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ECOLOGICAL SOUNDINGS

The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests

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ABSTRACT

Forests that regenerate exclusively from seed following high-severity fire are particularly vulnerable to local extinction if fire frequency leaves insufficient time for regenerating plants to reach sexual maturity. We evaluate the relative importance of extrinsic (such as fire weather and climate cycles) and intrinsic (such as proneness to fire due to stand age and structural development) factors in driving the decline of obligate seeder forests. We illustrate this using obligate seeding alpine ash (*Eucalyptus delegatensis*) forests in the montane regions of Victoria, Australia, that were burnt by megafires in 2003 (142,256 ha) or 2007 (79,902 ha), including some twice-burnt areas (11,599 ha). Geospatial analyses showed only a small effect of stand age on the remote sensing estimates of crown defoliation, but a substantial effect of forest fire weather, as measured by forest fire danger index (FFDI). Analysis of meteorological data over the last century showed that 5-year increases in FFDI precede cycle major fires in the *E. delegatensis* forests. Such strong extrinsic climate/weather driving of high-severity fires is consistent with the 'interval squeeze model' that postulates the vulnerability of obligate seeder forests to landscape-scale demographic collapse in response to worsening fire weather under climate change.

Keywords

Alternative stable state, Australia, climate change, disturbance ecology, *Eucalyptus*, forest regeneration, landscape ecology, wildfire.

INTRODUCTION

Around the world, forest ecosystems are under increasing environmental stress due to rapid environmental change, and this is particularly true for fire-dependent ecosystems. Fire seasons are lengthening and becoming more extreme (Jolly *et al.*, 2015), causing a global trend for more frequent, extensive high-severity fires that are becoming known as 'megafires' (Adams, 2013). According to alternative stable state theory, this tempo of fire activity is increasing the risk of shifts in the composition and structure of forests, and in some cases can drive replacement of forest by non-forest vegetation (Moritz *et al.*, 2004; Mermoz *et al.*, 2005; Savage & Mast, 2005; Odion *et al.*, 2010; Wood & Bowman, 2011; Bowman *et al.*, 2013). Recovery from such a loss of forests can be extremely slow, if not impossible. The most vulnerable ecosystems to such 'state shift' are forests that have limited capacity to regenerate vegetatively and rely on seedlings to recruit after fire disturbance, a strategy known as 'obligate seeding'. Obligate seeders require long fire-free intervals to allow trees to mature and accumulate seedbanks. Typically, they have seedbanks stored in the canopy (serotiny) or soil, and seed germination is dependent on, or stimulated by, fire. Most conifers in the Mediterranean basin are obligate seeders (Núñez & Calvo, 2000), and obligate seeders dominate the vast boreal forests of Eurasia and North America as well as the iconic conifer forests of the northern US Rocky Mountains (Turner *et al.*, 2003). These boreal and sub-alpine forests are characteristically subject to infrequent but severe stand-replacing fires that burn during unusually hot, dry periods (Turner *et al.*, 2003).

OBLIGATE SEEDER EUCALYPT FOREST

The shift between forest and non-forest states is well illustrated by reference to Australia's ash eucalypt forests,

