Title: Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire.

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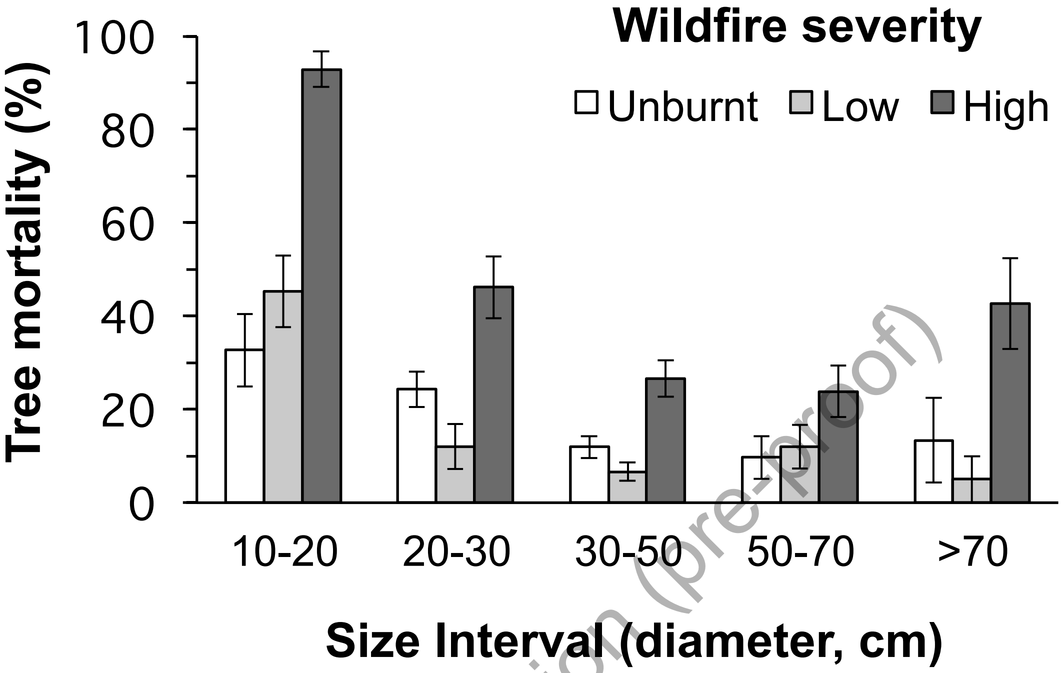
Highlights

- Mortalities of fire-tolerant eucalypts increased after high-severity wildfire
- Near loss of 10 to 20-cm diameter cohort after high-severity wildfire
- Eucalypt seedlings but not basal reprouts increased after high-severity wildfire
- Percentage mortalities of small eucalypts increased with recent prescribed fire
- Study indicates fire-tolerant eucalypts are not perpetually resistant to all fires

Graphical Abstract



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ABSTRACT

Mixed-species eucalypt forests of temperate Australia are assumed tolerant of most fire regimes based on the impressive capacity of the dominant eucalypts to resprout. However, empirical data to test this assumption are rare, limiting capacity to predict forest tolerance to emerging fire regimes including more frequent severe wildfires and extensive use of prescribed fire. We quantified tree mortality and regeneration in mixed-species eucalypt forests five years after an extensive wildfire that burnt under extreme fire weather. To examine combined site-level effects of wildfire and prescribed fire, our study included factorial replications of three wildfire severities, assessed as crown scorch and understorey consumption shortly after the wildfire (Unburnt, Low, High), and two times since last preceding fire (<10 years since prescribed fire, >30 years since any fire). Our data indicate that while most trees survived low-severity wildfire through epicormic resprouting, this capacity was tested by high-severity wildfire. Five years after the wildfire, percentage mortalities of eucalypts in all size intervals from 10 to >70 cm diameter were significantly greater at High severity than Unburnt or Low severity sites, and included the near loss of the 10 to 20 cm cohort (93% mortality). Prolific seedling regeneration at High severity sites, and unreliable basal resprouting, indicated the importance of seedling recruitment to the resilience of these fire-tolerant forests. Recent prescribed fire had no clear effect on forest resistance (as tree survival) to wildfire, but decreased site-level resilience (as recruitment) by increasing mortalities of small stems. Our study indicates that high-severity wildfire has the potential to cause transitions to more open, simplified stand structures through increased tree mortality, including disproportionate losses in some size cohorts. Dependence on seedling recruitment could increase vulnerabilities to subsequent fires and future climates, potentially requiring direct management interventions to bolster forest resilience.

Keywords: fire severity; prescribed burning; regeneration; resprouter; temperate forest; tree mortality.

1. Introduction

A growing number of studies have highlighted a range of threats to the health and persistence of temperate forests (Millar & Stephenson, 2015). Rising global temperatures have contributed to droughts of unprecedented severity in many parts of the world, affecting forest health directly through tree water stress and high temperature stress, and indirectly through increased vulnerability to other stressors (van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Grimm *et al.*, 2013; Reichstein *et al.*, 2013; Bennett *et al.*, 2015). Tree mortality is a key determinant of forest structure and composition (Dietze & Moorcroft, 2011), and increased tree mortality has the potential to shift forests to alternative states not dominated by trees (Millar & Stephenson, 2015). Persistent decreases in live tree biomass invariably means changes to key ecosystem services provided by forests, in particular to the strength and persistence of the land-based global carbon sink (Hicke *et al.*, 2012; Brienen *et al.*, 2015; Ghimire *et al.*, 2015).

Fire, as a global disturbance agent (Giglio *et al.*, 2013), is a key driver of tree mortality and regeneration in forests worldwide (e.g. Brando *et al.*, 2012; Abella & Fornwalt, 2014; Holz *et al.*, 2015). Fire's role in shaping tree demography varies according to a multitude of interactions between forest type, fire regime, and pre- and post-fire environmental conditions (van Mantgem *et al.*, 2013; Fernandes *et al.*, 2015; Coop *et al.*, 2016). These interactions are dynamic, and will likely be influenced by future climates, leading to a range of potential impacts on forest health (Grimm *et al.*, 2013; Enright *et al.*, 2015). For example, climate change is predicted to lead to more frequent, extensive and severe wildfires in many temperate regions of the world (Flannigan *et al.*, 2013). Such predictions have been made for southeast Australia (Clarke *et al.*, 2011), where, in the state of Victoria, the area burnt by wildfires increased in recent decades in two of three forest bioregions (Bradstock *et al.*, 2014), and the cumulative forest area burnt by wildfire in the decade to 2014 was roughly equivalent to that burnt in the preceding fifty years (Fairman *et al.*, 2016).

Whether or not current and emerging fire regimes threaten the health and persistence of temperate forests will depend on tree mortality and recovery. A critical emerging issue is whether extensive tree mortality is followed by recovery of the same or similar vegetation type, or whether large high-intensity fires produce changes in forest type, particularly in forests adapted to infrequent, moderate-severity fires (Stephens *et al.*, 2013). That is, using the definitions of Enright et al. (2014) in the context of plant-fire dynamics, are the forests 'resistant' to fire so that the extant trees survive through resprouting, and/or 'resilient' to fire – the trees have the 'capacity to recover to pre-disturbance abundance levels through [seedling] recruitment'? Or will there be changes not only in forest composition but also in forest structure through, for example, the disproportionate death of small tree stems (Bond *et al.*, 2012), or through a markedly simplified age-class distribution (Fairman *et al.*, 2016)?

