Diversity and Distributions, (Diversity Distrib.) (2016) **22**, 457–467

BIODIVERSITY RESEARCH

The dynamic regeneration niche of a forest following a rare disturbance event

Annabel L. Smith[1]*, Wade Blanchard[1], David P. Blair[1], Lachlan McBurney[1], Sam C. Banks[1], Don A. Driscoll[1,2] and David B. Lindenmayer[1,3]

[1]*Fenner School of Environment and Society, Australian National University, Frank Fenner Building 141, Linnaeus Way, Canberra, ACT 2601, Australia,* [2]*School of Life and Environmental Sciences, Deakin University Geelong, 221 Burwood Highway, Burwood, Vic. 3125, Australia,* [3]*Australian Research Council Centre of Excellence for Environmental Decisions and the Long-term Ecological Research Network, Canberra, ACT, Australia*

*Correspondence: Annabel Smith, Fenner School of Environment and Society, Australian National University, Frank Fenner Building 141, Linnaeus Way, Canberra, ACT 2601, Australia.
E-mail: annabel.smith@anu.edu.au

ABSTRACT

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

Location South-eastern Australia.

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

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

Main conclusions Our results describe how fire occurrence, fire severity and environmental gradients affected seedling establishment, persistence and growth. The dynamic constraints on regeneration likely reflect temporal changes in the biotic and abiotic environment and variation in resource requirements during the early post-fire years. Our findings will enable more accurate forecasts of species distributions to assist forest conservation in the face of global changes in climate and fire regimes.

Keywords
climate change, ecological disturbance, fire management, forest conservation, obligate seeder, ontogenetic niche shifts.

INTRODUCTION

Climate and fire regimes shape the distribution of many plant species (Swab *et al.*, 2012; Smith *et al.*, 2014) but climate change is driving fire regime shifts in many regions globally, including ecosystems adapted to large, infrequent disturbances (Romme *et al.*, 2011; Stephens *et al.*, 2013, 2014). Predicting the biogeographic effects of future climate

© 2016 John Wiley & Sons Ltd
DOI: 10.1111/ddi.12414
http://wileyonlinelibrary.com/journal/ddi

A Journal of Conservation Biogeography
Diversity and Distributions

and fire regimes relies on a solid understanding of these processes in driving current species distributions (Silvestrini *et al.*, 2011; King *et al.*, 2013; Aguirre-Gutiérrez *et al.*, 2015). For 'foundation' or 'keystone' species that have a dominant structural and functional role, such information is critical to the conservation of entire ecosystems (Bragg *et al.*, 2015; Yang *et al.*, 2015).

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

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

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

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

Beginning two months after the 'Black Saturday' wildfires in 2009, we studied distinct phases of the early regeneration niche (first four years) from initial establishment through different stages of growth. Annually, over four years, we surveyed 131 sites (61 burnt) in *E. regnans* forest (Table 1), spanning environmental gradients (elevation, temperature, precipitation, soil moisture and slope) and fire regime variables (fire severity and time since previous fire). This is an important study given that fires capable of initiating regeneration in *E. regnans* occur infrequently (75–150 years, McCarthy *et al.*, 1999) and fires of such large spatial scale (> 59,000 ha) have not occurred in these forests since 1939. The spatial extent of the Black Saturday fires allowed us to sample widely across the landscape, representing the range of environmental conditions in which *E. regnans* occurs. We tested the hypothesis that the importance of fire regimes and environmental gradients would shift during early seedling development, reflecting temporal changes in the biotic and abiotic environment and variation in resource requirements. Knowledge about the effects of climate and fire regimes on the regeneration niche is fundamental to forecasting future distributions of long-lived, foundation species and conserving the ecosystems in which they play a critical role.

Table 1 The total number of sites for each forest age and burn category.

	Burn category			
Forest age (years)	Unburnt	Moderate severity	High severity	Total (Forest age)
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

METHODS

Study region and seedling surveys

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

Following the 2009 wildfires, we surveyed 131 one-hectare sites (61 burnt, Fig. S1) where *E. regnans* is the dominant overstorey species (Lindenmayer *et al.*, 2000). Our sites were a subset of those established in 1997 for a long-term forest ecology and monitoring project (Lindenmayer *et al.*, 2003) that included only sites dominated by *E. regnans* (Lindenmayer *et al.*, 2000). Research on high-severity fire in forest ecosystems depends on infrequent, stochastic events, and achieving a balanced design is often impossible given the lack control over the placement of fire 'treatments' (Driscoll *et al.*, 2010). A key strength of our study was the ability to examine the effects of this rare disturbance event using our controlled, landscape-scale sampling approach (Lindenmayer *et al.*, 2010; Romme *et al.*, 2011). Several decades are likely to pass before a similar study can be conducted again in this system.

