

# Fire severity drives variation in post-fire recruitment and residual seed bank size of *Acacia* species

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**Abstract** Very high-severity fires are a component of many fire-prone ecosystems, yet are often viewed as detrimental to vegetation. However, species in such systems are likely to have adapted to persist under a fire regime that includes high-severity fires. We examined how fire severity affects post-fire recruitment and residual seed banks of *Acacia* species and whether severity may affect plant responses to fire intervals. Nine sites of either high or low burn severity were identified after a large-scale mixed-severity fire in Warrumbungle National Park, south-eastern Australia. Transects were used to sample above-ground woody plant density. Seed bank size was surveyed by

soil extraction from two depths and manual searching for seeds. Residual soil seed bank and recruitment were compared across the two burn severities. *Acacia* seedling density was higher in areas burnt at high severity, indicating that increased severity triggers increased germination from the seed bank. Size of residual seed bank was smaller after high-severity fire, but varied between species, with few *Acacia cheelii* seeds remaining despite high above-ground abundance. In contrast, *A. penninervis* retained a small residual seed bank. There was little evidence of negative effects on populations of *Acacia* species after high-severity burns. However, we found that high fire severity may impact on the ability of a species to persist in response to a subsequent short fire interval. Fire management for maintaining biodiversity needs to consider other key aspects of the fire regime, including severity and season, rather than focusing solely on fire frequency.

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## Introduction

To predict the response of plant populations and their ability to persist under altered fire regimes, we need to

understand the mechanisms that determine the magnitude and spatial and temporal patterns of post-fire recovery (Whelan 1995; Bond and van Wilgen 1996). This requires consideration of many interacting factors, from key life-history traits to variation in fire conditions. For many species from fire-prone habitats, particularly obligate seeders (i.e., those that are killed by fire and depend on recovery from seeds), the recovery of plant populations depends on the pre-fire abundance and distribution of seeds in a seed bank, as well as the fire response and resilience of their seed bank. Seed bank dynamics are, therefore, a critical determinant of population persistence.

In fire-prone regions, seedling emergence is related to fire-cued germination and contributes to the magnitude of recruitment, while the number of seeds remaining dormant (a post-fire residual seed bank) can contribute to a bet-hedging capacity, ensuring seeds are retained in the event of a lost seedling cohort (Whelan 1995; Bond and van Wilgen 1996; Auld and Denham 2006). Seed dormancy is one mechanism that influences both these outcomes, as it assists in maintaining a seed bank for long periods of time (Auld et al. 2000; Fenner and Thompson 2005; Ooi et al. 2007). Seed mortality resulting from fire can affect both the above and below ground population, resulting in lower levels of recruitment and a reduced residual seed bank. High seed mortality could compromise the capacity of a population to effectively recruit or retain a residual seed bank large enough to produce a subsequent seedling flush if a fire occurs soon after the first (i.e., increased fire frequency) (Auld and Denham 2006; Auld et al. 2007).

Many obligate seeding species have seeds with physical dormancy (also known as hard-seeded species), a dominant dormancy type in fire-prone ecosystems (Merritt et al. 2007; Ooi 2007), which is controlled by an impermeable seed coat. Physical dormancy is usually broken by high, short duration temperatures experienced during the passage of fire. For successful recruitment to occur, the seed bank must be heated to temperatures high enough to break the dormancy of such species, but not so high as to cause excessive levels of seed mortality. The general pattern for species from many fire-prone regions around the world is that germination increases in response to increasing heat shock temperatures for physically dormant species (Keeley and Meyers 1985; Jeffery et al. 1988; Auld and O'Connell 1991; Herranz

et al. 1998). In the field, this means that in areas where higher temperatures are generated in the soil during fire, a larger proportion of the seed bank would be exposed to dormancy-breaking thresholds (Bradstock and Auld 1995; Odion and Davis 2000; Ooi et al. 2014), resulting in a potentially higher abundance of seedlings and a greater diversity of species. However, once a high temperature threshold is exceeded, heat will cause seed mortality. Heat transfer into soil is dependent on the characteristics of the fire (e.g., energy release, temperature, and duration), composition of litter (Bradstock et al. 1992; Bradstock and Auld 1995) and thermal properties of the soil, which is influenced by its composition, density, and moisture content (Van Wijk 1963; Abu-Hamdeh and Reeder 2000; Stoof et al. 2011). Exposure of seeds to dormancy-breaking or mortality thresholds is also dependent on the depth that seeds occur in the soil, with soil temperatures attenuating steeply with soil depth (Bradstock et al. 1992; Bradstock and Auld 1995; Penman and Towerton 2008). Across regions with similar soil characteristics and litter composition, variation in fire intensity is likely to be a key determinant of recruitment response and seed mortality of physically dormant species.

