(A) DISCUSSION**

312

313 Our study demonstrated that the regeneration niche of *E. regnans* was not static. The relative
314 importance of fire severity and environmental variables, including elevation, temperature,
315 precipitation, soil moisture and slope varied during the first four years after fire. Seedlings
316 established most prolifically on sites burnt at both moderate and high severity and at high
317 elevations where rainfall is high and temperature is low. Three years into the regeneration
318 process, fire severity became important with high severity fire being the dominant driver of
319 seedling persistence. Our analysis of seedling height allowed us to identify temporal shifts in
320 the influence of fire regime and environmental factors on growth, likely reflecting biotic and
321 abiotic changes after fire and variation in resource requirements at different stages of
322 development (Fig. 3).

323

324 *(B) Seedling establishment*

325 In the first year after fire, the dominant driver of seedling establishment was the occurrence of
326 fire, irrespective of severity (Fig. 3). This reflects fire-dependent regeneration in obligate
327 seeders, with seed release and germination responding to heat and smoke cues (Moreira *et al.*,
328 2010) and to the flush of available soil nutrients that occur after fire (Wan *et al.*, 2001).

329 Although light and nutrient levels typically increase with fire severity (Wan *et al.*, 2001),
330 rates of establishment were similar on sites burnt at moderate and high severity. Seed reserves
331 at this early stage of regeneration might reduce their reliance on light and soil nutrients

332 (Pérez-Ramos *et al.*, 2012) and the greater shade and ground cover on moderately burnt sites
333 probably allowed seedlings to retain water (Smith *et al.*, 2014).

334

335 *(B) Effects on growth*

336 High severity fire became critically important for seedlings beyond the 25 cm growth stage,
337 likely driven by a number of differences between the severely and moderately burnt sites (Fig.
338 3). Ground-layer, mid-layer and dominant overstorey vegetation was killed on high-severity
339 sites, which likely resulted in high levels of light and reduced allelopathy from adult plants
340 (Ashton & Willis, 1982). The short-term flush of available N and P that occurs with soil
341 organic matter mineralisation after fire can increase with fire intensity (Weston & Attiwill,
342 1990; Wan *et al.*, 2001; Pausas *et al.*, 2003; Smithwick *et al.*, 2005), likely contributing to
343 high seedling growth on severely burnt sites (Launonen *et al.*, 2004). Seedling growth in *E.*
344 *regnans* can be suppressed by the fungal pathogen *Cylindrocarpon destructans*, but only
345 when soil nutrients and ectomycorrhizae are limited (Iles *et al.*, 2010). Such conditions occur
346 in moderately burnt *E. regnans* forest (Launonen *et al.*, 1999). Furthermore, the sparse
347 vegetation cover at high severity sites may have reduced pressure from herbivores that are
348 reluctant to browse in exposed landscapes (Knight & Holt, 2005) and large herbivores (e.g.
349 wallabies) in our study region were probably killed or displaced by high severity fire.

350

351 Growth over 50 and 200 cm increased with increasing elevation, precipitation and soil
352 moisture and with decreasing temperature. The key aspect of this result is that these
353 environmental variables did not influence earlier growth but became important as seedlings
354 grew larger (Fig. 3). The increasing influence of soil moisture on height might reflect
355 increased root growth and therefore increased ability to exploit soil water (Casper & Jackson,
356 1997). Seedling density had strongly declined by the time individuals reached 50 and 200 cm,

357 which might have reduced facilitative effects of conspecifics (le Roux *et al.*, 2013) and
358 increased reliance on abiotic factors.

359

360 A further explanation for why the environmental variables became important beyond the 50
361 cm growth stage is that the post-fire flush of N and P had returned to pre-fire levels by this
362 stage. Consequently, non-fire related abiotic factors probably became increasingly important
363 for growth. Post-fire levels of N and P can remain elevated for up to 16 months in *E. regnans*
364 forest (Weston & Attiwill, 1990) and up to three years in other forest types following large,
365 infrequent disturbances (Rau *et al.*, 2007; Turner *et al.*, 2007). Water use efficiency in plants
366 increases with N supply (Brueck, 2008) so effects of the moisture gradient in our study
367 probably became more important as nutrient levels dropped. Changes in the carbon balance
368 following depletion of seed reserves have driven regeneration niche shifts in a large seeded
369 species (*Quercus suber*) (Pérez-Ramos *et al.*, 2012). However, energy and nutrient stores in
370 tiny *E. regnans* seeds (< 1 mg) are unlikely to be sustained beyond the cotyledon stage
371 (Ashton & Kelliher, 1996). The shift towards a stronger influence of the climatic and
372 topographic environment is more likely to have been driven by a reduction in soil nutrients.