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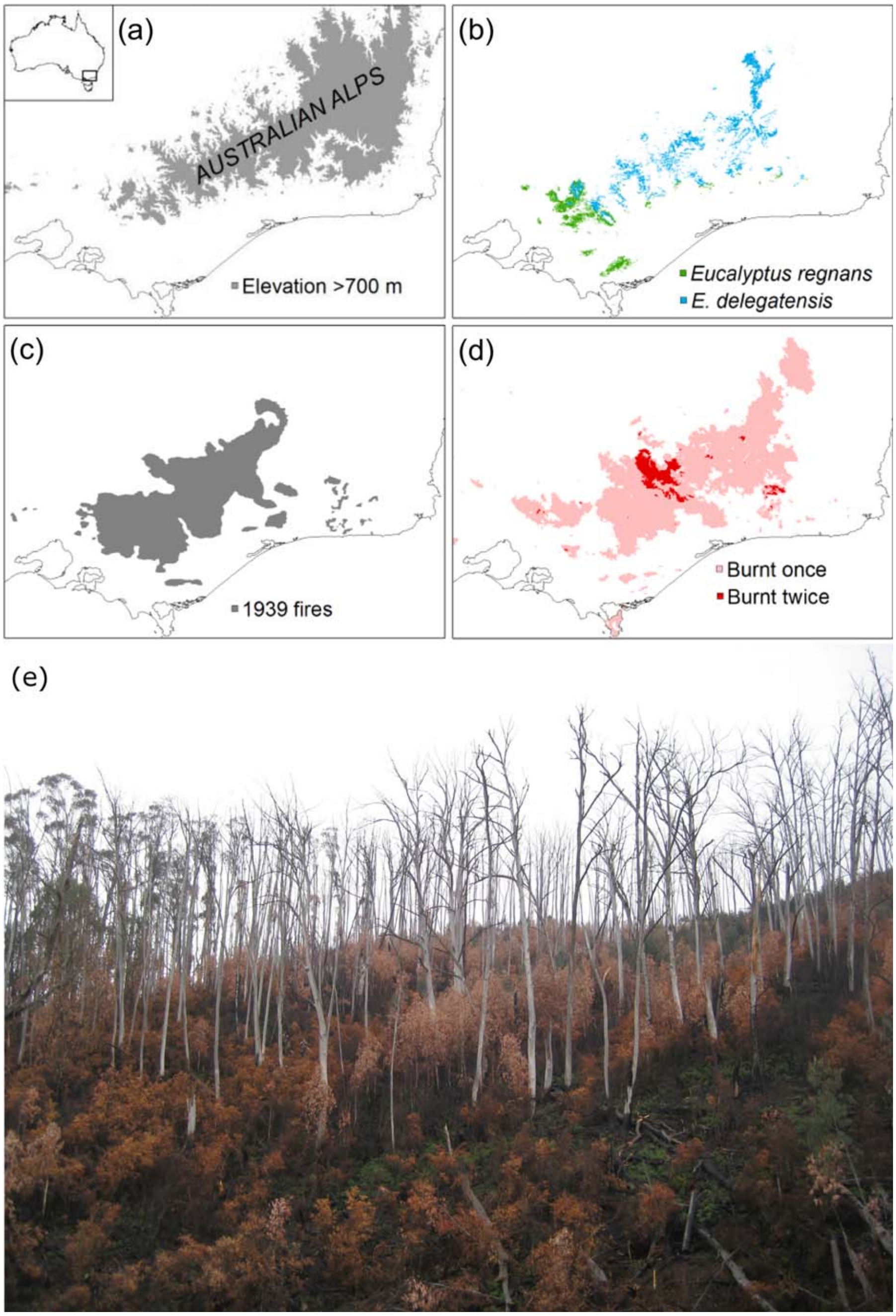

Figure 1 (a) Obligate seeder eucalypt forests (*Eucalyptus regnans*, *Eucalyptus delegatensis*) occur in the high-rainfall, montane areas of south-eastern Australia. (b) Within this high-rainfall zone, *E. regnans* is replaced by *E. delegatensis* at higher elevations. (c) Extensive fires occurred in the summer of 1939, converting large areas of obligate seeder eucalypt forest to even-aged stands. (d) Some areas of forest were burnt by both the 2003 and the 2007 fires, and this has resulted in the local population collapse of some stands (e). Photo: David Bowman.