Fire severity, a measure of the physical impact of fire on vegetation and, therefore, a correlate of intensity (Keeley 2009), is a key component of the fire regime. However, while several studies have reported on the vegetation response to varying fire severity, including survival, structure and magnitude of population recovery (e.g., Moreno and Oechel 1991; Morrison et al. 1992; Thaxton and Platt 2006), few have related this to the mechanisms driving these responses, such as temperature-related seed dormancy. Those that have are often focused on the potential negative effects of very cool fires on germination and recruitment (e.g., Bradstock et al. 1992; Bradstock and Auld 1995; Ooi et al. 2014). Very high-severity fires are an inherent component of many fire-prone ecosystems, yet are often considered detrimental to vegetation recovery and maintenance of biodiversity (e.g., Vivian et al. 2008; DellaSala et al. 2015). This is despite the fact that the majority of plant species in fire-prone vegetation are likely to have adapted to persist under a fire regime that includes high-severity fires. Quantification of the effects of very high fire severity on the persistence of plant populations is, therefore, required.

One basis for the perceived negative impact of extremely severe fires in naturally fire-prone systems, is the assumption that soil temperatures cause excessive seed mortality, to a much greater extent than during more moderate fire events (Bradstock and Auld 1995), potentially reducing both the magnitude of emergence and the size of the residual seed bank. Under this assumption, recruitment after extremely severe fire would depend on the resilience of seeds to high temperatures and/or the depth of burial of seeds. Soil offers highly effective insulation, and temperatures decrease considerably with increasing depth (Bradstock et al. 1992; Tozer 1998; Penman and Towerton 2008). During fire events, seeds that are closer to the surface, where soil heating is greatest, are much more likely to be exposed to dormancy-breaking temperatures, but may be at greater risk of mortality. The size of the residual soil seed bank, which can bet-hedge against a loss of a seedling cohort, would also be affected by increased seed mortality, potentially retaining fewer seeds and at greater depths (Auld and Denham 2006). Under extreme fire severity, it is, therefore, likely that a greater proportion of seeds will die, but seeds buried deeper will have less chance of suffering mortality. Thus, factors such as seed size, which can determine the ability to germinate successfully from depth (Bond et al. 1999; Auld and Denham 2005), and depth of burial will interact with fire severity to determine recruitment potential.

In this study, we investigated how fire severity impacts both recruitment and the residual soil seed bank of the dominant understorey species in a *Eucalyptus-Callitris* forest in south-eastern Australia. For the two key canopy species groups, high intensity, severe fire kills *Callitris* species which must then recruit from a canopy seed bank or from seeds dispersing into the burnt area, and causes above-ground mortality in *Eucalyptus* requiring resprouting from protected meristems below ground. However, these species are resilient to lower severity fires (Cohn et al. 2011; Denham et al. 2016). Extremely high-severity fires, therefore, retard the rate of recovery of these canopy species. The response to varying fire intensity of many of the understorey species is less well understood. Research identifying how fire regime shifts in temperate fire-prone regions may drive vegetation change has recently been highlighted as an important knowledge gap, and the impacts of extreme fire severity on critical life-history stages is

still required (e.g., see Fairman et al. 2016; Gordon et al. 2017). One such stage is the seed bank. A key aim of our study is to, therefore, assess how extreme fire events affect recruitment and persistence of understorey species in this system, where the majority of plant diversity occurs.

Our study focused on the Warrumbungle National Park in south-eastern Australia, where an extensive high-severity wildfire occurred in January 2013. It was the most severe fire in the recorded history of the park and burnt 90% of its total area. Post-fire, there was a large flush of physically dormant heat-responsive species, dominated by those within the genus *Acacia*. Previous studies had investigated whether post-fire *Acacia* recovery contributed to increases in fuel hazard (Gordon et al. 2017), but had not investigated the soil seed bank. We considered two hypotheses; first, that higher fire severity will increase recruitment in *Acacia* species, and second, that higher fire severity would reduce the abundance of seeds in the residual soil seed bank. To test these hypotheses, we quantified plant recruitment above-ground and the density of the corresponding residual soil seed bank below ground in areas burnt by either extremely high or relatively low severity fire. More specifically, we addressed the following questions:

1. Does fire severity impact recruitment of *Acacia* species from the seed bank and does the effect differ among species?
2. Does fire severity affect the residual seed bank, and if so, is this related to seed burial depth?
3. Is there evidence for negative effects of extremely high fire severity on the persistence of populations of fire-prone physically dormant species?

## Methods

### Study area

The Warrumbungle National Park (WNP) covers approximately 23 000 ha in the upper reaches of the Castlereagh River catchment, south-eastern Australia (31.29°S, 149.01°E). The region is topographically complex (elevation range 400–1200 m), with soils derived from basalts, trachyte and pyroclastic flows and from pre-volcanic sandstones. Summers are warm to hot (mean maximum temperature 23.7 °C), while

winters are mild (mean minimum temperature 7.4 °C), with an average annual rainfall of 750 mm (mostly in summer, though soil remains moist in winter).