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

We conducted surveys between April and November 2009 to assess fire severity (variation in vegetation consumption during the 2009 fires) and grouped sites into three burn categories (Table 1): unburnt ($N = 70$); moderate severity ($N = 40$) where the majority of the understorey and mid-storey was scorched but the overstorey remained unburnt; and high severity ($N = 21$) where the understorey, mid-storey and overstorey had been scorched or completely consumed.

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

We used spatial modelling software to derive values for environmental variables for each site that were important for first-year seedling emergence in *E. regnans* (Smith *et al.*, 2014). We used fixed values to model relative environmental variation among sites but also interpreted our findings in the context of annual variation in precipitation during the study (Fig. S2). Elevation (327–1054 m above sea level) was derived from a 20-m resolution digital elevation model (DEM, see Fig. S1) in ANUDEM (Hutchinson, 2011). Annual mean temperature (8–12 °C) and precipitation (1293–1776 mm yr^{-1}) were estimated from monthly mean climate surfaces from 1921–1995 for each cell in the DEM using the BIOCLIM module in ANUCLIM (Xu & Hutchinson, 2011). Slope (1–31° of inclination) was derived from neighbouring cell geometry in the DEM (M. Hutchinson,

unpublished software). Topographic wetness index (TWI, –4.34–6.95) was calculated as a measure of available soil moisture [log(specific catchment/slope)] (Beven & Kirkby, 1979).

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

Analysis

We analysed the regeneration niche of *E. regnans* using six response variables: probability of seedling occurrence, seedling density and the probability of growing through four different height categories: 10, 25, 50 and 200 cm. We analysed height data only from burnt sites (moderate and high severity) because seedlings were virtually absent on unburnt sites, and only from 2010–2012 because, in 2009, 99% of seedlings were < 10 cm. Few unburnt sites were included in the density analysis (see below), thus the unburnt sites were predominantly used to investigate probability of seedling occurrence. Site-within-year was the observational unit for the probability of occurrence and density analyses, with data from the three plots at each site pooled. This scale is appropriate for our landscape-scale focus (Dale & Fortin, 2014). Individual seedling was the observational unit for the height analyses.

For the probability of seedling occurrence, we fitted binomial generalized linear mixed-effects models (GLMM) using the lme4 library (Bates *et al.*, 2013) in R 3.0 (R Core Team, 2013). For seedling density, there was a high proportion of zeros in our data (70%), so we modelled density conditional on presence (Smith *et al.*, 2014). To do this, we fitted a truncated negative binomial GLMM to analyse only the positive values in the data, using the glmmADMB library (Skaug *et al.*, 2013) in R. This accounted for overdispersion, previously identified in a subset of the data (Smith *et al.*, 2014). For seedling height, we used binomial GLMMs to analyse four separate cumulative logits: height > 10, > 25, > 50 and > 200 cm. This allowed us to examine factors affecting the probability of

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

					Model terms								
d.f.	log(*L*)	BIC	ΔBIC	BIC weight	TSF	Burn	Age	PC1	PC2	TSF × burn	TSF × Age	TSF × PC1	TSF × PC2
Probability of seedling occurrence													
7	−162.80	359.73	0.00	0.72	+	+				+			
Seedling density, conditional on presence													
8	−538.80	1110.88	0.00	0.28	+	+		+	+				
10	−535.63	1112.85	1.97	0.10	+	+		+	+	+			
Height > 10 cm													
3	−226.05	463.30	0.00	0.30	+								
5	−222.89	464.47	1.17	0.17	+			+				+	
Height > 25 cm													
4	−353.39	721.73	0.00	0.45	+	+							
Height > 50 cm													
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	+	+		+	+	+		+	
Height > 200 cm													
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	+	+			+	+			

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

growth at different stages of development. Our approach was similar to cumulative ordinal logistic regression (Agresti, 2010) but we analysed each height variable separately because the proportionality assumption was not met.