dominated by the obligate seeding species mountain ash (*Eucalyptus regnans*) and alpine ash (*Eucalyptus delegatensis*). These two species are among the tallest flowering plants on Earth, and the forests they form are important for biodiversity as well as their extremely high carbon density (Jackson, 1968; Keith *et al*., 2009; Lindenmayer *et al*., 2011; Tng *et al*., 2012; Bowman *et al*., 2014; Enright *et al*., 2015) (Fig. 1). In brief, fire disturbance drives the stand dynamics of ash eucalypt forests because fire stimulates pulses of regeneration by creating a receptive seedbed (competition-free, nutrient-enriched mineral soil), stimulating the release of canopy-stored seeds and removing aboveground competition from established trees (Fagg *et al*., 2013). If fire intervals are shorter than the time required for regenerating seedlings to reach reproductive maturity (*c.* 20 years) then local populations collapse, resulting in local extinction of the ash eucalypts (Bassett *et al*., 2015). Ash eucalypts do not have a soil seedbank, so regeneration on sites where local populations have collapsed depends on dispersal of seeds from adjacent trees (Fig. 2a). Seed dispersal distances tend to be very short (up to approximately the height of one tree, typically 65 m; Cunningham, 1957), so recolonization of large areas is expected to be very slow. Bowman *et al.* (2013) have suggested that climate change could increase the likelihood of state change in these and other obligate seeder forests (Fig. 2b).

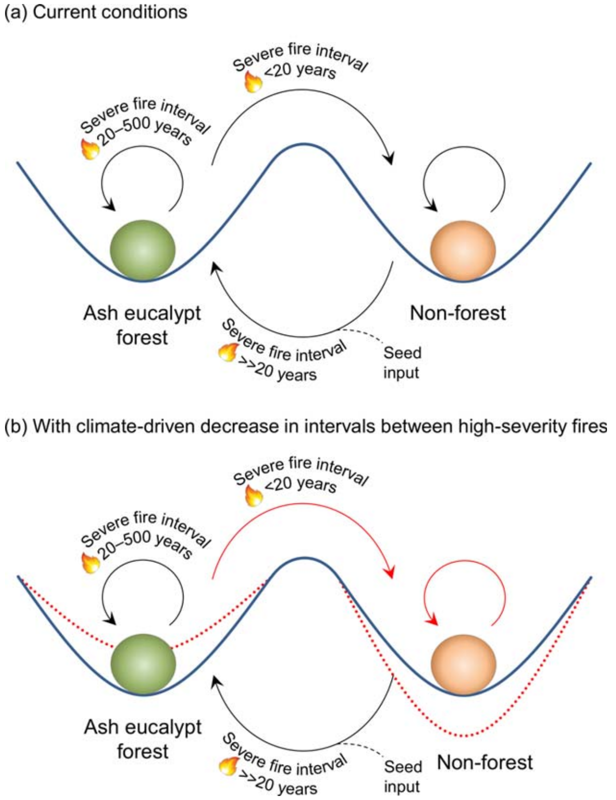

Figure 2 (a) 'Ball and cup' conceptual model of ash eucalypt forest dynamics in south-eastern Australia, consistent with Jackson (1968) and McCarthy *et al.* (1999). The troughs represent stable 'basins of attraction', or alternative stable states. The perpetuation of ash eucalypt forest depends on a regime of high-severity (i.e. stand-replacing) fires occurring at intervals greater than the time required for ash eucalypts to reach reproductive maturity (*c.* 20 years) and less than the lifespan of ash eucalypt trees (*c.* 500 years). If high-severity fires occur too frequently, then ash eucalypts are lost from a site and must recolonize from neighbouring mature forest. Panel (b) indicates how climate-driven shortening of intervals between high-severity fires (indicated by the red arrows) can increase both the rate of conversion of ash eucalypt forest to non-forest states, and the maintenance of non-forest vegetation in that state. This results in the forest 'basin of attraction' becoming shallower (i.e. a higher likelihood of departure from the forest state), and a deepening of the non-forest 'basin of attraction' (i.e. a higher likelihood of remaining in the non-forest state). Adapted from Bowman *et al.* (2013).

FIRE WEATHER OR STAND AGE?