The vegetation consists mostly of open *Eucalyptus-Callitris* forest (North-west Slopes Dry Sclerophyll Woodlands and Western Slopes Dry Sclerophyll Forests) (Keith 2004), with an understorey of sclerophyllous shrubs in low soil fertility areas, while grasses and forbs dominate high soil fertility areas (Denham et al. 2016). Canopy dominants vary among habitats, but *Callitris glaucophylla*, *Eucalyptus albens* and *E. crebra* are the predominant tree species present in most communities (Hunter 2008), and are 20–30 m tall. Obligate seeder species with physically dormant seeds dominate the understorey of most vegetation communities in the region, with genera such as *Acacia* and *Dodonaea* being very common. While these understorey species re-establish rapidly after fire, *Callitris* populations may take over 10 years to recover from a severe fire event, as population regeneration depends on relatively slow growing seedlings (Denham et al. 2016).

The recorded fire history of the WNP shows that there have been several relatively small fires scattered over the past 70 years, but that a majority of the park has not been burned for 40 years (OEH unpublished data, Storey et al. 2016). The Wambelong Fire, which occurred in 2013, is the largest and most severe fire in the recorded history of the park and is the focus of this study. During extreme fire conditions in January 2013, the fire burnt over 39 000 ha of vegetation within 24 h. Following the initial conflagration, the fire continued to burn in low–moderate fire conditions for several weeks, burning another 17 000 ha before being extinguished on the 21 Feb. Overall, approximately 84% of WNP was burnt, with 13% burnt at low severity, indicated by scorched low shrubs but tree canopies remaining unburnt. Around 64% of the park was burnt at high or extremely high intensity, with severity class in these areas based on top-killed trees and consumption of all vegetation and canopy (Denham et al. 2016).

#### Site selection

Potential study areas were initially selected based on remote sensing classification of burn severity (see Storey et al. 2016), with severity subsequently confirmed by field assessment. Sites were categorised

as being burnt at either low or high severity, which was a surrogate for fire intensity. While a number of woody species had recruited post-fire, *Acacia* species dominated the mid-storey within these sites and were, therefore, the target for this study (Table 2). Two species, *Acacia cheelii* and *A. penninervis*, occurred at each site and were, therefore, used as focal species in the study. Fire intensity was classed according to Chafer et al. (2004), who considered the amount of energy expended and type of burn. Classes were low–moderate (fire intensity < 500 kW/m, surface and low shrub fire) and high-extreme (500–70 000 kW/m, tall shrub fire with tree canopy scorch to total canopy consumption). Field assessment of severity was based on height of canopy scorch/consumption and the proportion of litter consumption. High-severity sites consisted of areas where all litter, shrubs, and most tree canopies (mainly *E. crebra*, *E. albens*, and *C. glaucophylla* canopies > 15 m) were consumed by fire, and only tree skeletons remained. At low severity sites, shrubs and litter were consumed, but tree canopies remained intact or partially burnt and *Eucalyptus* trees were observed resprouting from epicormic buds. Upon identification of suitable sites of high or low severity, a 20 × 20 m plot was established, within which surveys were conducted (see Table 1 for a description of sites).

Five sites burnt at low severity and four sites burnt at high severity were identified across different areas of the park, accounting for spatial variation of population distribution and fire characteristics. *Acacia*

**Table 1** Fire severity, dominant *Acacia* species (*A. cheelii*, *A. penninervis* or ‘both’ where present in similar numbers) and mean post-fire density of stems of all woody species for study sites

Site	Severity	Dominant <i>Acacia</i>	Stem density (per m <sup>2</sup> )
1	Low	<i>A. cheelii</i>	1.62
2	Low	<i>A. cheelii</i>	1.42
3	Low	<i>A. penninervis</i>	4.83
4	Low	<i>A. penninervis</i>	2.30
5	Low	Both	2.85
6	High	<i>A. cheelii</i>	10.73
7	High	<i>A. cheelii</i>	6.42
8	High	Both	6.07
9	High	<i>A. penninervis</i>	9.77

species within these sites were identified and targeted for the study (Table 2). We could not determine the pre-fire density of *Acacias*, because at many sites, no identifiable dead stems remained. Furthermore, it is reasonable to expect that above-ground populations of these species may decline with time-since-fire, persisting primarily in the soil as a seed bank. Topography was similar across all sites, being either flat or on gentle slopes (< 10% slope) and we, therefore, assumed that pre-fire densities of shrubs were not skewed towards either of our severity classes. The post-fire density of vegetation in the shrub layer varied among sites, ranging from scattered individuals to extremely dense (Table 1).