The fire-tolerant mixed-species eucalypt forests of southeastern Australia are thought to be highly resistant (*sensu* Enright *et al.*, 2014) to more frequent high-intensity wildfires due to the capacity of the dominant eucalypt species to resprout (Bowman *et al.*, 2013; Lavorel *et al.*, 2015). Fire-tolerant eucalypts have been termed 'the most accomplished post-fire resprouters' due to their capacity to resprout both from below-ground lignotubers, and from above-ground accessory buds and epicormic meristems (Burrows, 2013). This resprouting capacity typically keeps post-fire eucalypt mortalities low relative to, for example, fire-tolerant forests in temperate zones of the United States (Bennett *et al.*, 2013). However, while post-wildfire mortality rates of fire-tolerant eucalypt forests have rarely been quantified (as also noted by Gill, 1997), both historical observations (Fairman *et al.*, 2016), and a handful of recent small-scale studies, have indicated potential for elevated mortality of fire-tolerant eucalypts after some fires. For example, Prior et al. (, 2016) recently attributed 25% of eucalypt tree mortalities to moderate intensity wildfires in dry eucalypt forests of Tasmania, and two studies in central Victoria recorded up to 40% greater mortality of fire-tolerant eucalypts in high-severity than unburnt plots after the notorious ‘Black Saturday’ wildfire of 2009 (Benyon & Lane, 2013; Nolan *et al.*, 2014). While the Victorian data in particular were based on very few observations (total of five high severity plots, each <0.1 ha), these studies suggest that the tolerance of fire-tolerant eucalypt forests is not ‘boundless’ (Prior *et al.*, 2016), and that conceptual models for these forest types of perpetually resistant live tree biomass to fire (Bowman *et al.*, 2013) require further scrutiny.

The visibly impressive resprouting capacity of fire-tolerant eucalypt forests after most wildfires has led to conceptual understanding that regeneration from seeds was ‘unnecessary’ for their persistence under more frequent, high-intensity wildfires (Bowman *et al.*, 2013). However, resprouters in general often persist after fire through a combination of resprouting and regeneration from seed (Lamont *et al.*, 2011), with seedling recruitment considered ‘essential for population maintenance’ of some resprouters under shortening fire intervals (Enright *et al.*, 2014). Indeed, recent studies have recorded increased seedling regeneration with increasing wildfire intensity in the fire-tolerant eucalypt forests of southeastern Australia (Benyon & Lane, 2013; Nolan *et al.*, 2014). However, the relative frequency of seedling versus resprouter regeneration in these and comparable forest types remains under-examined (although see Prior *et al.*, 2016), and there has been limited evaluation of how the form of regeneration might influence forest persistence if fire intervals narrow (Enright *et al.*, 2015).

Wildfire risks in fire-tolerant forests throughout the world are often managed using prescribed fire (the planned introduction of fire under specified conditions; Burrows *et al.*, 2010) to decrease fuel hazards (Fernandes & Botelho, 2003; McCaw *et al.*, 2012; McIver *et al.*, 2013; Addington *et al.*, 2015). Low-intensity prescribed fires are used to decrease the incidence, extent and intensity (energy released; Keeley, 2009) of wildfires, with the aim of reducing hazards to humans, but also reducing the effects of wildfire severity – the impacts on the ecosystem (Keeley, 2009). In the fire-tolerant eucalypt forests of southern Australia, effective reduction of wildfire hazard requires regular prescribed burning at intervals of less than about 7 to 10 years (Boer *et al.*, 2009; Tolhurst & McCarthy, 2016). However, while prescribed fire regimes in these forests have been shown to reduce wildfire severity where fuel loads have governed fire intensity, this capacity to mitigate wildfire severity decreases under extreme fire weather (Price & Bradstock, 2012; Tolhurst & McCarthy, 2016). To date, there has been minimal examination of the combined effects of prescribed fires and wildfires on site-level tree mortality and regeneration in fire-tolerant eucalypt forests. For example, it remains unclear if a preceding low-intensity prescribed fire would decrease (by reducing fuel loads around individual stems; Aponte *et al.*, 2014) or increase (by decreasing bark thickness; Bennett *et al.*, 2013) site-level tree mortalities after a high-intensity wildfire that burnt under extreme weather conditions.

Our study assesses tree mortality and regeneration in fire-tolerant mixed-species eucalypt forests following the 2009 ‘Black Saturday’ wildfires of southeast Australia. We examine the effects of wildfire intensity as represented by fire severity, which was based on assessments of crown scorch and understorey consumption in the two months after the wildfire. Our in-field assessments were made five years after 2009 to adequately capture any medium-term secondary responses to the wildfire including post-fire mortality and/ or recovery through resprouting and regeneration. To examine the potential for prescribed fire to mitigate or exacerbate site-level wildfire effects, our study design included factorial combinations of two times since last fire prior to 2009 (<10 years since prescribed fire, >30 years since any fire) with three 2009-wildfire severities (unburnt, low, high). Our principal aims are to improve the empirical basis for predicting the resistance and resilience of fire-tolerant eucalypt forests under emerging fire regimes, and to highlight any potential vulnerabilities so that thresholds of sustainability might be identified and adaptively managed (Millar & Stephenson, 2015).

2. Materials and methods

2.1 Study area

Our study focused on native, mixed-species eucalypt forests in the foothills of the Great Dividing Range in central Victoria, south-eastern Australia (study area centre: 37°28’S, 145°32’E). Our study’s forests are a type of dry sclerophyll forest (Ashton, 2000) or ‘Open-forest’ (tree heights 10-30 m, projective foliage cover 30-70%; Specht, 1981), known locally as ‘Herb-rich Foothill Forest’ (Department of Sustainability and Environment, 2004). They are dominated by co-occurring eucalypts of different bark types, such as *Eucalyptus obliqua* L’Hér (deep fibrous ‘stringybark’), *E. radiata* Sieber ex DC. and *E. dives* Schauer (short fibrous bark), and *E. globulus* subsp. *bicostata* (Maiden, Blakely & Simmonds) J.B. Kirkp. (smooth ‘gum’ bark). Each of these bark types affords some degree of fire-tolerance to mature stems; for example, heat penetration to the cambium is decreased by the greater bark thickness of the stringybarks, but also by the relatively low inflammability of the smooth, non-decorticating bark on the gum stems (Gill & Ashton, 1968). The understoreys of these forests are characterised by a diverse and well-developed herb layer beneath a sparse to continuous sclerophyll shrub layer (Ashton, 2000). Current recommendations for minimum tolerable fire intervals to maintain the forests’ species compositions are 15 years for low-severity fires like typical prescribed fires (the maturation time of shorter-lived shrubs and herbs), and 15 years for high-severity crown fires (sufficient time for the longest-lived species to have the size or seed store to survive a second severe fire; Cheal, 2010).

Our forest sites encompassed a range of aspects, elevations (165 – 890 m above sea level), slopes (1 – 36°), and morphological types (Flat to Upper slope and Crest; Speight, 2009), reflecting the variable geomorphology of the area (Ashton, 2000). Soils are not well described in the study area; however, the dry sclerophyll forests frequently occur on yellow podzolic soils of relatively poor structure (Ashton, 2000). The regional climate is temperate, with annual rainfall in the range 800 to 1200 mm, and the least rain falling in summer (Ashton, 2000). Mean monthly minimum temperatures are in the range 4°C (July/August) to 12°C (February), and mean monthly maximum temperatures in the range 9°C (July) to 23°C (January/February; Toolangi weather station; Bureau of Meteorology, 2015).

Our study encompassed an area of about 720,000 ha (c. 60 x 120 km^2), including forest sites that were within and around the perimeter of two 2009 wildfires collectively known as the Kilmore East-Murrindindi fire complex. This wildfire complex led to the deaths of 159 people and the destruction of > 2200 buildings, and was the most damaging of the >300 fires that burnt in Victoria on ‘Black Saturday’, 7 February 2009 (Cruz *et al.*, 2012; Teague *et al.*, 2010). It burnt about 400,000 ha over three weeks, but most of the damage occurred in the first 12 hour period, which was characterised by forest crown fires of very high intensities (peaks of 90,000 kW m^{-1}), the result of ‘exceedingly dry’ fuels combined with extreme fire weather (high temperatures and strong hot winds; Cruz *et al.*, 2012). Widespread dry fuels were the result of a preceding twelve-year period of consistent rainfall deficit and above-average temperatures, combined with two periods of extreme heat (consecutive days > 40 °C; Bureau of Meteorology, 2009) in the fortnight before the wildfires.