373

374 (B) Effects on density

375 Unlike the dynamic drivers of establishment and growth, we found temporally consistent,
376 positive effects of high elevation, increased water availability and associated variables on
377 seedling density. Survival and growth are often negatively density dependent (Metz *et al.*,
378 2010; Nottebrock *et al.*, 2013) so the influence of these environmental variables on seedling
379 density might have limited influence on the longer-term viability of the species (ultimately
380 there are only 40-80 stems / ha in 150 yr old forest, Ashton & Attiwill 1994). However,
381 increases in initial seedling densities can buffer plant populations against herbivory (Clark *et*
382 *al.*, 2012) and drought (Yates & Ladd, 2005). High regeneration densities might also increase

383 fitness through both adaptive (Bailey *et al.*, 2013) and plastic (McNutt *et al.*, 2012) responses
384 to intraspecific competition. For example, intraspecific competition can drive niche
385 partitioning, making overall resource use more efficient (Boyden *et al.*, 2008) and can
386 increase tolerance to herbivory (McNutt *et al.*, 2012). The positive effects of cool, wet
387 environmental conditions on seedling density could therefore have positive effects on the
388 short- and long-term persistence of *E. regnans*. Further research into biotic interactions in *E.*
389 *regnans* forests is needed to assess the likelihood of elevational range shifts in this ecosystem
390 as the climate continues to change (le Roux *et al.*, 2013; Kopp & Cleland, 2014).

391

392 (B) Conclusions

393 The key insight gained from our study is that long-lived species that rely on fire for
394 regeneration pass through different ecological filters during early development. Seedlings
395 established only on burnt sites, persisted only where fire burned at high severity, and grew
396 taller where environmental conditions were most suitable. Such findings will help conserve
397 forest ecosystems generally, particularly montane systems that are characterised by large,
398 infrequent disturbance regimes (Romme *et al.*, 2011; Stephens *et al.*, 2014). Understanding
399 where high-severity fire intersects with optimal environmental conditions (e.g. high elevation
400 and soil moisture content for *E. regnans*), will enable accurate identification of the landscape
401 pattern driving species distributions. Mechanistic distribution models must consider the
402 dynamic regeneration niche, but also that climate change could alter environmental conditions
403 that interact with the regeneration niche to drive patterns of seedling establishment. This
404 understanding will help define target areas for conservation of species that are vulnerable to
405 changes in climate and fire regimes (King *et al.*, 2013; Yang *et al.*, 2015) and will facilitate
406 more realistic parameterisation of niche models for predicting future distributions (Aguirre-
407 Gutiérrez *et al.*, 2015).

408

409 **(A) ACKNOWLEDGEMENTS**

410

411 John Stein helped compile spatial data. This project was supported by funds from the
412 Australian Research Council, the Australian Government Department of Environment, the
413 Victorian Government Department of Primary Industries and Environment, Parks Victoria,
414 Melbourne Water and the Thomas Foundation. Input from four anonymous reviewers and the
415 editors greatly improved the manuscript.

416

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653

654 **(A) BIOSKETCH**

655 ALS investigates ecological and evolutionary aspects of fire regimes. Her co-authors have
656 interests in statistics, forest ecology, biodiversity conservation, dispersal, ecological genetics
657 and making movies about scientific research. Author contributions: All authors designed
658 study; DPB, LM, and DBL collected data; ALS and WB analysed data; and ALS wrote the
659 manuscript, incorporating input from all authors.

660

661 **(A) SUPPORTING INFORMATION**

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

663

664 **Table S1** Model selection results for six *Eucalyptus regnans* response variables.

665 **Table S2** Coefficients and standard errors from models of *Eucalyptus regnans* regeneration.

666 **Figure S1** Map of the study region showing the spatial distribution of sites.

667 **Figure S2** Total annual rainfall and long term rainfall averages.

668 **Figure S3** Estimates from models that differed in the Bayesian Information Criterion from the
669 top model by ≤ 2 .