### Recruitment response to fire severity

Field work to assess post-fire recruitment was conducted in August 2015, approximately two and a half years after the fire and recruited individuals had become woody but had not reached maturity. At each 20 m × 20 m plot within our five low- and four high-severity sites, we established three parallel 10 m long belt transects laid out equally spaced apart in an east–west orientation. Live stems of all shrub species in the plots, within 1 m either side of each transect, were identified and counted. This meant that in each

**Table 2** *Acacia* species identified in plots within the study area. Fire response categories are primarily from the NSW Flora Fire Response Database Version 1.3 (DECC 2002) and Gibson et al. (2011)

<i>Acacia</i> species	Height (m)	Fire response	Seed weight (mg)
<i>A. buxifolia</i>	1–4	Sr	20.8
<i>A. caesiella</i>	1–3.5	S	19.8
<i>A. cheelii</i>	~ 7	S	16.1
<i>A. cultriformis</i>	4	S	15.6
<i>A. deanei</i>	1.5–7	S	24.7
<i>A. decora</i>	1–4	S	14.7
<i>A. doratoxylon</i>	3–8	S	9.2
<i>A. gladiiformis</i>	1–3	S	21.4
<i>A. implexa</i>	5–12	Rs	25.0
<i>A. penninervis</i>	2–8	S	72.8

S = obligate seeder, R = resprouter, Sr = predominantly an obligate seeder, Rs = predominantly a resprouter. Seed weight is a mean, based on measurement of 30 seeds

transect we surveyed 20 m<sup>2</sup> and the total area surveyed at each plot was 60 m<sup>2</sup>.

Densities (plants per m<sup>2</sup>) were calculated separately for each transect. As previously described, *Acacia* occurred throughout all sites, and two species, either *A. cheelii*, *A. penninervis* (or both co-occurring), dominated all plots surveyed. We, therefore, calculated density by dividing the total number of live stems by area for four subgroups: all woody species (species pooled), all *Acacia* species, *A. cheelii* and *A. penninervis*, in order to highlight the pattern of distribution between high and low severity fires for these groups. Note that these subgroups sometimes overlapped within sites.

### Residual seed bank size

Post-fire recruits had not yet reached maturity, meaning that the residual seed bank could be surveyed (i.e., no new contributions to the seed bank prior to sampling). This allowed us to survey only the residual seed bank that persisted through the 2013 fire. Eight 30 × 30 cm seed bank plots were taken from each site. Locations of seed bank sample plots were stratified by the number of *Acacia* seedlings present. At each site, the eight 30 × 30 cm plots comprised of two each with 0, 1–2, 3–4, or 5+ seedlings. Once plots were located, seedlings were counted and removed. Soil from each plot was then removed to a depth of 5 cm, bagged and labelled. The soil was then dug to a depth of 10 cm (total volume of 9000 cm<sup>3</sup>/sample), ensuring soil from depth classes was kept separate. Soil was then taken to the laboratory, allowed to dry, and sieved to separate coarser particles to ease the sorting process. The remaining soil was then sorted by hand to search for seeds of all *Acacia* species, which were removed from the soil, identified and recorded. The mean number of seeds at each depth class was calculated for each severity class, using samples as replicates.

### Data analysis

To compare the density of above-ground species among sites burnt at different severities, we used a Generalised Linear Mixed Model (GLMM) with Poisson distribution. Fire severity was included as a fixed factor, while the random factor included transects nested within sites. Separate models were fitted

to compare the stem density of live woody species and the density of live *Acacia* stems (the dominant component of all sites) comparing high and low severity burn areas. Two further analyses explored the density of the two dominant species, *A. cheelii* and *A. penninervis*, using only the sites in which each target species occurred. *Acacia cheelii* was dominant in four sites, and *Acacia penninervis* dominant in three, with both species co-occurring in only two of the nine sites (see Table 1.)

To assess the effect of fire severity on residual seed bank density and whether this varied with depth, a two-factor Generalised Linear Model (GLM) with Poisson distribution was used, with the number of seeds recorded of all *Acacia* species as the dependent variable, and fire severity (high versus low) and depth class (0–5 cm and 5–10 cm) as the two factors. To examine the difference in residual seed bank density between *A. cheelii* and *A. penninervis*, depth classes were pooled and a two-factor GLM was used. To test whether seeds were abundant in areas that we did not sample, we used logistic regression to model the likelihood of seeds being present in the residual seed bank in relation with the number of seedlings present, fire severity, and species (*A. cheelii* or *A. penninervis*).