2.2 Study design

Our 71 study sites were replicated combinations of two times since the last preceding fire (‘Recently burnt’, ‘Long unburnt’), and three 2009-wildfire severities (‘Unburnt’, ‘Low’, ‘High’). Time since the last fire was as recorded in the state environment department’s spatial database of fire history, which contained records of wildfires back to 1927 but was considered most accurate after 1972. Sites were classified as ‘Recently burnt’ (32 sites) if last burnt by low-intensity prescribed fire within 10 years of 2009 (i.e. less than the above-mentioned minimum tolerable fire interval of 15 years), and as ‘Long unburnt’ if there were no records of any fire (wildfire or prescribed fire) for more than 30 years prior to 2009 (39 sites). To limit the number of fire conditions examined, we excluded sites burnt by recent wildfire and by any fire between 10 and 30 years before 2009.

Our wildfire severity classes were from a 1:25 000 map produced in 2009 by the state environment department that was based on change in the Normalised Burn Ratio (dNBR) as estimated from pre- and post-fire SPOT images, and extensive ground-truthing in the two months after the wildfires (Department of Sustainability and Environment, 2009). Sites were classified as ‘Low severity’ if burnt by low-intensity surface fire, which caused patchy combustion of the understorey and no or light crown scorch (<35%); ‘Medium severity’ if there was a mixed mosaic of crown burning and scorching ranging from 30 to 100%; and as ‘High severity’ if burnt by an intense fire that consumed the entire understorey and 70 to 100% of the overstorey crowns (Department of Sustainability and Environment, 2009; Table 1). Our study design included 21 Low severity sites and 24 High severity sites, representing the low and high ends of the 2009 severity assessment. We did not include Medium severity sites due to logistical constraints, but also to avoid ambiguities in interpreting wildfire effects associated with the uncertainties of mapping mixed wildfire severities in the middle range. Our 26 ‘Unburnt’ sites showed no signs of wildfire in the 2009 assessment, and were selected using the following criteria: same forest type (i.e. ‘Herb-rich Foothill Forest’); close as possible to wildfire boundary (within c. 30 km); and as evenly distributed as possible around the wildfire boundary.

Within the boundaries of the Kilmore East-Murrindindi fire complex, the predominant time-since-fire by wildfire severity combinations examined in this study were Long unburnt with Low severity (9958 ha; 15% of the total wildfire area), and Long unburnt with High severity (6574 ha; 10%; Table 1). In comparison, the ‘Recently burnt’ combinations occupied much smaller areas – 2370 ha (3%) in the Low severity class, and 357 ha (1%) in the High severity class (Table 1).

We made our assessments (detailed below) of large eucalypts (≥20 cm dbhub; diameter at breast height underbark, 1.3 m height) at all 71 sites from October 2013 to March 2014. This was followed by assessments of small- to medium-sized eucalypts and eucalypt regeneration at a subset of 42 sites (7 replicates of each of the six fire combinations) from April to October 2014. That is, while our 2009 wildfire severity classes were based on immediate fire effects, our field assessments were made some five years after the wildfire, allowing for medium-term secondary effects and responses to fire including potential for recovery through tree resprouting and regeneration (Morgan *et al.*, 2014).

2.3 Field assessments

We assessed the status of eucalypts in four size classes: regeneration (<2.5 cm basal diameter), small stems (2.5 – <10 cm dbh), medium stems (10 – <20 cm dbh), and large stems (≥20 cm dbhub; divided into four size intervals: 20 – <30, 30 – <50, 50 – <70, ≥70 cm dbhub). Our focus was on eucalypts because they were the predominant overstorey genus, comprising >99% of standing live large trees. Assessable small to large eucalypt stems were defined as upright or leaning, >1.3 m height, and rooted in the ground (i.e. not fallen ‘coarse woody debris’). We ignored burnt-out stumps and stem fragments of <1.3 m height because low numbers and sometimes dense understorey meant that they could not be reliably detected.

At each of 71 sites, we assessed large eucalypt stems in two 10 x 50 m plots, one with the long side running at 0° and the other at 240° from the plot centre (total plot area 0.1 ha).

We classified large stems as ‘live’ if live leaves were present in the canopy (unburnt, and/ or epicormic resprouts) or on the stem (epicormic resprouts), and ‘dead’ if the canopy and stem held no live leaves (i.e. no likelihood of producing new leaves given that the assessment was made five years after the wildfire). We assessed all large stems for: over-bark dbh (mm), presence of charring at 1.3 m height, and bark thickness on the north and south side (using a ‘Gill-type’ needle gauge; Gill *et al.*, 1982). We also recorded species for large live stems, but not dead stems, which were usually not identifiable.

At a subset of 42 sites, we counted small- and medium-sized eucalypt stems in two 10 x 25 m sub-plots located at the centre of the large tree plots (total area 0.05 ha). To gain insights into regeneration forms, we allocated counts of small- and medium-sized live and dead stems (classified as above) to one of three sub-classes: stem with live basal resprout, stem alone (no live basal resprout), and stem as basal resprout (either live or dead). In addition, to assess tree seedling regeneration, we tallied all live and dead eucalypt seedlings (i.e. <2.5 cm basal diameter, not basal resprouts) that were rooted within 1 m of the long sides of the small/medium tree sub-plots (total area 0.01 ha).

2.4 Statistical analyses

Effects of time since last fire and of 2009 wildfire severity class (as assessed soon after the wildfire) on medium-term (i.e. five years after the wildfire) eucalypt stem/ seedling densities and tree mortalities (percentages of standing trees that were dead) were tested using the two-way Analysis of Variance models of GenStat (15th edition, VSN International Ltd, Hemel Hempstead, UK). These models cater for unbalanced designs by automatically using regression analyses (Payne, 2012). Assumptions of normality and variance homogeneity were checked, and dependent variables transformed as necessary (fourth-root for densities, arcsine for percentages; Quinn & Keough, 2002).

In addition to Analysis of Variance models, Random Forest analyses (see below) were used to identify explanatory variables that were most important in explaining site-level patterns in eucalypt stem and seedling densities, and in tree mortalities by size class (all large size intervals combined; medium; and small). A total of 21 explanatory variables were initially considered for the 71-site analyses of large stems, and up to 24 for the 42-site analyses of medium- and small-sized stems and eucalypt seedling regeneration (Table 2).

Location and topography explanatory variables included field measures of aspect and slope, and elevation and vertical-distance-above-stream measures that were estimated using a 20-m resolution digital elevation model (Table 2). In addition, site easting and northing coordinates were included to acknowledge unknown elements of the study area's variable environment including geology and soils, and subtle differences in management histories. In the absence of detailed local climate data, climate explanatory variables were estimated using the WorldClim climate grids (http://www.worldclim.org). Fire history variables were derived from the previously mentioned state environment department's spatial database, and encompassed numbers of years since previous fires, and total numbers of fires (Table 2). For a continuous measure of 2009 wildfire severity (rather than the severity classes used in the above ANOVAs), we used a site-level composite burn index (CBI), which was derived using an empirical additive model based on optical and radar remote sensing data. The empirical model was calibrated and validated using field estimates of fire severity based on the above-mentioned ground-truthing in the two months after the 2009 wildfires (Department of Sustainability and Environment, 2009). Detailed information on field-estimated fire severity, remote sensing data processing, and the modelling approach and validation can be found in Tanase *et al.* (2015). Finally, additional estimates of wildfire severity were based on ancillary field measures, and included: the percentage number of large trees that were charred; the mass of rotten coarse woody debris (since the mass of rotten woody debris proved responsive to fire effects in a similar forest type, and was presumably less influenced by post-wildfire accessions than sound woody debris; Aponte *et al.*, 2014); and – for consideration in eucalypt seedling regeneration models only – measures of stand structure (basal area of large live and dead trees, large stump number; Table 2).