There are two prominent ecological models that provide a mechanistic basis for abrupt vegetation changes as predicted by alternative stable state theory: the 'landscape trap' model (Lindenmayer *et al.*, 2011) and the 'interval squeeze model' (Enright *et al.*, 2015). A key point of difference between these models is the emphasis on the relative importance of *intrinsic* and *extrinsic* drivers of state change. The 'landscape trap' model posits that changes to forest structure following disturbance (from both fire and logging) can render forested landscapes vulnerable to re-burning, and hence increase the likelihood of state change because of increased fire hazard (McCarthy *et al.*, 1999; Hardy, 2005) due to changed fuel arrays and understorey microclimate. By contrast, the 'interval squeeze' model stresses the extrinsic drivers of climatic warming and drying that simultaneously increase the frequency of high-severity fires and affect vital demographic rates (such as time to maturity, fecundity and seedling establishment) (Enright *et al.*, 2015). Interval squeeze is also affected by the interactions between climate, fire and demographic processes. For example, in low-elevation lodgepole pine (*Pinus contorta*) forests, serotiny increases markedly with stand age (Schoennagel *et al.*, 2003), and in *E. delegatensis*, there is very little seed produced by surviving trees for 3–5 years following fire because floral buds are aborted at the time of the fire (Fagg *et al.*, 2013). Furthermore, under climate change, fire seasons are starting earlier at a time when the aerial seed crop of *E. delegatensis* is immature, increasing the risk of regeneration failure (Fagg *et al.*, 2013). However, some of these effects could be offset by possible increases in fecundity as a result of elevated CO_2, as has been demonstrated for loblolly pine (*Pinus taeda*) (Way *et al.*, 2010).

Understanding the relative importance of intrinsic and extrinsic drivers is critical for evaluating the risk to obligate seeder forests, thereby progressing the development of predictive models of species distributions and land-cover change (Porfirio *et al.*, 2014; Keppel *et al.*, 2015) and as well as guiding managers as to the most appropriate fire regimes to conserve flammable forests at risk of abrupt state change (Bowman *et al.*, 2013; Fairman *et al.*, 2015). To date, the only test of the landscape trap model has been a landscape ecology study by Taylor *et al.* (2014) in *E. regnans* forests in Victoria, Australia, that were burnt by the extreme bushfires of 2009. These authors found that young stands of *E. regnans* were more likely to be affected by high-severity fires than older stands, as predicted by the landscape trap model. This finding led them to conclude that logging in *E. regnans* forests is increasing the risk of abrupt state change, a view that has been disputed by some forest managers (Ferguson & Cheney, 2011).

Closely following the analytical approach of Taylor *et al.* (2014), we compared the extrinsic effect of extreme fire with the intrinsic effect of stand age in predicting high-severity fires in obligate seeder eucalypt forests. We used *E. delegatensis* forests burnt in the 2003 and 2007 alpine fires in the state of Victoria, Australia, as our study system (Fig. 1). The 2003 fires burnt 142,000 ha of *E. delegatensis* forest over 44 days and the 2007 fires burnt 80,000 ha over 60 days, thereby occurring over a wide range of fire weather conditions and disturbance histories, including large areas of *E. delegatensis* forest, some of which were burnt by both fires (Fairman *et al.*, 2015). Of the 71,802 ha of *E. delegatensis* forest burnt by high-severity or very high-severity fires in 2003, 6.3% was reburnt by fires of similar severity in 2007 (Table 1). Since the 1970s there has been a steady increase in the severity of fire weather (Clarke *et al.*, 2013) that has led to a sharp

Table 1 Areas of *Eucalyptus delegatensis* burnt by extensive fires in 2003 and 2007, including some areas burnt in both 2003 and 2007.

	Area burnt (ha)		
Severity Class	2003	2007	2003 and 2007
Very high severity (crown burn)	12,175	16,880	2181
High severity	59,627	20,239	2311
Moderate severity	19,804	19,171	3963
Low severity	50,650	23,612	3144
Total	142,256	79,902	11,599

increase the area burnt in *E. delegatensis* forests (Fairman *et al.*, 2015).

Using a statistical model that controlled for variation in terrain and past disturbance history, we found the dominant influence to be fire weather (indicated by the forest fire danger index, FFDI) with only minor effects of stand age on the probability of stands being killed by fire (Fig. 3). Under extreme fire weather conditions ($FFDI > 50$) the probability of crown-defoliating fires is 63–73% and this falls to 33–40% under low to moderate conditions ($FFDI < 10$). This relationship is the same for both young and old stands, albeit with a small offset of 7% (Fig. 3). We found a much stronger effect of fire weather than stand age in predicting high-severity fires in *E. delegatensis* obligate seeder forests. As outlined below, we argue that these results suggest that extrinsic factors more strongly influence the risk of state change in obligate seeder forests than do intrinsic factors.