## Results

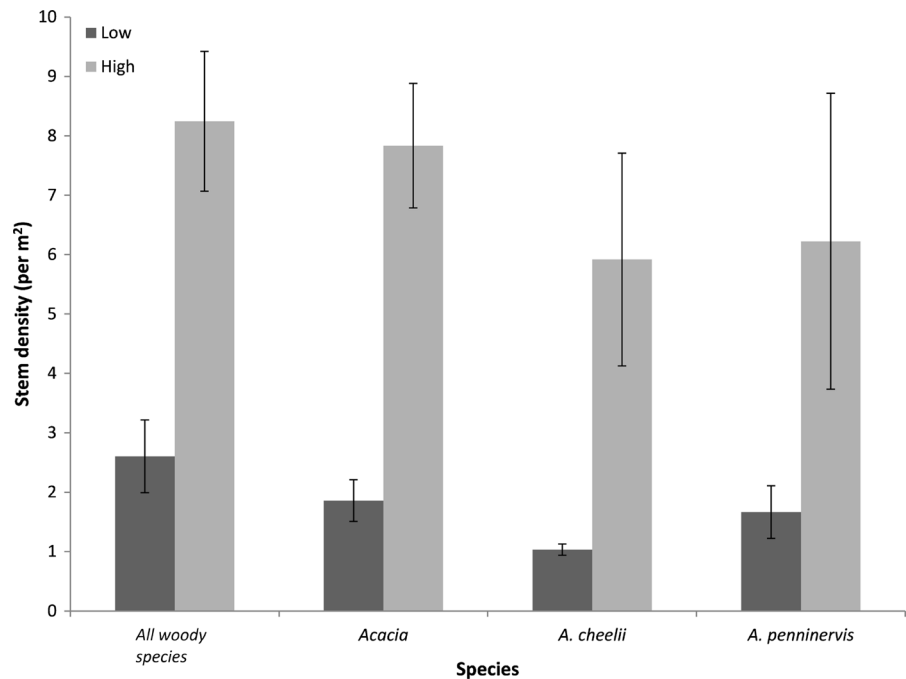
### Recruitment response to fire severity

The mean density of live woody stems (all species combined) in high-severity burn areas was 8.25/m<sup>2</sup> compared to only 2.6/m<sup>2</sup> in the low severity burn areas (Fig. 1, Table 1). All four comparisons with GLMMs of above-ground vegetation demonstrated that high-severity burn sites had a higher density of recruitment than low severity sites (although *A. penninervis* was only near significant; Table 3). This consistent relationship indicated that *Acacia* species, and in particular, *A. cheelii* and *A. penninervis*, drove the overall

**Table 3** Results for generalised linear mixed models of above-ground woody stem density comparing high and low severity sites

	<i>df</i>	$\chi^2$	<i>P</i>
All species	1	11.552	< 0.0001
All <i>Acacia</i> species	1	16.071	< 0.0001
<i>Acacia penninervis</i>	1	3.598	0.0578
<i>Acacia cheelii</i>	1	7.237	0.0071

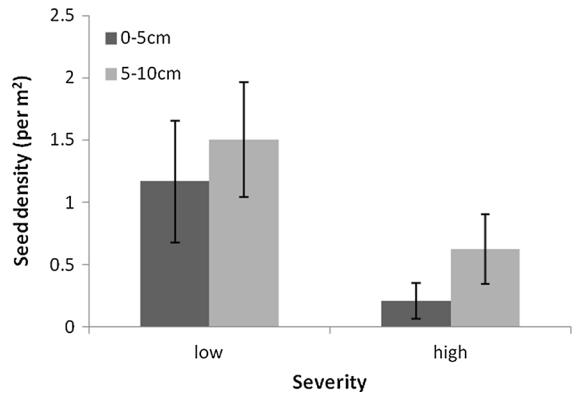
**Fig. 1** Density (mean  $\pm$  standard error per m<sup>2</sup>) of live stems for woody plants recruiting post-fire. Data are for the four subgroups All woody species, All *Acacia* species, and the single species *A. cheelii* and *A. penninervis* in low (dark grey) and high (light grey) severity sites. Note that there is overlap among these groups within sites