670 **Figure S4** Variograms of model residuals for each response variable.

671

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676

677 **Table 1** The total number of sites for each fire return interval and burn category.

Forest age (years)	Burn category			Total (Forest age)
	Unburnt	Moderate severity	High severity	
Old-growth (100-300)	9	6	7	22
70 year-old (70-83)	46	30	7	83
Young (26-54)	15	4	7	26
Total (burn category)	70	40	21	Overall total: 131

678

679

680 **Table 2** Supported models for different phases of the regeneration niche in *Eucalyptus*
681 *regnans*, selected using the Bayesian Information Criterion (BIC). The + indicates included
682 terms. All models that differed in BIC from the top model (Δ BIC) by ≤ 2 are shown. Models
683 with Δ BIC > 2 had little support ($< 13\%$ BIC weight, Table S1). See Table S2 for
684 coefficients and standard errors.

685

df	log(L)	BIC	Δ BIC	BIC weight	Model terms								
					TSF	Burn	Age	PC1	PC2	TSF x burn	TSF x Age	TSF x PC1	TSF x PC2
<i>Probability of seedling occurrence</i>													
7	-162.80	359.73	0.00	0.72	+	+					+		
<i>Seedling density, conditional on presence</i>													
8	-538.80	1110.88	0.00	0.28	+	+		+	+				
10	-535.63	1112.85	1.97	0.10	+	+		+	+		+		
<i>Height > 10 cm</i>													
3	-226.05	463.30	0.00	0.30	+								
5	-222.89	464.47	1.17	0.17	+			+					+
<i>Height > 25 cm</i>													
4	-353.39	721.73	0.00	0.45	+	+							
<i>Height > 50 cm</i>													
7	-333.64	693.45	0.00	0.21	+	+		+			+		+
6	-336.01	694.44	1.00	0.13	+	+		+			+		
8	-332.55	695.00	1.55	0.10	+	+		+	+		+		+
<i>Height > 200 cm</i>													
6	-155.17	332.76	0.00	0.21	+	+		+			+		
7	-153.38	332.93	0.17	0.19	+	+		+			+		
8	-151.88	333.66	0.90	0.13	+	+		+	+		+		+
5	-157.58	333.84	1.08	0.12	+	+					+		
6	-155.77	333.96	1.19	0.12	+	+			+		+		

686
687 df = degrees of freedom; log(L) = log-likelihood; TSF = Time (in years) since fire, Burn =
688 burn category (unburnt, moderate severity, high severity); Age = forest age (young, 70 year-
689 old, old-growth) representing time since previous fire; PC1 = principal component 1
690 (accounts for correlations among elevation (loading = -0.58), temperature (0.58) and
691 precipitation (-0.56)); PC2 = principal component 2 (accounts for the correlation between
692 available soil moisture (0.69) and slope (-0.72)).

693
694

695 **FIGURE LEGENDS**

696

697 **Figure 1** The regeneration niche in *Eucalyptus regnans* characterised by (a) the probability of
698 seedling occurrence and (b-d) seedling density, conditional on presence (estimates and 95%
699 confidence intervals from the first-ranked models). (a) Fire, regardless of severity, was the
700 dominant driver of seedling establishment in the first year after fire (2009). Three years after
701 fire, seedling occurrence on moderately burnt sites declined while severely burnt sites
702 retained seedlings. (b) Seedling density was initially high after fire (estimates shown for mean
703 principal component scores) and declined rapidly on burnt sites, regardless of severity. In all
704 survey years, the greatest number of seedlings occurred on sites characterised by (c) high
705 elevation, high precipitation and low temperature and by (d) high soil moisture availability
706 (estimates shown for high severity sites in 2009). Points are staggered within years to make
707 error bars visible.