For each response, we fitted a global model with five main effects (time since fire + burn category + forest age + PC1 + PC2) and four interactions between time since fire and all other terms. Site was fitted as a random effect in all models to account for repeated sampling. In all models, time since fire was treated as ratio variable (0, 1, 2, 3) (Howitt & Cramer, 2011) as seedlings experience exponential declines over time (West *et al.*, 2009), corresponding to linear on the link (log) scale. There were no patterns (e.g. quadratic) in plots of final model residuals and time since fire, supporting the treatment of time as a ratio variable. We did not fit an interaction between burn category and forest age as this overparameterized our models given the limited number of sites when these categories were combined. To find a parsimonious model or set of models, we used a modified 'all subsets' model selection procedure, appropriate when all terms have potential importance (Stephens *et al.*, 2007; Doherty *et al.*, 2012). We included time in all models because we were interested in temporal changes and fitted all plausible combinations of the other terms using the MuMIn library (Bartoń, 2013) in R. This produced 81 candidate models for each response variable. We ranked models using the Bayesian information criterion (BIC) [−2 ln likelihood + (ln number of sites) (number of fitted parameters)] (Jones, 2011). We considered all models that differed in BIC from the top-ranked model (ΔBIC) by ≤ 2 to have support from the data (Hegyi & Garamszegi, 2011). We did not conduct model averaging because it biases parameter estimates, particularly when interactions are present (Freckleton, 2011; Hegyi & Garamszegi, 2011), but made inference from all models with a ΔBIC ≤ 2 (Table 2; see Table S1 for all models with ΔBIC ≤ 4; see Table S2 and Fig. S3 for estimates of models with ΔBIC ≤ 2). For factorial variables, we estimated the difference and 95% confidence interval between each pair of levels (e.g. moderate versus high severity fire) within the parameter (Fisher's Least Significant Difference). Differences were considered significant when confidence intervals did not include zero on the log scale.

To determine whether there was spatial autocorrelation in the residuals of our models, we produced variograms using the GEOR package (Ribeiro Jr & Diggle, 2001) in R for each year separately. We visually assessed autocorrelation at three spatial scales. For each scale, we divided the data into 10 evenly distributed spatial distance classes where the first class began at the minimum distance between sites. We generated three sets of distance classes representing three spatial scales by modifying the maximum distance class using the first quartile, third quartile and maximum distance between sites.

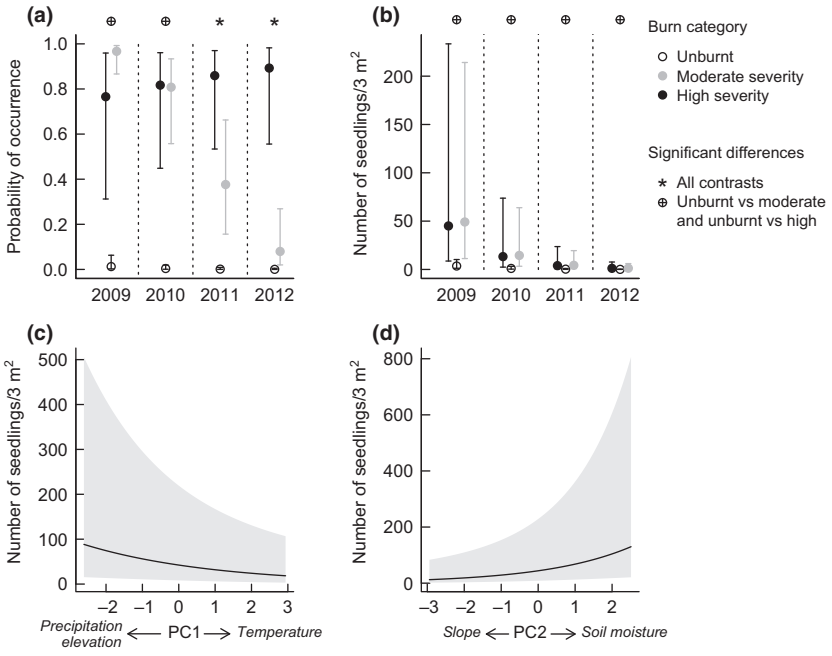

Figure 1 The regeneration niche in *Eucalyptus regnans* characterized by (a) the probability of seedling occurrence and (b–d) seedling density, conditional on presence (estimates and 95% confidence intervals from the first-ranked models). (a) Fire, regardless of severity, was the dominant driver of seedling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

There was no strong or consistent evidence of a sill that would indicate spatial autocorrelation in the model residuals (Liebhold & Sharov, 1998) (Fig. S4).

RESULTS

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

The probability of seedling growth over 10 cm was high on all burnt sites (Fig. 2a) and not strongly influenced by fire regime or environmental variables (Table 2). In 2010, growth over 10 cm was higher at low elevations (second-ranked model, Table 2, Fig. S3b), probably reflecting heavy snowfall suppressing growth at high elevations in 2010 (Fig. S2). In all survey years, the probability of growing over 25 cm was greater on severely burnt compared to moderately burnt sites (Table 2, Fig. 2b). Growth over 50 cm and 200 cm was also promoted by high-severity fire (Fig. 2c,e) and by increasing elevation and precipitation and decreasing temperature (PC1, Fig. 2d,f). Growth over 50 cm and 200 cm was more likely on flat terrain with high soil moisture availability (Table 2, Fig. S2c, d). Forest age did not affect any of the six response variables (Table 2).