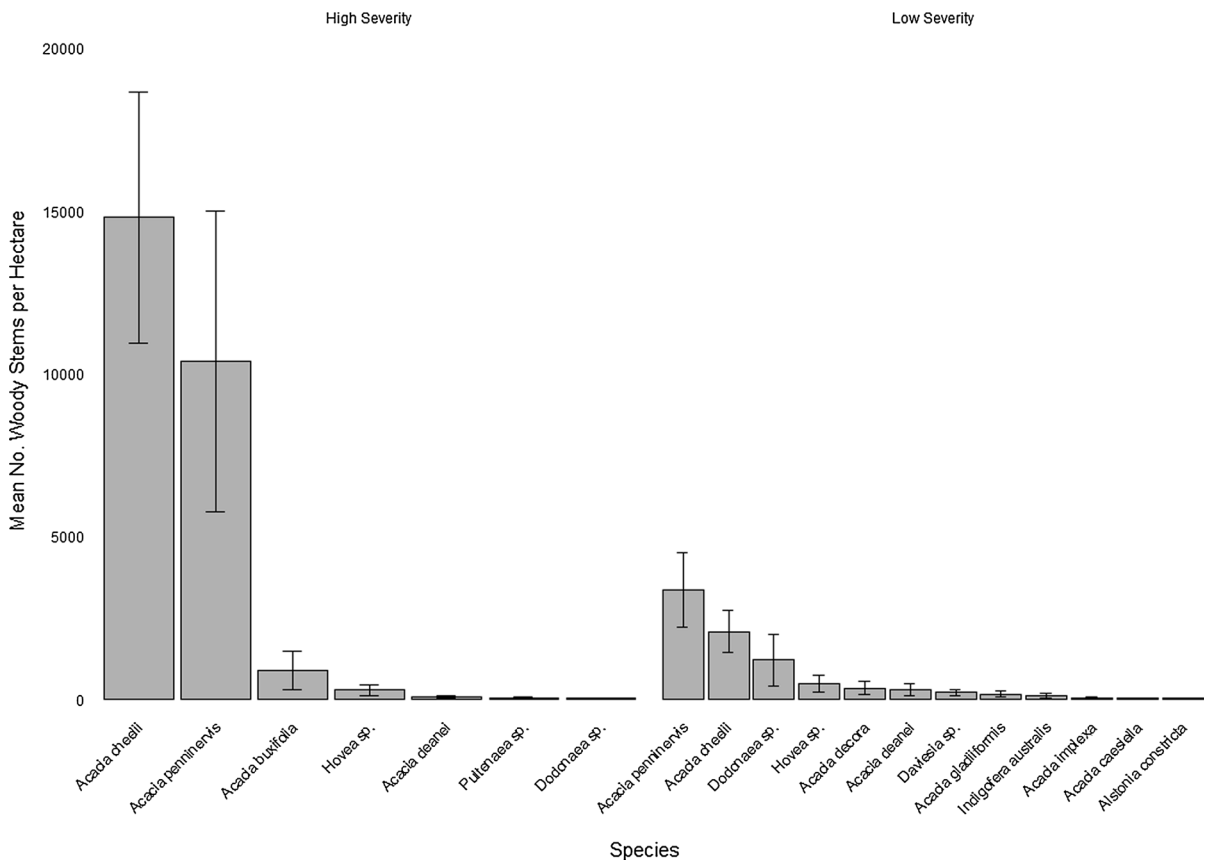
patterns of understorey shrub response. *Acacia cheelii* and *A. penninervis* were the dominant components in the studied sites, evident by their high density in both low- and high-severity burn areas when compared to other surveyed plant species (Fig. 2).

Residual seed bank size

The number of seeds recovered from soil seed bank samples was very low across all sites (Fig. 3). Nevertheless, there was a significant effect of fire severity ( $df = 1, \chi^2 = 4.993, P = 0.025$ ) on seed bank density, with higher densities of seeds in areas burnt at low severity (0–13 seeds/m<sup>2</sup>) than at high severity (0–7 seeds/m<sup>2</sup>). While there was no significant effect of depth ( $df = 1, \chi^2 = 1.625, P = 0.202$ ), there was a trend for more seeds at greater depths at both fire severity classes.



**Fig. 3** Number of seeds (mean ± standard error per m<sup>2</sup>) at two depths in the soil profile, at low- or high-severity sites subjected to either high or low severity burn. There were significantly more seeds found in low severity sites ( $P = 0.0254$ ), but no significant differences between different depths



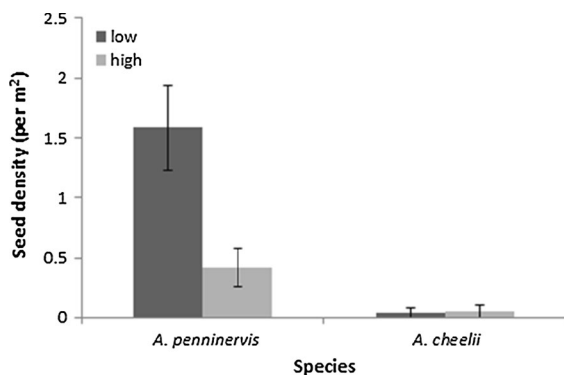
**Fig. 2** Density of individual stems (mean ± standard error per hectare) of woody species at low and high severity, averaged across all sites. Density of species is approximately four times higher after high-severity fire than after low severity fire

Comparison of the residual seed banks of the two dominant *Acacia* species in relation to fire severity uncovered striking differences. *Acacia penninervis* seed density was much higher than for *A. cheelii* (Fig. 4). There was a significant interaction between species and severity ( $df = 1$ ,  $\chi^2 = 8.033$ ,  $P = 0.005$ ), indicating that high-severity fire significantly reduced the size of the residual seed bank, but only for *A. penninervis*. *Acacia cheelii* seed density was negligible regardless of fire severity (Fig. 4).