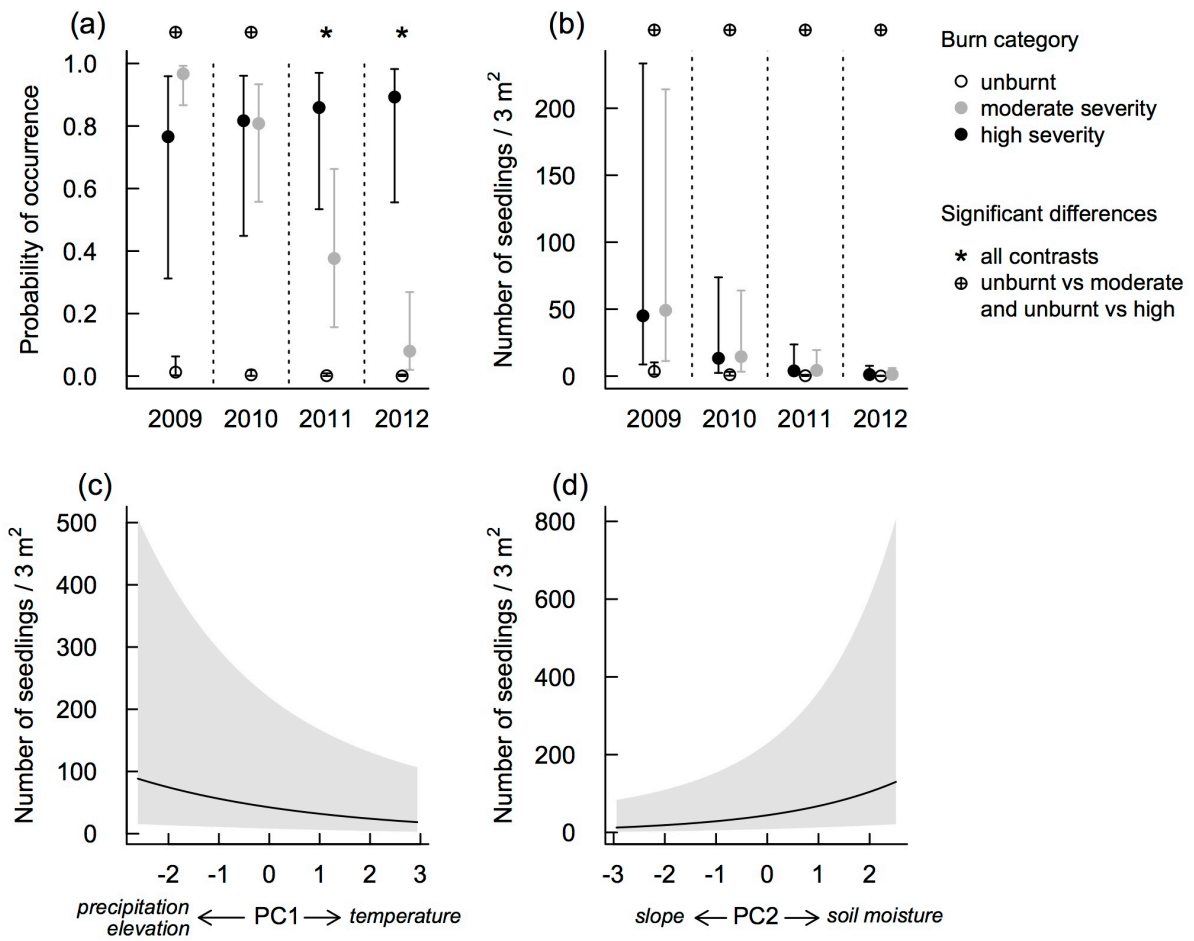
708

709 **Figure 2** The regeneration niche in *Eucalyptus regnans* characterised by growth at different
710 height stages on burnt sites (estimates and 95% confidence intervals from the first-ranked
711 models). (a) The probability of growing > 10 cm was affected by time since fire. (b) High
712 severity fire increased the probability of growing > 25 cm. Growth over (c-d) 50 cm and (e-f)
713 200 cm was promoted by high severity fire (estimates shown for mean principal component 1
714 (PC1) scores) and by high precipitation and low temperatures that occurred at high elevations
715 (estimates shown for high severity fire). Open squares = time effects only; Black circles =
716 high severity fire; Grey circles = moderate severity fire; * = significant differences. Points are
717 staggered within years to make error bars visible.