The non-parametric decision tree-learning approaches of Random Forest were used to examine relationships of eucalypt stem and seedling response variables with explanatory variables on the basis that they are robust to non-linear and complex interactions among variables, which can be both discrete (as in the case of some of this study's fire history variables) and continuous (Breiman, 2001). In addition, Random Forest can be used to identify the variables of most importance to a response variable, and, within a permutation test framework (rather than a prediction accuracy framework), be used to estimate the significance of each variable's importance (Hapfelmeier & Ulm, 2013). All Random Forest models were run using R (version 3.2.1; R Core Team, 2015). First, explanatory variables that were highly correlated with others (Pearson's correlation coefficient > 0.75) were excluded (see Table 2) on the basis that while Random Forest can cope with correlated variables the interpretation of any models that included closely correlated explanatories would be unnecessarily complex. Next, the 'NAP' ('new approach') method of Hapfelmeier and Ulm (2013) was used to identify the most important explanatory variables; this approach uses permutation tests to estimate the importance of all potential explanatory variables in a conditional Random Forest model (R 'party' package; Hothorn *et al.*, 2008) and selects those with a p-value ≤ 0.05. To assess the variance explained, the selected explanatory variables were then included in a Random Forest model containing 100 trees, with the number of input variables for each split set to the square root of the number of available variables (Díaz-Uriarte & Alvarez de Andrés, 2006).

3. Results

3.1 Fire effects on medium-term tree mortality

Five years after the 2009 wildfire, densities and mortalities of established eucalypt stems (medium stems 10 – 20 cm, and large stems ≥20 cm dbh) were significantly different among the 2009 wildfire severity classes, but were not influenced by time since fire prior to 2009, nor by interactions between time since fire and wildfire severity class. Densities and mortalities of established stems are thus discussed in terms of the overall effects of the 2009-wildfire severity classes.

Live stem densities in the medium size class (10 – 20 cm dbh) and in the next large size interval (20 – 30 cm dbh) were significantly lower at sites classified as High severity in 2009 compared with those classified as Unburnt or Low severity (Figure 1). Mean live stem densities in the remaining large size intervals (30 – 50, 50 – 70, ≥70 cm dbh) were also lower in the High severity compared with the Unburnt class although these differences were not significant (Figure 1).

Densities of dead stems in all large size intervals were consistently greater at High severity than either Unburnt or Low severity sites (Figure 1). In contrast, there was no clear effect of fire severity on densities of standing dead medium-sized stems despite significantly fewer live stems in this size class at High severity sites (Figure 1). This suggested greater combustion and/or collapse of medium-sized stems at High severity than Unburnt and Low severity sites.

As a result of the effects on live and dead stem densities, percentage tree mortalities five years after 2009 were significantly greater in the medium size class and in all large size intervals at sites that were classified in 2009 as High severity than those classified as Unburnt or Low severity (Figure 1). This effect was greatest in the medium size class where mean percentage mortality at High severity sites was 93%, compared with 45% at Low severity and

33% at Unburnt sites (Figure 1). In comparison, mean tree mortalities for the four large size intervals (20 – 30, 30 – 50, 50 – 70, ≥70 cm dbh) ranged from 24 to 46% at High severity sites, 5 to 12% at Low severity sites, and 10 to 24% at Unburnt sites (Figure 1).

3.2 Fire effects on medium-term eucalypt seedling regeneration

Densities of live eucalypt seedlings were significantly greater at High severity than Low Severity and Unburnt sites, reaching values in excess of 10,000 seedlings ha^{-1} five years after the 2009 wildfire (Figure 2). Similarly, densities of dead eucalypt seedlings were significantly greater at High severity than Low severity or Unburnt sites (Figure 2).

Time since fire prior to 2009 had no overall effect on live and dead eucalypt seedling densities, although recent prescribed fire was associated with a decrease in live seedling densities at Low wildfire severity sites (as indicated by a significant severity class by time-since-fire interaction; Figure 2).

3.3 Fire effects on new eucalypt establishment

The five years between the 2009 wildfire and our assessment provided sufficient time for some new eucalypt seedlings to grow into the next size class to become established small stems (2.5 – 10 cm dbh). As such, consistent with the effects on seedlings, densities of small live eucalypt stems were significantly greater at High severity than Low severity and Unburnt sites (overall means of 465 stems ha^{-1} at High severity and 40 stems ha^{-1} at Unburnt sites; Figure 3). Time since fire prior to 2009 did not affect densities of small live eucalypt stems five years after the 2009 wildfire (Figure 3). However, there were significantly greater mean densities of small dead eucalypt stems at Recently burnt than Long unburnt sites, mostly evident at High severity sites (Figure 3). This led to significantly greater mean small stem mortality at Recently burnt sites (64% vs. 38% at Long unburnt sites; Figure 3).

Very few of all small live eucalypt stems either originated from basal resprouts (sub-class ‘stem as basal resprout’; 1.3%), or supported a live basal resprout (3.1%) five years after the 2009 wildfire. These proportions were not influenced by 2009 wildfire severity class, or by time since fire prior to 2009 (data not shown). Similarly, the percentage of small dead eucalypt stems that originated from basal resprouts was universally small (1.8%), and very few supported live basal resprouts (6.6%) irrespective of wildfire severity class or of time since fire (data not shown). Few basal resprouts and lack of fire effects on resprouting frequency were also evident in the medium-sized stem class (10 – 20 cm dbh; data not shown). That is, very few medium eucalypt stems clearly originated from basal resprouts (live 1.3%; dead 3.2%), or supported live basal resprouts five years after the 2009 wildfire (live 4.4%; dead 5.4%).

3.4 Most important explanatory variables

The Random Forest analyses confirmed an overriding influence of wildfire severity as assessed in 2009 (here as the continuous variable Composite Burn Index, CBI) on eucalypt stem and seedling densities five years after the wildfire. CBI was ranked as the most important variable for explaining densities of live large- and medium-sized eucalypts (both negative associations), and of live small eucalypts and live eucalypt seedling regeneration (both positive; Table 3). It was also most important in explaining percentage mortalities of large- and medium-sized eucalypts (positive associations; Table 3). The variances explained by Random Forest models that included all significant explanatory variables were greatest for medium-sized eucalypt stems (55% of live density, 61% of percentage mortalities), consistent with the very clear effects of the High severity wildfire class on mortalities in this size class (Figure 1).

CBI was also included as a significant explanatory variable in models of small eucalypt percentage mortalities (negative association), although number of years since the preceding fire was ranked higher (negative; Table 3), which was consistent with significantly greater mean mortalities at Recently burnt than Long unburnt sites in this size class (Figure 3). In addition, another measure of wildfire severity, percentage number of large stems that were charred (TCHAR), was a significant explanatory variable of percentage mortalities of medium-sized eucalypts, of small live eucalypt densities, and of live eucalypt seedling densities (all positive associations; Table 3).

4. Discussion

4.1 Increased medium-term tree mortality with increased wildfire severity

Our tree mortality data challenge current conceptual models of perpetually resistant live tree biomass to high-severity wildfires in the fire-tolerant eucalypt forests of southern Australia (Bowman *et al.*, 2013). Mortalities of medium to large trees in the five years after the wildfire increased with fire severity as it was assessed (either as a class or as a continuous variable) shortly after the wildfire. Our data are consistent with previous shorter-term indications of elevated mortality of fire-tolerant eucalypts in high-severity areas after the ‘Black Saturday’ fires (Benyon & Lane, 2013; Nolan *et al.*, 2014; Bassett *et al.*, 2015a). Nonetheless, they represent much higher mortality rates than those recorded elsewhere in comparable mixed-species eucalypt forests after high-severity wildfire (Strasser *et al.*, 1996; Vivian *et al.*, 2008), and are the first to record significantly greater mortality of medium to large trees in all size intervals. This included the largest trees, greater than 50 and 70 cm dbh, which are considered the most fire resistant (Gill & Ashton, 1968; Burrows, 2013). Thus, while our tree mortality data support current understanding of high resistance of the medium- to large-sized eucalypts to low-severity wildfire, they provide clear evidence of decreased resistance to high-severity wildfire.

