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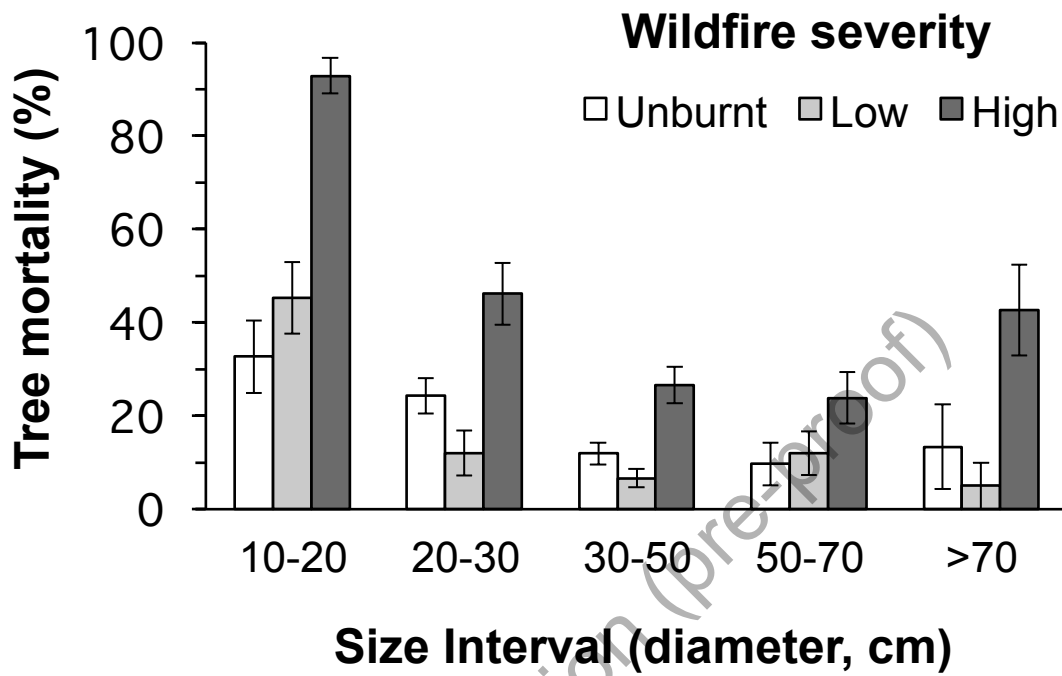
Title: Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire.

Authors: Lauren T. Bennett^{a*}, Matthew J. Bruce^b, Josephine MacHunter^b, Michele Kohout^b, Mihai A. Tanase^c, Cristina Aponte^c

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 reprints 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

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1 **ABSTRACT**

2 Mixed-species eucalypt forests of temperate Australia are assumed tolerant of most fire
3 regimes based on the impressive capacity of the dominant eucalypts to resprout. However,
4 empirical data to test this assumption are rare, limiting capacity to predict forest tolerance to
5 emerging fire regimes including more frequent severe wildfires and extensive use of
6 prescribed fire. We quantified tree mortality and regeneration in mixed-species eucalypt
7 forests five years after an extensive wildfire that burnt under extreme fire weather. To
8 examine combined site-level effects of wildfire and prescribed fire, our study included
9 factorial replications of three wildfire severities, assessed as crown scorch and understorey
10 consumption shortly after the wildfire (Unburnt, Low, High), and two times since last
11 preceding fire (<10 years since prescribed fire, >30 years since any fire). Our data indicate
12 that while most trees survived low-severity wildfire through epicormic resprouting, this
13 capacity was tested by high-severity wildfire. Five years after the wildfire, percentage
14 mortalities of eucalypts in all size intervals from 10 to >70 cm diameter were significantly
15 greater at High severity than Unburnt or Low severity sites, and included the near loss of the
16 10 to 20 cm cohort (93% mortality). Prolific seedling regeneration at High severity sites, and
17 unreliable basal resprouting, indicated the importance of seedling recruitment to the resilience
18 of these fire-tolerant forests. Recent prescribed fire had no clear effect on forest resistance (as
19 tree survival) to wildfire, but decreased site-level resilience (as recruitment) by increasing
20 mortalities of small stems. Our study indicates that high-severity wildfire has the potential to
21 cause transitions to more open, simplified stand structures through increased tree mortality,
22 including disproportionate losses in some size cohorts. Dependence on seedling recruitment
23 could increase vulnerabilities to subsequent fires and future climates, potentially requiring
24 direct management interventions to bolster forest resilience.