A feature of regenerating flammable forests in the Southern Hemisphere is that fire hazard initially increases with time as fuel loads increase, and then decreases as the forest matures and fuel moisture increases (Jackson, 1968; Perry *et al.*, 2015; Whitlock *et al.*, 2015), a pattern described by McCarthy *et al.* (1999) as the 'moisture model'. Such a pattern is in marked contrast to fire-adapted ponderosa pine (*Pinus ponderosa*) forests in the USA, where fire suppression has led to an intrinsically increased risk of high-severity fires (Allen *et al.*, 2002). These contrasting patterns in probability of fire produce very different levels of resilience to changes in ignition rates and climatic variability (Kitzberger *et al.*, 2011). In forests where flammability declines as the trees mature (as observed in Southern Hemisphere forests), fire regimes and community states are more likely to shift in response to climate change (Kitzberger *et al.*, 2011). Stands of *E. delegatensis* regenerating after a recent high-severity fire have been shown to have a higher mass of shrubs than long-unburnt stands (Bowman *et al.*, 2014), and this no doubt contributes to the observed higher risk of high-severity fires in young compared with older stands found in our study (Fig. 3). Taylor *et al.* (2014) also found that immature (<25 years) *E. regnans* forests had a slightly higher probability of experiencing high-severity fires (defoliating entire crowns and killing trees). However, in both these studies the difference in the risk of high-severity fires in regenerating stands compared with older stands was quite small (Fig. 4a; *E. regnans* 96% vs. 76% and *E. delegatensis* 48% vs. 40%). It is important to note that the comparison between these studies is valid, given that our method closely followed that of Taylor *et al.* (2014).

Our finding that the intrinsic effect of stand age on fire hazard is minor, relative to extrinsic effects, also harmonizes with the modelling by McCarthy *et al.* (1999). Those authors investigated the effect of increased fire hazard in regenerating forests of the obligate seeder *E. regnans* relative to the effect of mean fire interval (Fig. 4b). To do this, they contrasted a hazard function termed the 'moisture model' with a null model where fire hazard remains constant through time. Their moisture model hazard function is a reasonable approximation of the observed increase in risk of high-severity fire found in our study and that of Taylor *et al.* (2014). The analysis by McCarthy *et al.* (1999) demonstrated that, compared with the dominant effect of shortening fire intervals below *c.* 50 years, there was a negligible difference between the 'moisture model' and null model hazard functions in terms of changing the extent of *E. regnans* forests (Fig. 4c).

The strong extrinsic effect of fire weather, regardless of stand age, in *E. delegatensis* forests (Fig. 3) is consistent with the analysis by Price & Bradstock (2012) of the 2009 Victorian fires using the same remotely sensed estimates of fire severity as used in our study. Those authors found that under extreme fire weather conditions, high-severity fires occurred in *Eucalyptus* forests regardless of past disturbance history, supporting the observations of Ferguson & Cheney (2011) who argue that fire intensity and rate of spread depend more on terrain and weather than on fuels. A

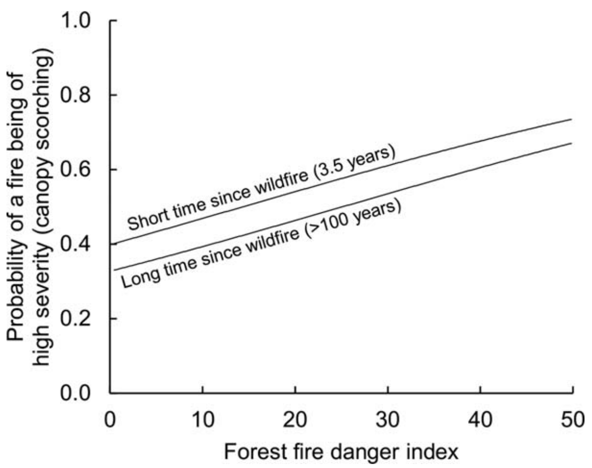

Figure 3 Empirically derived variation in the probability of a fire being of high severity (scorching the canopy), and probably stand-replacing, in *Eucalyptus delegatensis* forest, in response to fire weather (forest fire danger index). The effect of time since wildfire is shown, with separate predictions for short (3.5 years, the interval at which the probability of high-severity fire peaks) and long (>100 years) times since wildfire.