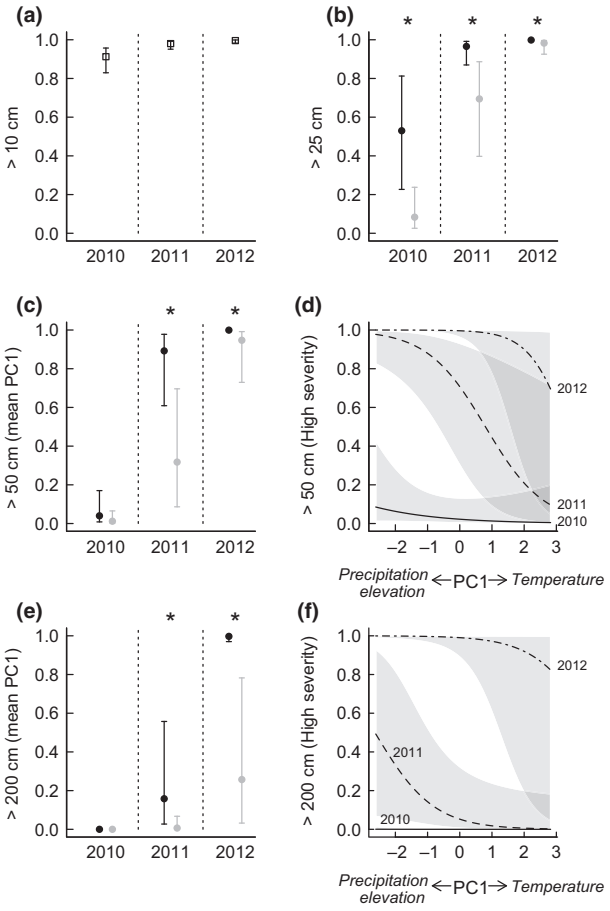

Figure 2 The regeneration niche in *Eucalyptus regnans* characterized by growth at different height stages on burnt sites (estimates and 95% confidence intervals from the first-ranked models). (a) The probability of growing > 10 cm was affected by time since fire. (b) High-severity fire increased the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

DISCUSSION

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

Seedling establishment

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

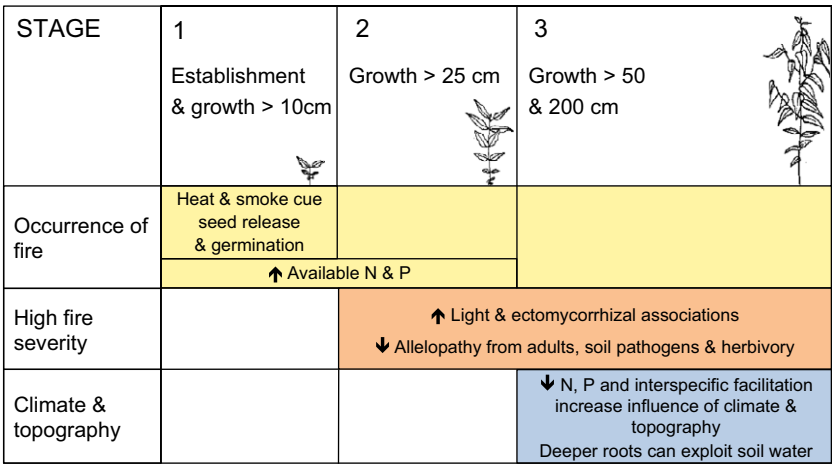

Figure 3 Fire severity and environmental variation drove regeneration niche shifts in *Eucalyptus regnans*. Factors affecting different stages of regeneration are indicated by the shaded panels and the potential mechanisms are listed within the panels (references for all mechanisms are given in the Discussion). Seedling pictures from Ashton (1975a).

establishment were similar on sites burnt at moderate and high severity. Seed reserves at this early stage of regeneration might reduce their reliance on light and soil nutrients (Pérez-Ramos *et al.*, 2012), and the greater shade and ground cover on moderately burnt sites probably allowed seedlings to retain water (Smith *et al.*, 2014).

Effects on growth

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

Growth over 50 cm and 200 cm increased with increasing elevation, precipitation and soil moisture and with decreasing temperature. The key aspect of this result is that these environmental variables did not influence earlier growth but became important as seedlings grew larger (Fig. 3). The increasing influence of soil moisture on height might reflect increased root growth and therefore increased ability to exploit soil water (Casper & Jackson, 1997). Seedling density had strongly declined by the time individuals reached 50 cm and 200 cm, which might have reduced facilitative effects of conspecifics (le Roux *et al.*, 2013) and increased reliance on abiotic factors.