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

27 **1. Introduction**

28 A growing number of studies have highlighted a range of threats to the health and
29 persistence of temperate forests (Millar & Stephenson, 2015). Rising global temperatures
30 have contributed to droughts of unprecedented severity in many parts of the world, affecting
31 forest health directly through tree water stress and high temperature stress, and indirectly
32 through increased vulnerability to other stressors (van Mantgem *et al.*, 2009; Allen *et al.*,
33 2010; Grimm *et al.*, 2013; Reichstein *et al.*, 2013; Bennett *et al.*, 2015). Tree mortality is a
34 key determinant of forest structure and composition (Dietze & Moorcroft, 2011), and
35 increased tree mortality has the potential to shift forests to alternative states not dominated by
36 trees (Millar & Stephenson, 2015). Persistent decreases in live tree biomass invariably means
37 changes to key ecosystem services provided by forests, in particular to the strength and
38 persistence of the land-based global carbon sink (Hicke *et al.*, 2012; Brien *et al.*, 2015;
39 Ghimire *et al.*, 2015).

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

50 wildfires increased in recent decades in two of three forest bioregions (Bradstock *et al.*,
51 2014), and the cumulative forest area burnt by wildfire in the decade to 2014 was roughly
52 equivalent to that burnt in the preceding fifty years (Fairman *et al.*, 2016).

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

64 The fire-tolerant mixed-species eucalypt forests of southeastern Australia are thought to
65 be highly resistant (*sensu* Enright *et al.*, 2014) to more frequent high-intensity wildfires due to
66 the capacity of the dominant eucalypt species to resprout (Bowman *et al.*, 2013; Lavorel *et*
67 *al.*, 2015). Fire-tolerant eucalypts have been termed ‘the most accomplished post-fire
68 resprouters’ due to their capacity to resprout both from below-ground lignotubers, and from
69 above-ground accessory buds and epicormic meristems (Burrows, 2013). This resprouting
70 capacity typically keeps post-fire eucalypt mortalities low relative to, for example, fire-
71 tolerant forests in temperate zones of the United States (Bennett *et al.*, 2013). However, while
72 post-wildfire mortality rates of fire-tolerant eucalypt forests have rarely been quantified (as
73 also noted by Gill, 1997), both historical observations (Fairman *et al.*, 2016), and a handful of
74 recent small-scale studies, have indicated potential for elevated mortality of fire-tolerant

75 eucalypts after some fires. For example, Prior *et al.* (, 2016) recently attributed 25% of
76 eucalypt tree mortalities to moderate intensity wildfires in dry eucalypt forests of Tasmania,
77 and two studies in central Victoria recorded up to 40% greater mortality of fire-tolerant
78 eucalypts in high-severity than unburnt plots after the notorious ‘Black Saturday’ wildfire of
79 2009 (Benyon & Lane, 2013; Nolan *et al.*, 2014). While the Victorian data in particular were
80 based on very few observations (total of five high severity plots, each <0.1 ha), these studies
81 suggest that the tolerance of fire-tolerant eucalypt forests is not ‘boundless’ (Prior *et al.*,
82 2016), and that conceptual models for these forest types of perpetually resistant live tree
83 biomass to fire (Bowman *et al.*, 2013) require further scrutiny.

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

96 Wildfire risks in fire-tolerant forests throughout the world are often managed using
97 prescribed fire (the planned introduction of fire under specified conditions; Burrows *et al.*,
98 2010) to decrease fuel hazards (Fernandes & Botelho, 2003; McCaw *et al.*, 2012; McIver *et*
99 *al.*, 2013; Addington *et al.*, 2015). Low-intensity prescribed fires are used to decrease the

100 incidence, extent and intensity (energy released; Keeley, 2009) of wildfires, with the aim of
101 reducing hazards to humans, but also reducing the effects of wildfire severity – the impacts on
102 the ecosystem (Keeley, 2009). In the fire-tolerant eucalypt forests of southern Australia,
103 effective reduction of wildfire hazard requires regular prescribed burning at intervals of less
104 than about 7 to 10 years (Boer *et al.*, 2009; Tolhurst & McCarthy, 2016). However, while
105 prescribed fire regimes in these forests have been shown to reduce wildfire severity where
106 fuel loads have governed fire intensity, this capacity to mitigate wildfire severity decreases
107 under extreme fire weather (Price & Bradstock, 2012; Tolhurst & McCarthy, 2016). To date,
108 there has been minimal examination of the combined effects of prescribed fires and wildfires
109 on site-level tree mortality and regeneration in fire-tolerant eucalypt forests. For example, it
110 remains unclear if a preceding low-intensity prescribed fire would decrease (by reducing fuel
111 loads around individual stems; Aponte *et al.*, 2014) or increase (by decreasing bark thickness;
112 Bennett *et al.*, 2013) site-level tree mortalities after a high-intensity wildfire that burnt under
113 extreme weather conditions.