Greater percentage mortalities of medium- than large-sized stems was consistent with findings elsewhere that smaller eucalypts lack sufficient bark thickness or crown height to survive high-intensity fire (Gill & Ashton, 1968; Wilkinson & Jennings, 1993; Lawes *et al.*, 2001). We recorded almost complete medium-term mortality of medium-sized eucalypt stems after high-severity wildfire (93%), representing the near loss of an entire cohort of stems. This indicates potential for a decrease in the woody complexity of mixed-species eucalypt stands after high-severity wildfire. Such demographic legacies could also influence stand recovery after the next fire, for example, the development of bottlenecks in the transition from juvenile to mature tree stages, akin to those in savannahs where smaller stems are killed by a subsequent fire before they have a chance to be recruited into the large size classes (Bond *et al.*, 2012).

The ‘Black Saturday’ wildfires occurred towards the end of an extended drought in which southeast Australia recorded the driest 7- to 11-year periods on record (Bureau of Meteorology, 2012). Thus, chronic ‘hydraulic deterioration’ (Anderegg *et al.*, 2013) associated with this drought might have contributed to relatively high baseline mortalities at our Unburnt sites (*cf.* Bennett *et al.*, 2013), leading to unusually high mortalities at our High severity sites. This is consistent with atypically high post-fire mortalities confounded by antecedent drought in a recent study in the dry eucalypt forests of Tasmania (Prior *et al.*, 2016). Nonetheless, we suggest that our findings will be increasingly relevant to fire/ climate interactions in the near future given predictions of more frequent high-severity wildfires (Clarke *et al.*, 2011; King *et al.*, 2013), and of more frequent severe droughts (CSIRO & Bureau of Meteorology, 2015) in southern Australia under climate change projections.

How increased site-level mortalities after high-severity wildfire will influence mortality patterns at broader landscape scales remains unclear. Just c. 15% of the area of the Kilmore East-Murrindindi fire complex in mixed-species eucalypt forest was classified as High severity, compared with nearly two-thirds as Medium severity (Table 1). Limited field assessments shortly after the fire recorded tree mortalities in Medium-severity plots that were about half those in High-severity plots (Benyon & Lane, 2013; Nolan *et al.*, 2014), suggesting that there would be high mean percentage survival over the entire area of mixed-species eucalypt forest. However, a comprehensive field assessment of the fire complex concluded that unburnt patches within the fire boundary were rare, particularly where mixed-species eucalypt forests were burnt by high-severity wildfire (Leonard *et al.*, 2014). This indicates a potential for large contiguous areas (> c. 1000 ha) of increased tree mortality after high-severity wildfires in these forest landscapes.

4.2 New stem recruitment dominated by seedlings rather than basal resprouts

Our study's findings support general understanding that resprouter species recover from fire through a combination of resprouting and regeneration from seed (Lamont *et al.*, 2011). Despite increased mortality (as above), many small to large eucalypt stems survived high-severity fire, which consumed up to 100% of crowns, through epicormic resprouting from branches and stems. The predominance of epicormic resprouting was consistent with other studies of eucalypt recovery after high-severity wildfire (Wardell-Johnson, 2000; McCaw & Middleton, 2015), and with general understanding that epicormic resprouting has been critical to the success of eucalypts in fire-prone Australia (Gill, 1997; Burrows, 2013). High-severity wildfire also induced prolific regeneration from seed leading to significant increases five years later in the densities of both eucalypt seedlings and small stems. High seedling densities in mixed-species eucalypt forests after high-intensity wildfire have been previously recorded (Wardell-Johnson, 2000; Benyon & Lane, 2013), providing further evidence that the tolerance of these forests to high-severity wildfire involves a combination of 'resilience' through seedling recruitment and 'resistance' through epicormic resprouting (Enright *et al.*, 2014).

In contrast to seedling regeneration, we found very little evidence of recruitment of new stems after fire through basal resprouting. This was surprising given observations in comparable forests of multiple basal resprouts from small eucalypts (<20 cm diameter) that were top-killed by high-intensity wildfire (Wilkinson & Jennings, 1993; Strasser *et al.*, 1996). That is, we anticipated that prolific basal resprouting would follow mortality of small- and medium-sized stems after wildfire, consistent with understanding that basal resprouting capacity is greater in smaller rather than larger eucalypt stems (Gill, 1997; Prior *et al.*, 2016). Instead, we found very little evidence of basal resprouting in these size classes irrespective of wildfire occurrence and severity. This paucity of basal resprouting could be due to multiple factors including inherent intra-specific variation in resprouting capacity (Gill, 1997; Bellingham & Sparrow, 2000), and to the effects of the protracted drought prior to and including 2009, which, through a combination of carbohydrate depletion and hydraulic failure, could have limited bud initiation as well as resprout vigour and survival (Moreira *et al.*, 2012; Pausas *et al.*, 2016). Whatever the reasons, our study indicates that basal resprouting might not be a reliable strategy for recruiting new stems in this forest type, and that regeneration from seeds will be far from ‘unnecessary’ (Bowman *et al.*, 2013) if fire-killed stems are to be replaced by new cohorts.

4.3 Effects of recent prescribed fire on medium-term mortality and regeneration

Our study indicated that recent prescribed fire had limited impact on site-level resistance, but had the potential to decrease site-level resilience (*sensu* Enright *et al.*, 2014) of mixed-species eucalypt forests to wildfire. That is, while there were no effects on medium and large stem mortalities, recent prescribed fire was associated with greater mortalities of small stems, and with decreases in live seedling densities after low-severity wildfire (an effect masked by the prolific regeneration after high-severity wildfire). Both of these effects are consistent with previous findings of increased mortalities of small eucalypts with more frequent fire, even low-intensity prescribed fire (Abbott & Loneragan, 1984; Bennett *et al.*, 2013; Collins *et al.*, 2014). That is, shorter intervals associated with more frequent fires provide insufficient time for new seedlings that regenerated after one fire to establish sufficient protective mechanisms (bark thickness, crown height) to survive the next, and/or for small stems that survived the preceding fire to recover adequate bark thickness to escape cambial death from the next fire (Lawes *et al.*, 2001; Bennett *et al.*, 2013). As such, there were no indications that recent prescribed fires mitigated wildfire effects on tree dynamics at the site level. This does not discount the potential for prescribed fires to mitigate wildfire effects at the landscape level by reducing the extent of high-severity wildfires (most likely under moderate fire weather; Price & Bradstock, 2012), and increasing the likelihood of unburnt patches (Leonard *et al.*, 2014). However, low encounter rates with recent prescribed fire areas (c. 9%; Table 1) arguably decreased the potential for landscape-scale mitigation of the 'Black Saturday' wildfires.

5. Conclusions and management implications

Our study indicates potential for elevated mortality of fire-tolerant eucalypts of all sizes after high-severity wildfire. Such mortalities, including the near loss of medium-sized trees, could portend changes towards more open and less structurally complex forest, albeit at variable scales from patches to potentially large contiguous areas (up to c. 1000 ha in this example) depending on the continuity of high-severity fires.

High percentage mortalities of small stems coupled with unreliable basal resprouting, highlighted the importance of seedling recruitment to fill size gaps in these resprouter forests. A binary response of seedling recruitment with (predominantly) epicormic resprouting of mature stems also fits general understanding that these forest types can persist under a range of fire conditions (Gill, 1997). However, over-reliance on seedling recruitment could increase vulnerability to subsequent fires, particularly if a warmer drier future climate decreases seedling establishment and growth rates (Enright *et al.*, 2015). Potential feedback mechanisms associated with more open forest structures can include changes in understorey composition, fuel distribution, and associated flammability (Dobrowski *et al.*, 2015; Holz *et al.*, 2015; Coppoletta *et al.*, 2016), although such feedbacks remain under-examined in eucalypt forests (Fairman *et al.*, 2016). Other knowledge gaps include understanding the effects of compounded disturbances on tree mortality and regeneration in temperate forests, particularly the recent succession of short-interval wildfires in southeast Australia (Fairman *et al.*, 2016), and of potential stabilizing processes that both mitigate and compensate for tree mortality after severe wildfire (Lloret *et al.*, 2012).