718

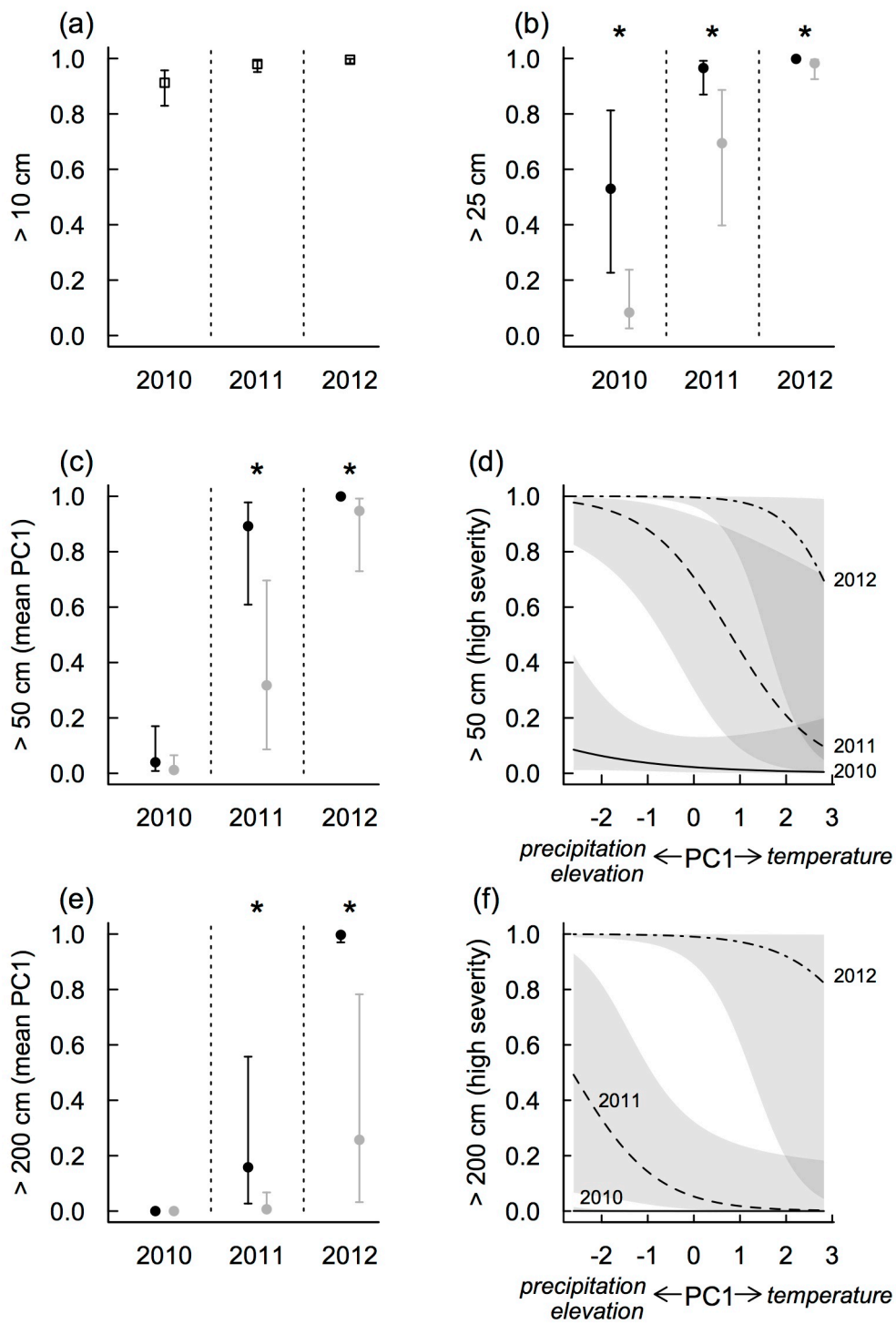
719 **Figure 3** Fire severity and environmental variation drove regeneration niche shifts in
720 *Eucalyptus regnans*. Factors affecting different stages of regeneration are indicated by the

721 shaded panels and the potential mechanisms are listed within the panels (references for all
722 mechanisms are given in the Discussion). Seedling pictures from Ashton (1975a).
723



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730 **Figure 3**

STAGE	1 Establishment & growth > 10cm 	2 Growth > 25 cm 	3 Growth > 50 & 200 cm 
Occurrence of fire	Heat & smoke cue seed release & germination		
	↑ Available N & P		
High fire severity		↑ Light & ectomycorrhizal associations ↓ Allelopathy from adults, soil pathogens & herbivory	
Climate & topography			↓ N, P and interspecific facilitation increase influence of climate & topography Deeper roots can exploit soil water

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