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

Effects on density

Unlike the dynamic drivers of establishment and growth, we found temporally consistent, positive effects of high elevation, increased water availability and associated variables on seedling density. Survival and growth are often negatively

density-dependent (Metz *et al.*, 2010; Nottebrock *et al.*, 2013) so the influence of these environmental variables on seedling density might have limited influence on the longer-term viability of the species (ultimately there are only 40–80 stems/ha in 150 year old forest, Ashton & Attiwill, 1994). However, increases in initial seedling densities can buffer plant populations against herbivory (Clark *et al.*, 2012) and drought (Yates & Ladd, 2005). High regeneration densities might also increase fitness through both adaptive (Bailey *et al.*, 2013) and plastic (McNutt *et al.*, 2012) responses to intraspecific competition. For example, intraspecific competition can drive niche partitioning, making overall resource use more efficient (Boyden *et al.*, 2008) and can increase tolerance to herbivory (McNutt *et al.*, 2012). The positive effects of cool, wet environmental conditions on seedling density could therefore have positive effects on the short- and long-term persistence of *E. regnans*. Further research into biotic interactions in *E. regnans* forests is needed to assess the likelihood of elevational range shifts in this ecosystem as the climate continues to change (le Roux *et al.*, 2013; Kopp & Cleland, 2014).

CONCLUSIONS

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

ACKNOWLEDGEMENTS

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

REFERENCES

Agresti, A. (2010) Logistic regression models using cumulative logits. *Analysis of ordinal categorical data*, pp. 44–87. John Wiley & Sons, Inc., New Jersey.

Aguirre-Gutiérrez, J., Serna-Chavez, H.M., Villalobos-Arambula, A.R., Pérez de la Rosa, J.A. & Raes, N. (2015) Similar but not equivalent: ecological niche comparison across closely–related Mexican white pines. *Diversity and Distributions*, **21**, 245–257.

Ashton, D.H. (1975a) The root and shoot development of *Eucalyptus regnans* F. Muell. *Australian Journal of Botany*, **23**, 867–887.

Ashton, D.H. (1975b) The seasonal growth of *Eucalyptus regnans* F. Muell. *Australian Journal of Botany*, **23**, 239–252.

Ashton, D.H. (1975c) Studies of flowering behaviour in *Eucalyptus regnans* F. Muell. *Australian Journal of Botany*, **23**, 399–411.

Ashton, D.H. & Attiwill, P.M. (1994) Tall open-forests. *Australian vegetation* (ed.by R.H. Groves), pp. 157–196. Cambridge University Press, Melbourne.

Ashton, D.H. & Kelliher, K.J. (1996) The effect of soil desiccation on the nutrient status of *Eucalyptus regnans* F. Muell seedlings. *Plant and Soil*, **179**, 45–56.

Ashton, D.H. & Willis, E.J. (1982) Antagonisms in the regeneration of *Eucalyptus regnans* in the mature forest. *The plant community as a working mechanism* (ed.by E.I. Newman), pp. 113–128. British Ecological Society, London.

Bailey, S.F., Dettman, J.R., Rainey, P.B. & Kassen, R. (2013) Competition both drives and impedes diversification in a model adaptive radiation. *Proceedings of the Royal Society B*, **280**, 20131253.

Bartoń, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M. & Bolker, B. (2013) lme4: linear mixed-effects models using S4 classes. R package, version 0.999999-2. http://lme4.r-forge.r-project.org/.

Bell, D.M., Bradford, J.B. & Lauenroth, W.K. (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, **23**, 168–180.

Beven, K.J. & Kirkby, M.J. (1979) A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin*, **24**, 43–69.

Bowman, D.M.J.S., Murphy, B.P., Neyland, D.L.J., Williamson, G.J. & Prior, L.D. (2014) Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Global Change Biology*, **20**, 1008–1015.

Boyden, S., Binkley, D. & Stape, J.L. (2008) Competition among *Eucalyptus* trees depends on genetic variation and resource supply. *Ecology*, **89**, 2850–2859.

Bragg, J.G., Supple, M.A., Andrew, R.L. & Borevitz, J.O. (2015) Genomic variation across landscapes: insights and applications. *New Phytologist*, **207**, 953–967.

Brueck, H. (2008) Effects of nitrogen supply on water-use efficiency of higher plants. *Journal of Plant Nutrition and Soil Science*, **171**, 210–219.

Bykova, O., Chuine, I., Morin, X. & Higgins, S.I. (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography*, **39**, 2191–2200.