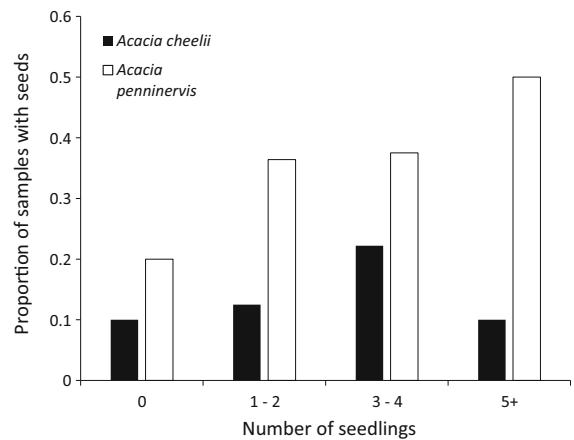
Neither fire severity nor number of seedlings present significantly influenced the likelihood of finding a residual seed bank according to the logistic regression model. However, species was significant, such that the likelihood of finding seeds in the soil was approximately five times greater for *A. penninervis* than for *A. cheelii* (*A. cheelii* odds ratio 0.21, 95% CI 0.06–0.81). There was a greater proportion of samples that had seeds in samples with more seedlings of *A. penninervis*, but this trend was not significant (Fig. 5). The low proportion of samples with seeds where there were no seedlings (less than 20%) suggests that there are unlikely to be large numbers of seeds in areas where we did not sample.

## Discussion

High-severity fire resulted in a greater recruitment response of the dominant physically dormant *Acacia* species than low severity fire, with *Acacia* species dominating the mid-storey vegetation in sites subjected to high-severity fire. The corollary of this



**Fig. 4** Residual seed bank density (mean  $\pm$  standard error per  $m^2$ ) of the two dominant *Acacia* species, *A. cheelii* and *A. penninervis* at low (dark grey) and high (light grey) severity sites



**Fig. 5** Proportion of soil seed bank samples that contained viable *Acacia* seeds after fire in relation to the number of seedlings within the sample

response is that high-severity fire resulted in a greatly reduced residual seed bank. A combination of large seeds and a relatively large store of seeds in the soil, in conjunction with adequate soil heating from the fire, is likely to contribute to promoting the rapid establishment and growth of these species. The known heat response for breaking dormancy of *Acacia* seeds (Auld and O'Connell 1991; Ooi et al. 2014) provides a clear mechanism to explain the patterns of recruitment observed, with the dense recovery in high-severity areas indicating that more seeds were exposed to temperatures high enough to break dormancy. These findings also suggest that high-severity fire does not necessarily result in negative outcomes for species with physically dormant seeds, and that species are adapted to such events. Results from our assessment of residual seed banks demonstrate that some risk-spreading capacity can be maintained after high-severity fires. However, the interaction of fire severity and fire frequency is important when trying to determine appropriate fire intervals for the persistence of a species.

The above-ground recruitment recorded in our study is consistent with the hypothesis that higher severity fire will produce hotter soil temperatures and subsequently greater recruitment of physically dormant heat-responsive species (Ooi et al. 2014; Wright et al. 2016). Across regions with similar litter composition, it is clear that other factors, such as air temperature and soil moisture, contribute to fire intensity and, therefore, soil temperature (Whelan



1995; Stoof et al. 2011; Mondal and Sakumar 2014). Higher levels of recruitment 2.5 years post-fire in areas of high severity, compared to that in low severity areas, indicate that this is a key driver of the magnitude of recruitment of physically dormant species, as suggested by some other studies (e.g., Knox and Morrison 2005), including at other sites in relation to the same fire (Gordon et al. 2017). However, few studies have quantified this, or incorporated the dynamics and role of residual seed banks in determining persistence.