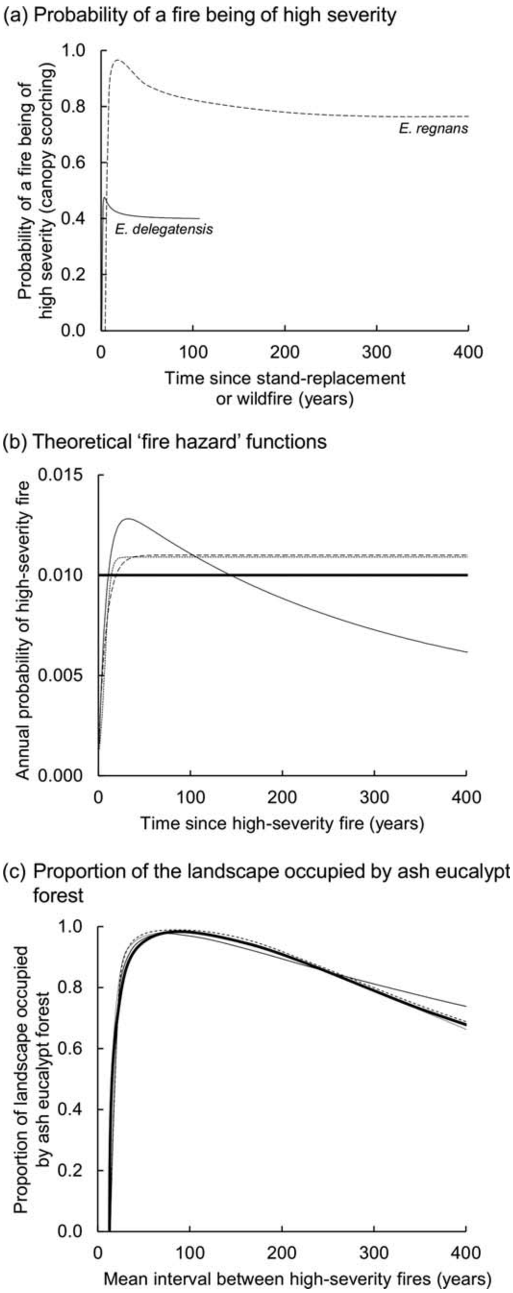

Figure 4 (a) Empirically derived variation in the probability of a fire being of high severity (scorching the canopy), and probably stand-replacing, in *Eucalyptus regnans* forest (Taylor *et al.*, 2014) (varying with time since stand replacement) and *E. delegatensis*, in this study (varying with time since previous wildfire; see Appendix S1 in the Supporting Information). These conform most closely to the moisture model (solid thin line in b). (b) Annual probability of high-severity stand-replacing fires in ash eucalypt forest as a function of time since the last high-severity fire, according to two theoretical 'hazard functions' examined by McCarthy *et al.* (1999): null model, with a constant hazard, and the 'moisture model', with an initially increasing, then a decreasing, hazard. (c) Results of simulation modelling by McCarthy *et al.* (1999), showing the proportion of the landscape with *E. regnans* as a function of mean fire interval, using the two contrasting theoretical hazard functions shown in (b).