Casper, B.B. & Jackson, R.B. (1997) Plant competition underground. *Annual Review of Ecology and Systematics*, **28**, 545–570.

Clark, C.J., Poulsen, J.R. & Levey, D.J. (2012) Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality. *Ecology*, **93**, 554–564.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, **111**, 1119–1144.

Cunningham, T.M. (1957) Seed production and seed fall of *Eucalyptus regnans* (F. Muell). *Australian Forestry*, **21**, 30–39.

Dale, M.R. & Fortin, M.-J. (2014) Spatial concepts and notions. *Spatial analysis: a guide for ecologists*, pp. 1–31. Cambridge University Press, Cambridge, UK.

Doherty, P.F., White, G.C. & Burnham, K.P. (2012) Comparison of model building and selection strategies. *Journal of Ornithology*, **152**, S317–S323.

Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J., Clarke, M.F., Dexter, N., Fensham, R., Friend, G., Gill, A.M., James, S., Kay, G., Keith, D.A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J.E.M., Williams, R.J. & York, A. (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation*, **143**, 1928–1939.

Eriksson, O. (2002) Ontogenetic niche shifts and their implications for recruitment in three clonal *Vaccinium* shrubs: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Vaccinium oxycoccos*. *Canadian Journal of Botany*, **80**, 635–641.

Freckleton, R. (2011) Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioral Ecology and Sociobiology*, **65**, 91–101.

Gabler, C.A. & Siemann, E. (2013) Rapid ontogenetic niche expansions in invasive Chinese tallow tree permit establishment in unfavourable but variable environments and can be exploited to streamline restoration. *Journal of Applied Ecology*, **50**, 748–756.

Gill, A.M. (1975) Fire and the Australian flora: a review. *Australian Forestry*, **38**, 4–25.

Gill, A.M. & Catling, P.C. (2002) Fire regimes and biodiversity of forested landscapes of southern Australia. *Flammable Australia: the fire regimes and biodiversity of a continent* (ed.by R.A. Bradstock, J.E. Williams and A.M. Gill), pp. 351–369. Cambridge University Press, Cambridge.

Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.

Hegyi, G. & Garamszegi, L. (2011) Using information theory as a substitute for stepwise regression in ecology and behavior. *Behavioral Ecology and Sociobiology*, **65**, 69–76.

Hollingsworth, T.N., Johnstone, J.F., Bernhardt, E.L. & Chapin, F.S. III (2013) Fire severity filters regeneration traits to shape community assembly in Alaska's boreal forest. *PLoS One*, **8**, e56033.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Lima, M., López, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtali, M.A., Richter, M., Sabaté, S. & Squeo, F.A. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87–95.

Howitt, D. & Cramer, D. (2011) *Introduction to statistics in psychology*, 5th edn. Pearson Education Limited, Essex, UK.

Hutchinson, M.F. (2011) *ANUDEM version 5.3, user guide*. Fenner School of Environment and Society, Australian National University, Canberra.

Iles, T.M., Ashton, D.H., Kelliher, K.J. & Keane, P.J. (2010) The effect of *Cylindrocarpon destructans* on the growth of *Eucalyptus regnans* seedlings in air-dried and undried forest soil. *Australian Journal of Botany*, **58**, 133–140.

Johnstone, J.F. & Chapin, F.S. III (2006) Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems*, **9**, 14–31.

Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S. & Mack, M.C. (2010) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, **16**, 1281–1295.

Jones, R.H. (2011) Bayesian information criterion for longitudinal and clustered data. *Statistics in Medicine*, **30**, 3050–3056.

King, D.A., Bachelet, D.M. & Symstad, A.J. (2013) Climate change and fire effects on a prairie–woodland ecotone: projecting species range shifts with a dynamic global vegetation model. *Ecology and Evolution*, **3**, 5076–5097.

Knight, T.M. & Holt, R.D. (2005) Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. *Ecology*, **86**, 587–593.

Knox, K.J.E. & Clarke, P.J. (2006) Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands. *Oecologia*, **149**, 730–739.

Kopp, C.W. & Cleland, E.E. (2014) Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. *Journal of Vegetation Science*, **25**, 135–146.

Launonen, T.M., Ashton, D.H. & Keane, P.J. (1999) The effect of regeneration burns on the growth, nutrient acquisition and mycorrhizae of *Eucalyptus regnans* F. Muell. (mountain ash) seedlings. *Plant and Soil*, **210**, 273–283.

Launonen, T.M., Ashton, D.H., Kelliher, K.J. & Keane, P.J. (2004) The growth and P acquisition of *Eucalyptus regnans*

F. Muell. seedlings in air-dried and undried forest soil in relation to seedling age and ectomycorrhizal infection. *Plant and Soil*, **267**, 179–189.