Options for management to mitigate wildfire effects on tree mortality in mixed-species eucalypt forests will rely on decreasing the incidence and extent of high-severity wildfire however possible, including through wildfire suppression and effective prescribed fire programs (Fernandes & Botelho, 2003; Boer *et al.*, 2009; Cheney, 2010). However, extensive use of prescribed fires will need careful consideration of the fire intervals required to maintain new cohorts of eucalypt stems, including intervals close to the minimum tolerable fire interval for these forests (c. 15 years; Cheal, 2010), and/ or a diversity of intervals within any given landscape as non-burnt patches within prescribed fire boundaries or using a mosaic of prescribed fire intervals at broader scales (Burrows, 2008). If tree mortality is increased in extent by, for example, two wildfires in quick succession, management options might need to include re-seeding the dominant eucalypts in mixed-species forests in a manner akin to the fire-sensitive ‘ash-type’ eucalypt forests dominated by obligate seeder trees (Bassett *et al.*, 2015b). That is, rather than assuming perpetual resistance and resilience to fire, our study highlights the need to carefully monitor tree population dynamics in even the most fire-tolerant forests, particularly in light of the many emerging threats to forest health posed by changing disturbance and climate regimes (Millar & Stephenson, 2015).

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Figure Captions

Fig. 1 Effects of 2009 wildfire severity class (Unburnt, Low, High) on live and dead eucalypt stem densities and mortalities (percentages of standing stems that were dead) five years after the 2009 wildfire. Values are means (± SE) by medium size class (10 to 20 cm) and by large size intervals (dbh, diameter breast height). For live and stem densities, *n*=14 for the medium size class, and *n*=21 to 26 for the large size intervals. Mortality means (%) are based on fewer sites because sites without live or dead stems in that size interval were treated as a missing value. Letters indicate significant differences between 2009 wildfire severity classes within each size interval (based on the non-inclusion of zero in the 95% confidence interval for the difference between two means).

Fig. 2 Densities of live and dead eucalypt seedlings by combinations of 2009 wildfire severity class and time since fire (TSF: left grey bars, Recently burnt: <10 years since prescribed fire prior to 2009; right white bars, Long unburnt: >30 years since any fire prior to 2009). Values (provided for clarity) are the mean densities five years after the wildfire (fourth-root back-transformed) at 7 sites, with 95% confidence intervals. Significant effects of severity (S: High severity HS, Low severity LS, Unburnt UB), and severity by TSF interactions are indicated by asterisks (* $P < 0.05$, *** $P < 0.001$).

Fig. 3 Densities and mortalities of small eucalypt stems by combinations of 2009 wildfire severity class and time since fire (left grey bars, Recently burnt: <10 years since prescribed fire prior to 2009; right white bars, Long unburnt: >30 years since any fire prior to 2009). Values are the means of small (2.5 – 10 cm dbh) live and dead densities (fourth-root back-transformed), and associated mortalities at 7 sites, with 95% confidence intervals. Significant effects of severity (S: High severity HS, Low severity LS, Unburnt UB), and time since fire

(TSF: Recently Burnt RB, Long unburnt LUB) are indicated by asterisks (* $P < 0.05$, *** $P < 0.001$).

Figure 1

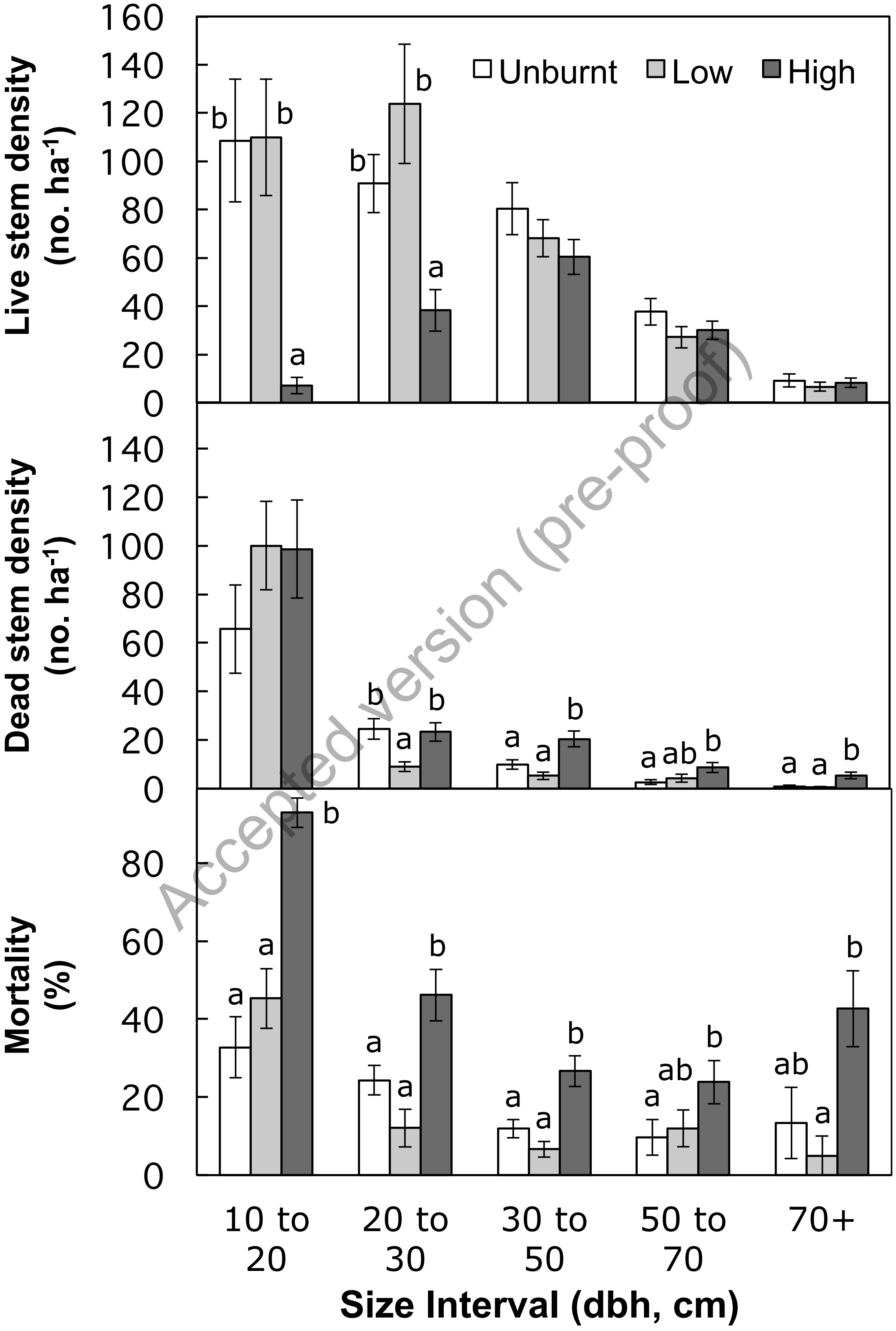
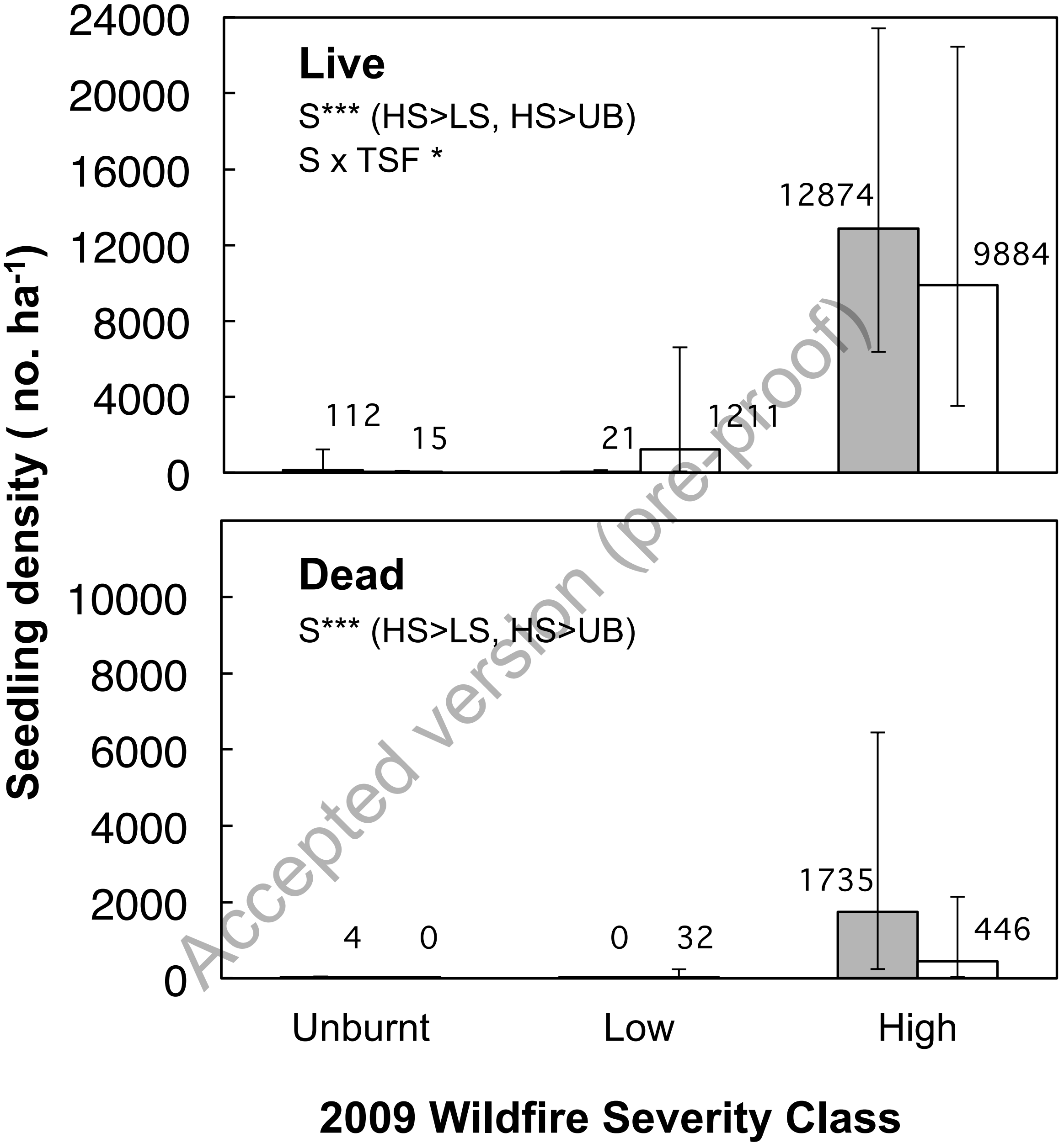