Extreme fire events, such as the one studied here, increase soil temperatures to very high levels, and, therefore, also increase the likelihood of greater amounts of seed mortality. However, despite this, high levels of above-ground recruitment were observed in higher severity burnt areas. This suggests that seed mortality alone, as a result of hotter fires, is unlikely to limit recruitment in these fire-adapted species. While lethal temperatures could cause greater seed mortality, this is likely to be restricted to the upper few centimetres due to the insulating effects of soil. Suitable dormancy-breaking temperatures would, therefore, shift further down the soil profile, and germination (rather than mortality) would be possible for depths beyond the first few centimetres. Seed size would subsequently be a critical determinant of recruitment success under increasingly severe fire, because smaller seeds are unable to emerge from greater depths (Bond et al. 1999). *Acacia* species have large seeds in comparison to most other species within the study region, and they would have some capacity to emerge from depths of at least 5 cm (Denham and Auld 2006; Liyanage and Ooi 2018). However, the fact that there is a range of seed sizes, even within our study group (9.2–72.8 mg, Table 2), means that there could still be relative differences in response. Understanding recruitment of different species to fire severity, therefore, requires knowledge of seed dormancy-breaking temperature and mortality thresholds (Ooi et al. 2014; Liyanage and Ooi 2015), along with their ability to emerge from depth (Bond et al. 1999; Hanley et al. 2003). Further work is required to estimate dormancy-breaking and mortality temperature thresholds for physically dormant species in fire-prone regions.

Fire severity had a clear effect on the size of the residual soil seed bank. For *A. penninervis*, there was more than three times the number of seeds remaining

in the seed bank in the low severity compared to high-severity areas. In contrast, there was almost no evidence of a residual seed bank for *A. cheelii* or any other *Acacia* species at sites of either high or low severity, despite the high abundance of above-ground recruits. Above-ground recruitment of *A. cheelii* was comparable to *A. penninervis*, suggesting that there were either fewer *A. cheelii* seeds prior to the fire or that more were killed during the fire or died prior to emergence. *Acacia cheelii* seeds have a mass less than 25% that of *A. penninervis*, and would have a lower probability of successful emergence if dormancy was broken at depth. Individuals of larger seeded species, such as *Acacia penninervis*, would be able to emerge from greater depths where they are protected from the most extreme temperatures and have the resources to reach the surface.

We found no evidence that the size of the residual seed bank size is moderated by burial depth. In contrast, Auld and Denham (2006) showed that post-fire *Acacia* soil seed banks contained fewer seeds in the top 5 cm of soil than layers from 5 to 10 cm and 10–15 cm, indicating that heat shock cues declined with depth and caused more germination and mortality close to the surface. The lack of significance of burial depth in our study could be attributed to the extremely severe fire causing very high soil temperatures, even in low severity burn areas, a clear demonstration of the extreme nature of the event. These high soil temperatures were likely sufficient to produce seed mortality or promote germination down to a depth of at least 10 cm. The residual seed bank density (0–13 seeds/m<sup>2</sup>) was low in comparison to other post-fire studies. Auld et al. (2007) found approximately 21 seeds/m<sup>2</sup> of *Persoonia lanceolata* (an obligate seeder) in heath and woodlands in coastal New South Wales, 9 years after fire. Another study found that several shrub species (including *A. suaveolens*) in open woodlands in south-eastern Australia maintained sizeable seed banks through low–moderate severity fires (Auld and Denham 2006). However, there has been little study regarding the size of residual soil seed banks following high-severity wild fires. We suggest that further studies are required after natural fires to gain a clearer understanding of the role that residual seed banks play.

Our estimation of fire effects is based on two components of genets of these species after fire—the above-ground recruits and the residual seed bank. We were unable to estimate the losses of genets due to

excessive heating of seeds or early seedling mortality, nor were we able to assess pre-fire abundance of plants. There is some possibility, therefore, of an underlying difference in the landscape in which high and low severity sites occurred. Alternatively, there may be a relationship between severity and the abundance of *Acacias*, with these species establishing more successfully in sites subject to high-severity fire, or that the presence of *Acacias* predisposes these sites to high-severity fire. Although further elucidating this relationship is an important area for future research, our finding of a residual seed bank in low severity sites that was larger in absolute terms (Fig. 3) rather than in proportion to the total number of genets, demonstrates that any sampling bias did not influence the conclusions of this study.

Despite significant levels of above-ground recruitment of physically dormant species post-fire, the limited residual seed bank we observed suggests that a short interval before a subsequent fire event would threaten populations of many of the species in the study region. Frequent fire poses a risk of population decline and extinction for obligate seeding species, as individuals can be killed before they mature, and seed banks are not replenished (Keith 1996; Bowman et al. 2014a; Enright et al. 2015). Depending on the length of the juvenile period (from emergence to flowering), this can take many years (Keith 1996). While *A. penninervis* has some capacity to respond to a subsequent fire in the short term, due to a small residual seed bank, many other *Acacia* species are unlikely to have such a buffer. Here importantly, we have demonstrated that severity of the previous fire has important consequences for a species response to subsequent fire interval, similar to studies investigating obligate seeders in other regions (e.g., Bowman et al. 2014b in alpine habitat). This highlights that an understanding of key elements of the fire regime beyond only fire frequency, including severity and season (Ooi 2010; Mackenzie et al. 2016), need to be incorporated into implemented fire strategies when managing for biodiversity or the persistence of threatened species.

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