Liebhold, A. & Sharov, A. (1998) Testing for correlation in the presence of spatial autocorrelation in insect count data. *Population and community ecology for insect management and conservation* (ed. by J. Baumgartner), pp. 111–117. A.A. Balkema, Rotterdam, Netherlands.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F. & Franklin, J.F. (2000) Structural features of old-growth Australian montane ash forests. *Forest Ecology and Management*, **134**, 189–204.

Lindenmayer, D.B., Cunningham, R.B., MacGregor, C., Incoll, R.D. & Michael, D. (2003) A survey design for monitoring the abundance of arboreal marsupials in the central highlands of Victoria. *Biological Conservation*, **110**, 161–167.

Lindenmayer, D.B., Likens, G.E. & Franklin, J.F. (2010) Rapid responses to facilitate ecological discoveries from major disturbances. *Frontiers in Ecology and the Environment*, **8**, 527–532.

Lindenmayer, D.B., Blanchard, W., McBurney, L., Blair, D., Banks, S.C., Driscoll, D.A., Smith, A.L. & Gill, A.M. (2014) Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers. *Diversity and Distributions*, **20**, 467–477.

Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, **18**, 797–805.

Mackey, B.G., Lindenmayer, D.B., Gill, A.M., McCarthy, M.A. & Lindesay, J. (2002) *Wildlife, fire and future climate: a forest ecosystem analysis*. CSIRO Publishing, Collingwood.

Matías, L., Zamora, R. & Castro, J. (2011) Repercussions of simulated climate change on the diversity of woody-recruit bank in a Mediterranean-type ecosystem. *Ecosystems*, **14**, 672–682.

McCarthy, M.A., Gill, A.M. & Lindenmayer, D.B. (1999) Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. *Forest Ecology and Management*, **124**, 193–203.

McNutt, D., Halpern, S., Barrows, K. & Underwood, N. (2012) Intraspecific competition facilitates the evolution of tolerance to insect damage in the perennial plant *Solanum carolinense*. *Oecologia*, **170**, 1033–1044.

Metz, M.R. (2012) Does habitat specialization by seedlings contribute to the high diversity of a lowland rain forest? *Journal of Ecology*, **100**, 969–979.

Metz, M.R., Sousa, W.P. & Valencia, R. (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology*, **91**, 3675–3685.

Moreira, B., Tormo, J., Estrelles, E. & Pausas, J.G. (2010) Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. *Annals of Botany*, **105**, 627–635.

Morrison, D.A. (2002) Effects of fire intensity on plant species composition of sandstone communities in the Sydney region. *Austral Ecology*, **27**, 433–441.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, **23**, 638–647.

Nottebrock, H., Esler, K.J. & Schurr, F.M. (2013) Effects of intraspecific and community density on the lifetime fecundity of long-lived shrubs. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 150–161.

Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T. & Vallejo, R. (2003) Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. *Plant Ecology*, **169**, 205–213.

Pérez-Ramos, I.M., Urbieta, I.R., Zavala, M.A. & Marañón, T. (2012) Ontogenetic conflicts and rank reversals in two Mediterranean oak species: implications for coexistence. *Journal of Ecology*, **100**, 467–477.

R Core Team. (2013) *R: a language and environment for statistical computing*. http://www.R-project.org, R Foundation for Statistical Computing, Vienna, Austria.

Rau, B.M., Blank, R.R., Chambers, J.C. & Johnson, D.W. (2007) Prescribed fire in a Great Basin sagebrush ecosystem: dynamics of soil extractable nitrogen and phosphorus. *Journal of Arid Environments*, **71**, 362–375.

Ribeiro, P.J. Jr & Diggle, P.J. (2001) geoR: A package for geostatistical analysis. *R News*, **1**, 14–18.

Romme, W.H., Boyce, M.S., Gresswell, R., Merrill, E.H., Minshall, G.W., Whitlock, C. & Turner, M.G. (2011) Twenty years after the 1998 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems*, **14**, 1196–1215.

le Roux, P.C., Shaw, J.D. & Chown, S.L. (2013) Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist*, **200**, 241–250.

Silvestrini, R.A., Soares-Filho, B.S., Nepstad, D., Coe, M., Rodrigues, H. & Assunção, R. (2011) Simulating fire regimes in the Amazon in response to climate change and deforestation. *Ecological Applications*, **21**, 1573–1590.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. (2013) Generalized linear mixed models using AD Model Builder. R package, version 0.7.4. http://glmmadmb.r-forge.r-project.org/.