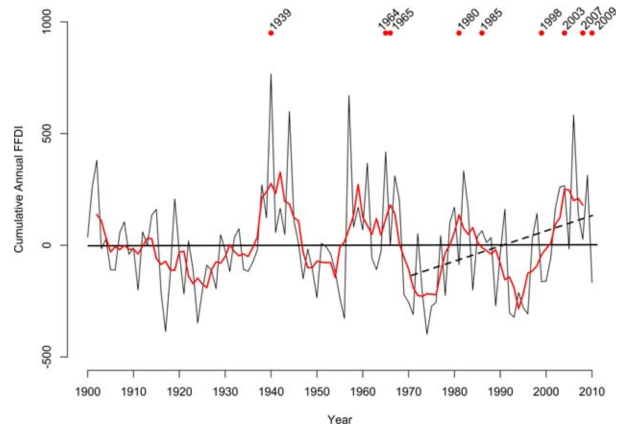

Figure 5 Forest fire danger index (FFDI) for the Australian Alps bioregion since 1900, showing the annual sum of daily deviations from the mean daily FFDI, averaged across all weather stations in the bioregion. The positive trend since the 1970s (dashed line) is well documented (Clarke *et al.*, 2013). Over the whole 114-year record, there is no trend (solid black line), yet there are distinct phases of high and low FFDI, with a period of about 20 years (solid red line: 5-year running mean). The years when fires burnt more than 5000 ha of *E. delegatensis* are shown by red dots.

number of studies from obligate seeder communities around the world have shown how fire weather can override the influence of fuels on the occurrence of stand-replacing fires (Salvador *et al.*, 2005). Examples include the Californian chaparral (Moritz *et al.*, 2004), and high-elevation conifer forests in the western USA (Turner *et al.*, 2003).

TRENDS IN FIRE WEATHER

Trends in FFDI over the last century in the domain of *E. delegatensis* have clear multi-decadal cycles driven by inter-annual drought, but with no long-term trend yet apparent (Fig. 5) (White *et al.*, 2003). Major fires that burnt at least 5000 ha of *E. delegatensis* forest generally occurred following a period of above average FFDI. In particular the 2003 and 2007 fires are associated with high FFDI (Figs 1 & 5). The decades following the 1939 fires were characterized by moderate fire weather conditions, allowing large expanses of immature forest, vulnerable to high-severity fires, to remain unburnt and thus avoid state change (Fig. 5). The projected trend for more extreme fire weather in the Australian Alps (Clarke *et al.*, 2011; King *et al.*, 2011; Bradstock *et al.*, 2014) suggests that stands regenerating after the fires of the 2000s could be more likely to experience repeat fires (<20-year intervals) than those regenerating after the 1939 fires.

We argue that the available evidence supports the recent 'interval squeeze' model (Enright *et al.*, 2015) by showing the pronounced effect of weather and climate on the occurrence of high-severity fires. While fire hazard is shown to increase after disturbance, as predicted by the landscape trap model (Lindenmayer *et al.*, 2011), this intrinsic effect is much smaller than the extrinsic effect of fire weather and climate.

The predominance of extrinsic drivers of high-severity fires is concerning given global warming and associated severe fire weather, which can potentially threaten diverse obligate seeder ecosystems around the world. Westerling *et al.* (2011), for instance, concluded that by the mid-21st century, increased fire frequency and extent driven by climate change would be 'inconsistent with the persistence of the current suite of conifer species' in Yellowstone National Park, USA. Predictive species distribution models for obligate seeder species that do not include the demographic impacts of frequent high-severity fires are likely to underestimate the rate of change in the distribution of obligate seeder forests (Porfirio *et al.*, 2014; Keppel *et al.*, 2015).

Mitigating the effect of climate-driven fires on obligate seeder forests constitutes an enormous challenge to land managers given that fuel treatments are likely to be ineffective under extreme fire conditions (Price & Bradstock, 2012; Fairman *et al.*, 2015). While reseeding of thrice-burnt forests has re-established obligate seeders where population collapse has occurred (Bassett *et al.*, 2015), this is unlikely to be possible should large areas of forest be lost, due to inadequate seed supplies and the costs of aerial sowing (Ferguson, 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Methods.

BIOSKETCH

David Bowman leads the Environmental Change Biology Lab at the University of Tasmania. A key focus of the group is understanding the impacts of global environmental change on Australian forests and woodlands and their fire regimes. The group has led a series of recent papers on the impacts of repeated high-severity fire on the obligate seeding eucalypt forests of the Australian Alps bioregion.

All authors contributed to the initial idea for the paper. B.P.M. and G.J.W. conducted the analyses. D.M.J.S.B. led the writing. All authors edited early versions of the manuscript.

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