Live stem density (no. ha^{-1})
160
140
120
100
80
60
40
20
0
Unburnt
Low
High
b
b
a
b
b
a
Dead stem density (no. ha^{-1})
140
120
100
80
60
40
20
0
b
a
b
a
a
b
a
ab
b
a
a
b
Mortality (%)
80
60
40
20
0
b
a
a
a
a
b
a
a
b
a
ab
b
ab
a
b
10 to 20
20 to 30
30 to 50
50 to 70
70+
Size Interval (dbh, cm)

Figure 2



Live
S*** (HS>LS, HS>UB)
S x TSF *
24000
20000
16000
12000
8000
4000
0
112
15
21
1211
12874
9884
Dead
S*** (HS>LS, HS>UB)
10000
8000
6000
4000
2000
0
4
0
0
32
1735
446
Seedling density (no. ha^{-1})
Unburnt
Low
High
2009 Wildfire Severity Class

Figure 3

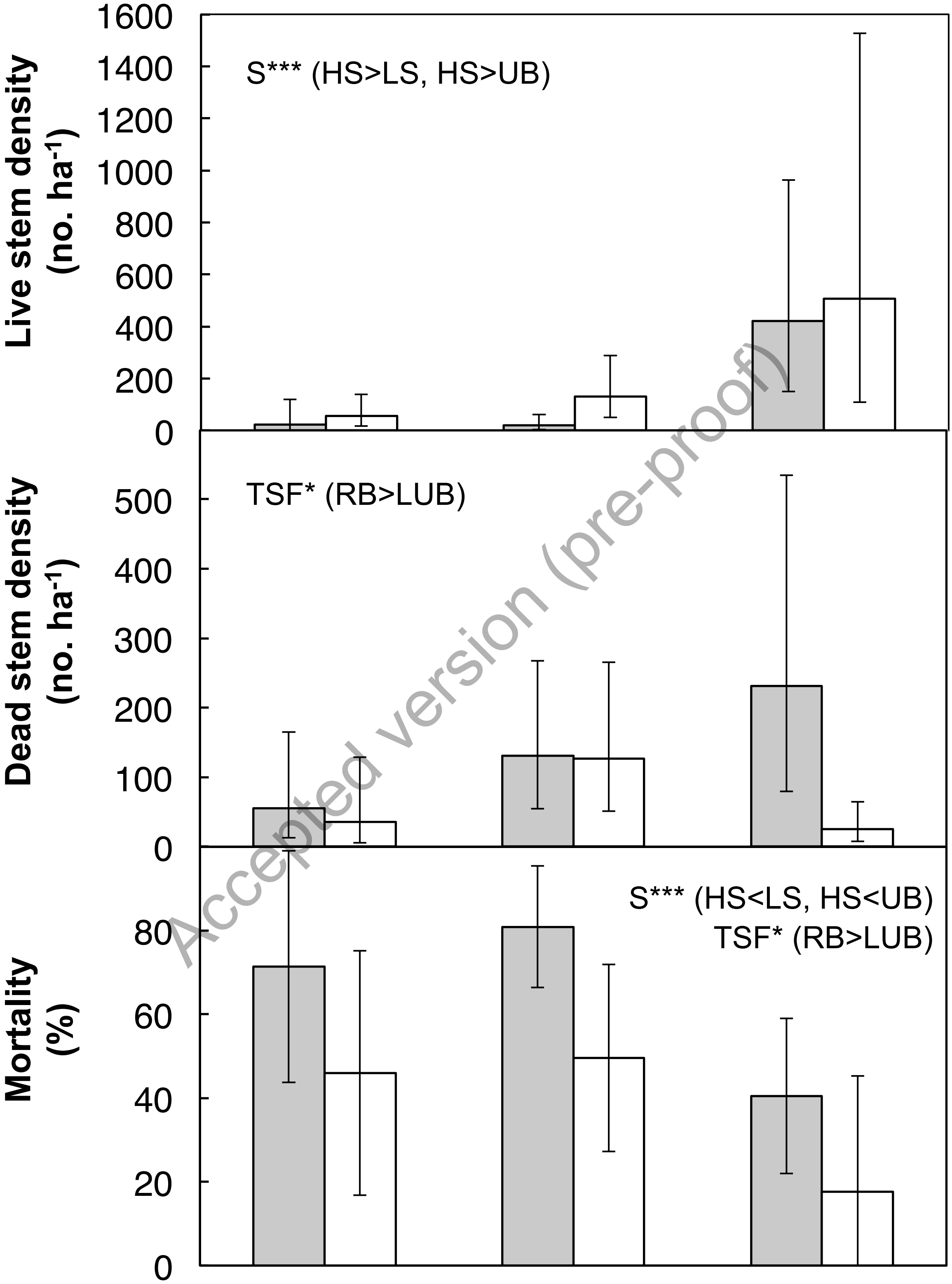

Live stem density (no. ha^{-1})
1600
1400
1200
1000
800
600
400
200
0
S*** (HS>LS, HS>UB)
Dead stem density (no. ha^{-1})
500
400
300
200
100
0
TSF* (RB>LUB)
Mortality (%)
80
60
40
20
0
S*** (HS<LS, HS<UB)
TSF* (RB>LUB)
Unburnt
Low
High
2009 Wildfire Severity Class