114 Our study assesses tree mortality and regeneration in fire-tolerant mixed-species
115 eucalypt forests following the 2009 ‘Black Saturday’ wildfires of southeast Australia. We
116 examine the effects of wildfire intensity as represented by fire severity, which was based on
117 assessments of crown scorch and understorey consumption in the two months after the
118 wildfire. Our in-field assessments were made five years after 2009 to adequately capture any
119 medium-term secondary responses to the wildfire including post-fire mortality and/ or
120 recovery through resprouting and regeneration. To examine the potential for prescribed fire to
121 mitigate or exacerbate site-level wildfire effects, our study design included factorial
122 combinations of two times since last fire prior to 2009 (<10 years since prescribed fire, >30
123 years since any fire) with three 2009-wildfire severities (unburnt, low, high). Our principal
124 aims are to improve the empirical basis for predicting the resistance and resilience of fire-

125 tolerant eucalypt forests under emerging fire regimes, and to highlight any potential
126 vulnerabilities so that thresholds of sustainability might be identified and adaptively managed
127 (Millar & Stephenson, 2015).

128 **2. Materials and methods**

129 *2.1 Study area*

130 Our study focused on native, mixed-species eucalypt forests in the foothills of the Great
131 Dividing Range in central Victoria, south-eastern Australia (study area centre: 37°28'S,
132 145°32'E). Our study's forests are a type of dry sclerophyll forest (Ashton, 2000) or 'Open-
133 forest' (tree heights 10-30 m, projective foliage cover 30-70%; Specht, 1981), known locally
134 as 'Herb-rich Foothill Forest' (Department of Sustainability and Environment, 2004). They
135 are dominated by co-occurring eucalypts of different bark types, such as *Eucalyptus obliqua*
136 L'Hér (deep fibrous 'stringybark'), *E. radiata* Sieber ex DC. and *E. dives* Schauer (short
137 fibrous bark), and *E. globulus* subsp. *bicostata* (Maiden, Blakely & Simmonds) J.B. Kirkp.
138 (smooth 'gum' bark). Each of these bark types affords some degree of fire-tolerance to mature
139 stems; for example, heat penetration to the cambium is decreased by the greater bark
140 thickness of the stringybarks, but also by the relatively low inflammability of the smooth,
141 non-decortivating bark on the gum stems (Gill & Ashton, 1968). The understoreys of these
142 forests are characterised by a diverse and well-developed herb layer beneath a sparse to
143 continuous sclerophyll shrub layer (Ashton, 2000). Current recommendations for minimum
144 tolerable fire intervals to maintain the forests' species compositions are 15 years for low-
145 severity fires like typical prescribed fires (the maturation time of shorter-lived shrubs and
146 herbs), and 15 years for high-severity crown fires (sufficient time for the longest-lived species
147 to have the size or seed store to survive a second severe fire; Cheal, 2010).

148 Our forest sites encompassed a range of aspects, elevations (165 – 890 m above sea
149 level), slopes (1 – 36°), and morphological types (Flat to Upper slope and Crest; Speight,
150 2009), reflecting the variable geomorphology of the area (Ashton, 2000). Soils are not well
151 described in the study area; however, the dry sclerophyll forests frequently occur on yellow
152 podzolic soils of relatively poor structure (Ashton, 2000). The regional climate is temperate,
153 with annual rainfall in the range 800 to 1200 mm, and the least rain falling in summer
154 (Ashton, 2000). Mean monthly minimum temperatures are in the range 4°C (July/August) to
155 12°C (February), and mean monthly maximum temperatures in the range 9°C (July) to 23°C
156 (January/February; Toolangi weather station; Bureau of Meteorology, 2015).