Smith, A.L., Blair, D., McBurney, L., Banks, S.C., Barton, P.S., Blanchard, W., Driscoll, D.A., Gill, A.M. & Lindenmayer, D.B. (2014) Dominant drivers of seedling establishment in a fire-dependent obligate seeder: climate or fire regimes? *Ecosystems*, **17**, 258–270.

Smithwick, E.A.H., Turner, M.G., Mack, M.C. & Chapin, F.S. III (2005) Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems*, **8**, 163–181.

Staver, A.C., Bond, W.J., Cramer, M.D. & Wakeling, J.L. (2012) Top-down determinants of niche structure and adaptation among African Acacias. *Ecology Letters*, **15**, 673–679.

Stephens, P.A., Buskirk, S.W. & Martínez del Rio, C. (2007) Inference in ecology and evolution. *Trends in Ecology and Evolution*, **22**, 192–197.

Stephens, S.L., Agee, J.K., Fulé, P.Z., North, M.P., Romme, W.H., Swetnam, T.W. & Turner, M.G. (2013) Managing forests and fire in changing climates. *Science*, **342**, 41–42.

Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G. & van Wagtendonk, J.W. (2014) Temperate and boreal forest mega-fires: characteristics and challenges. *Frontiers in Ecology and the Environment*, **12**, 115–122.

Swab, R.M., Regan, H.M., Keith, D.A., Regan, T.J. & Ooi, M.K.J. (2012) Niche models tell half the story: spatial context and life-history traits influence species responses to global change. *Journal of Biogeography*, **39**, 1266–1277.

Syphard, A.D., Regan, H.M., Franklin, J., Swab, R.M. & Bonebrake, T.C. (2013) Does functional type vulnerability to multiple threats depend on spatial context in Mediterranean-climate regions? *Diversity and Distributions*, **19**, 1263–1274.

Turner, M.G., Romme, W.H. & Tinker, D.B. (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.

Turner, M.G., Smithwick, E.A.H., Metzger, K.L., Tinker, D.B. & Romme, W.H. (2007) Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proceedings of the National Academy of Sciences USA*, **104**, 4782–4789.

Vivian, L.M., Cary, G.J., Bradstock, R.A. & Gill, A.M. (2008) Influence of fire severity on the regeneration, recruitment and distribution of eucalypts in the Cotter River Catchment, Australian Capital Territory. *Austral Ecology*, **33**, 55–67.

Wan, S., Hui, D. & Luo, Y. (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications*, **11**, 1349–1365.

West, G.B., Enquist, B.J. & Brown, J.H. (2009) A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences USA*, **106**, 7040–7045.

Weston, C.J. & Attiwill, P.M. (1990) Effects of fire and harvesting on nitrogen transformations and ionic mobility in soils of *Eucalyptus regnans* forests of south-eastern Australia. *Oecologia*, **83**, 20–26.

Wood, S.W., Hua, Q., Allen, K.J. & Bowman, D.M.J.S. (2010) Age and growth of a fire prone Tasmanian temperate old-growth forest stand dominated by *Eucalyptus regnans*, the world's tallest angiosperm. *Forest Ecology and Management*, **260**, 438–447.

Xu, T. & Hutchinson, M.F. (2011) *ANUCLIM version 6.1, user guide*. Fenner School of Environment and Society, Australian National University, Canberra.

Yang, J., Weisberg, P., Shinneman, D., Dilts, T., Earnst, S. & Scheller, R. (2015) Fire modulates climate change response of simulated aspen distribution across topoclimatic gradients in a semi-arid montane landscape. *Landscape Ecology*, **30**, 1055–1073.

Yates, C.J. & Ladd, P.G. (2005) Relative importance of reproductive biology and establishment ecology for persistence of a rare shrub in a fragmented landscape. *Conservation Biology*, **19**, 239–249.

Zimmermann, J., Higgins, S.I., Grimm, V., Hoffmann, J., Münkemüller, T. & Linstädter, A. (2008) Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. *Journal of Ecology*, **96**, 1033–1044.

SUPPORTING INFORMATION

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

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

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

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

Figure S2 Total annual rainfall and long-term rainfall averages.

Figure S3 Estimates from models that differed in the Bayesian information criterion from the top model by ≤2.

Figure S4 Variograms of model residuals for each response variable.

BIOSKETCH

ALS investigates ecological and evolutionary aspects of fire regimes. Her co-authors have interests in statistics, forest ecology, biodiversity conservation, dispersal, ecological genetics and making movies about scientific research.

Author contributions: All authors designed study; D.P.B., L.M. and D.B.L. collected data; A.L.S. and W.B. analysed data; and A.L.S. wrote the manuscript, incorporating input from all authors.

Editor: David Richardson