Table 1

Areas (ha) of combinations of 2009 wildfire severity classes and time since fire classes (combinations assessed in this study are in bold; values in brackets indicate the percentage of the total 68119 ha of the wildfire). Areas were estimated from the intersection of two spatial data layers[a] within the boundaries of the 2009 Kilmore East-Murrindindi fire complex, and relate only to the forest type considered in this study (Herb-rich Foothill Forest).

	Time since fire prior to 2009				
Wildfire severity class [b]	<10 years since prescribed fire ('Recently burnt')	<10 years since wildfire	10 to 30 years since any fire	>30 years since any fire ('Long unburnt')	Total
Low	**2370 (3)**	933 (1)	1829 (3)	**9958 (15)**	15090 (22)
Medium	3309 (5)	343 (1)	10854 (16)	28313 (42)	42819 (63)
High	**357 (1)**	11 (0)	3268 (5)	**6574 (10)**	10210 (15)
Total	5986 (9)	1287 (2)	15951 (23)	44845 (66)	68119

[a] 1:25 000 map of 2009 wildfire severity classes (Department of Sustainability and Environment, 2009) intersected with the state environment department's spatial database of fire history

[b] Low severity: low-intensity surface fire causing patchy combustion of the understorey and no or light crown scorch (<35%); Medium severity: mixed mosaic of crown burning and scorching from 30 to 100%; High severity: intense fire that consumed the entire understorey and 70 to 100% of the overstorey crowns (Department of Sustainability and Environment, 2009)

Table 2

Summary of the study area’s environment, fire history, and stand structure, and of measures of severity of the 2009 wildfire. Bolded variables were included as potential explanatory variables in Random Forest models of large eucalypt densities at 71 sites (non-bolded were excluded due to high correlations with one or more of the bolded variables). Bolded and italicised variables were also included in models of eucalypt seedling regeneration (all three variables), and of small- and medium-sized tree densities (CWDR_M only) based on 42 sites.

Variable group and variable name	Abbreviated name	Unit	Mean [a] (min, max)
Location/ topography			
Easting [b]	EAST	m	371952 (328877, 434459)
Northing [b]	NORTH	m	5861065 (5831962, 5889044)
Elevation	ELEVATION	m asl	520 (165, 890)
Aspect (predominant) [c]	ASPECT	°	177 (0, 345)
Slope (predominant)	SLOPE	°	13.5 (1.0, 36.0)
Vertical distance above stream	VDIST	m	56 (0, 207)
Climate			
Annual mean temperature	TEMP_MEAN	°	12.0 (10.0, 13.7)
Max temp. of warmest month	TEMP_MAX	°	25.8 (23.9, 27.6)
Min temp. of coldest month	TEMP_MIN	°	2.2 (0.1, 4.2)
Annual precipitation	RAIN_TOT	mm	1233 (913, 1673)
Precipitation of wettest quarter	RAIN_WQ	mm	424 (272, 641)
Precipitation of driest quarter	RAIN_DQ	mm	174 (148, 219)
Annual solar radiation	RAD_MEAN	$W\ m^{-2}$	23.2 (16.0, 26.6)
Fire history			
Years since last fire of any type [d]	LASTFIREYR	years	39 (1, 82)
Years since last wildfire [d]	LASTFIREYR_W	years	69 (26, 82)
Total fire number on record [e]	FIRENO_TOT	count	2.1 (0.0, 4.0)
Total fire number after 1972 [e]	FIRENO72_TOT	count	1.3 (0.0, 3.0)
Wildfire number on record [e]	FIRENO_W	count	1.5 (0.0, 3.0)
Prescribed fire number on record [e]	FIRENO_P	count	0.7 (0.0, 2.0)
Wildfire severity [f]			
Composite Burn Index	CBI	score	1.62 (0.39, 2.75)
Percentage no. large trees charred	TCHAR	%	73 (0, 100)
Coarse woody debris rotten mass	CWDR_M	$Mg\ ha^{-1}$	6.0 (0.0, 28.9)
Stand structure [g]			
Basal area (large live and dead)	TBA	$m^2\ ha^{-1}$	29 (19, 48)
Stump number (large)	STU_NO	$no.\ ha^{-1}$	59 (0, 260)

[a] Values are across 71 study sites with the exception of CWDR_M, STU_NO, and TLD_BA, which are across 42 sites

[b] Map Grid of Australia (GDA 94), UTM Zone 55

[c] Cosine radian

[d] Years since last fire before 2009; the earliest fires on record were wildfires in 1927 (this date was used as the earliest fire year for sites that had no known fires on record)

[e] Total fires includes prescribed fires plus wildfires (including the 2009 wildfire); fire records started in 1927 and were considered most reliable after 1972; the earliest prescribed fires on record were in 1977

[f] CBI was a continuous variable assessed using 2009 remotely sensed data shortly after the wildfire (see text for details); percentage number of large trees that were charred and the mass of rotten coarse woody debris were measured as part of the field campaign five years after the wildfire

[g] Stand structure/ history variables were assessed five years after the 2009 wildfire; ‘large’ ≥20 cm diameter at 30 cm height for stumps, and at breast height for trees (1.3 m).

Table 3

Table 3

Most important explanatory variables in Random Forest models of live eucalypt stem or seedling densities, and of eucalypt stem mortalities in small, medium and large size classes (dbhob, diameter breast height).

Response variables	Most important explanatory variables (and p-value) [a]				Variance explained (%) [b]
Large eucalypt stems (≥20 cm dbh)					
Live density (no ha^{-1})	–CBI	–RAINDQ			14*
	(0.00)	(0.03)			
Mortality (%)	+CBI	– NORTH	+TEMP_MEAN		24
	(0.00)	(0.02)	(0.02)		
Medium eucalypt stems (10 – <20 cm dbh)					
Live density (no ha^{-1})	–CBI	+EAST	+SLOPE		55
	(0.00)	(0.02)	(0.03)		
Mortality (%)	+CBI	–EAST	–SLOPE	+TCHAR	61
	(0.00)	(0.00)	(0.00)	(0.00)	
Small eucalypt stems (2.5 – <10 cm dbh)					
Live density (no ha^{-1})	+CBI	–SLOPE	+TCHAR		19
	(0.00)	(0.00)	(0.01)		
Mortality (%)	–LASTFIREYR	–CBI	+EAST	–TEMP_MEAN	22
	(0.00)	(0.00)	(0.01)	(0.02)	
Eucalypt seedlings (<2.5 cm diameter)					
Live density (no ha^{-1})	+CBI	–EAST	+TCHAR		39*
	(0.00)	(0.01)	(0.02)		

[a] See Table 2 for description of explanatory variables. The most important explanatory variables were selected using the 'NAP' ('new approach') method of Hapfelmeier and Ulm (2013), which uses permutation tests to indicate the importance of all potential explanatory variables in a Random Forest model and selects those with a p-value ≤ 0.05; variables are in order of importance in the Random Forest model (p-values in brackets); + or – indicates a positive or negative association with the response variable.

[b] Variance explained by a Random Forest model that only includes the listed explanatory variables; asterisks indicate the response variable was fourth-root transformed.