157 Our study encompassed an area of about 720,000 ha (c. 60 x 120 km²), including forest
158 sites that were within and around the perimeter of two 2009 wildfires collectively known as
159 the Kilmore East-Murrindindi fire complex. This wildfire complex led to the deaths of 159
160 people and the destruction of > 2200 buildings, and was the most damaging of the >300 fires
161 that burnt in Victoria on ‘Black Saturday’, 7 February 2009 (Cruz *et al.*, 2012; Teague *et al.*,
162 2010). It burnt about 400,000 ha over three weeks, but most of the damage occurred in the
163 first 12 hour period, which was characterised by forest crown fires of very high intensities
164 (peaks of 90,000 kW m⁻¹), the result of ‘exceedingly dry’ fuels combined with extreme fire
165 weather (high temperatures and strong hot winds; Cruz *et al.*, 2012). Widespread dry fuels
166 were the result of a preceding twelve-year period of consistent rainfall deficit and above-
167 average temperatures, combined with two periods of extreme heat (consecutive days > 40 °C;
168 Bureau of Meteorology, 2009) in the fortnight before the wildfires.

169 2.2 Study design

170 Our 71 study sites were replicated combinations of two times since the last preceding
171 fire (‘Recently burnt’, ‘Long unburnt’), and three 2009-wildfire severities (‘Unburnt’, ‘Low’,
172 ‘High’). Time since the last fire was as recorded in the state environment department’s spatial

173 database of fire history, which contained records of wildfires back to 1927 but was considered
174 most accurate after 1972. Sites were classified as ‘Recently burnt’ (32 sites) if last burnt by
175 low-intensity prescribed fire within 10 years of 2009 (i.e. less than the above-mentioned
176 minimum tolerable fire interval of 15 years), and as ‘Long unburnt’ if there were no records
177 of any fire (wildfire or prescribed fire) for more than 30 years prior to 2009 (39 sites). To
178 limit the number of fire conditions examined, we excluded sites burnt by recent wildfire and
179 by any fire between 10 and 30 years before 2009.

180 Our wildfire severity classes were from a 1:25 000 map produced in 2009 by the state
181 environment department that was based on change in the Normalised Burn Ratio (dNBR) as
182 estimated from pre- and post-fire SPOT images, and extensive ground-truthing in the two
183 months after the wildfires (Department of Sustainability and Environment, 2009). Sites were
184 classified as ‘Low severity’ if burnt by low-intensity surface fire, which caused patchy
185 combustion of the understorey and no or light crown scorch (<35%); ‘Medium severity’ if
186 there was a mixed mosaic of crown burning and scorching ranging from 30 to 100%; and as
187 ‘High severity’ if burnt by an intense fire that consumed the entire understorey and 70 to
188 100% of the overstorey crowns (Department of Sustainability and Environment, 2009; Table
189 1). Our study design included 21 Low severity sites and 24 High severity sites, representing
190 the low and high ends of the 2009 severity assessment. We did not include Medium severity
191 sites due to logistical constraints, but also to avoid ambiguities in interpreting wildfire effects
192 associated with the uncertainties of mapping mixed wildfire severities in the middle range.
193 Our 26 ‘Unburnt’ sites showed no signs of wildfire in the 2009 assessment, and were selected
194 using the following criteria: same forest type (i.e. ‘Herb-rich Foothill Forest’); close as
195 possible to wildfire boundary (within c. 30 km); and as evenly distributed as possible around
196 the wildfire boundary.

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

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

211 2.3 Field assessments

212 We assessed the status of eucalypts in four size classes: regeneration (< 2.5 cm basal
213 diameter), small stems (2.5 – < 10 cm dbh), medium stems (10 – < 20 cm dbh), and large stems
214 (≥ 20 cm dbh; divided into four size intervals: 20 – < 30 , 30 – < 50 , 50 – < 70 , ≥ 70 cm
215 dbh). Our focus was on eucalypts because they were the predominant overstorey genus,
216 comprising $> 99\%$ of standing live large trees. Assessable small to large eucalypt stems were
217 defined as upright or leaning, > 1.3 m height, and rooted in the ground (i.e. not fallen ‘coarse
218 woody debris’). We ignored burnt-out stumps and stem fragments of < 1.3 m height because
219 low numbers and sometimes dense understorey meant that they could not be reliably detected.

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

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

229 At a subset of 42 sites, we counted small- and medium-sized eucalypt stems in two 10 x
230 25 m sub-plots located at the centre of the large tree plots (total area 0.05 ha). To gain insights
231 into regeneration forms, we allocated counts of small- and medium-sized live and dead stems
232 (classified as above) to one of three sub-classes: stem with live basal resprout, stem alone (no
233 live basal resprout), and stem as basal resprout (either live or dead). In addition, to assess tree
234 seedling regeneration, we tallied all live and dead eucalypt seedlings (i.e. <2.5 cm basal
235 diameter, not basal resprouts) that were rooted within 1 m of the long sides of the
236 small/medium tree sub-plots (total area 0.01 ha).

237 2.4 Statistical analyses

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

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

252 Location and topography explanatory variables included field measures of aspect and
253 slope, and elevation and vertical-distance-above-stream measures that were estimated using a
254 20-m resolution digital elevation model (Table 2). In addition, site easting and northing
255 coordinates were included to acknowledge unknown elements of the study area's variable
256 environment including geology and soils, and subtle differences in management histories. In
257 the absence of detailed local climate data, climate explanatory variables were estimated using
258 the WorldClim climate grids (<http://www.worldclim.org>). Fire history variables were derived
259 from the previously mentioned state environment department's spatial database, and
260 encompassed numbers of years since previous fires, and total numbers of fires (Table 2). For
261 a continuous measure of 2009 wildfire severity (rather than the severity classes used in the
262 above ANOVAs), we used a site-level composite burn index (CBI), which was derived using
263 an empirical additive model based on optical and radar remote sensing data. The empirical
264 model was calibrated and validated using field estimates of fire severity based on the above-
265 mentioned ground-truthing in the two months after the 2009 wildfires (Department of
266 Sustainability and Environment, 2009). Detailed information on field-estimated fire severity,
267 remote sensing data processing, and the modelling approach and validation can be found in
268 Tanase *et al.* (2015). Finally, additional estimates of wildfire severity were based on ancillary
269 field measures, and included: the percentage number of large trees that were charred; the mass
270 of rotten coarse woody debris (since the mass of rotten woody debris proved responsive to

271 fire effects in a similar forest type, and was presumably less influenced by post-wildfire
272 accessions than sound woody debris; Aponte *et al.*, 2014); and – for consideration in eucalypt
273 seedling regeneration models only – measures of stand structure (basal area of large live and
274 dead trees, large stump number; Table 2).

275 The non-parametric decision tree-learning approaches of Random Forest were used to
276 examine relationships of eucalypt stem and seedling response variables with explanatory
277 variables on the basis that they are robust to non-linear and complex interactions among
278 variables, which can be both discrete (as in the case of some of this study’s fire history
279 variables) and continuous (Breiman, 2001). In addition, Random Forest can be used to
280 identify the variables of most importance to a response variable, and, within a permutation
281 test framework (rather than a prediction accuracy framework), be used to estimate the
282 significance of each variable’s importance (Hapfelmeier & Ulm, 2013). All Random Forest
283 models were run using R (version 3.2.1; R Core Team, 2015). First, explanatory variables that
284 were highly correlated with others (Pearson’s correlation coefficient > 0.75) were excluded
285 (see Table 2) on the basis that while Random Forest can cope with correlated variables the
286 interpretation of any models that included closely correlated explanatories would be
287 unnecessarily complex. Next, the ‘NAP’ (‘new approach’) method of Hapfelmeier and Ulm
288 (2013) was used to identify the most important explanatory variables; this approach uses
289 permutation tests to estimate the importance of all potential explanatory variables in a
290 conditional Random Forest model (R ‘party’ package; Hothorn *et al.*, 2008) and selects those
291 with a p-value ≤ 0.05 . To assess the variance explained, the selected explanatory variables
292 were then included in a Random Forest model containing 100 trees, with the number of input
293 variables for each split set to the square root of the number of available variables (Díaz-
294 Uriarte & Alvarez de Andrés, 2006).

295 3. Results

296 3.1 *Fire effects on medium-term tree mortality*

297 Five years after the 2009 wildfire, densities and mortalities of established eucalypt
298 stems (medium stems 10 – 20 cm, and large stems ≥ 20 cm dbh) were significantly different
299 among the 2009 wildfire severity classes, but were not influenced by time since fire prior to
300 2009, nor by interactions between time since fire and wildfire severity class. Densities and
301 mortalities of established stems are thus discussed in terms of the overall effects of the 2009-
302 wildfire severity classes.

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

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

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

320 33% at Unburnt sites (Figure 1). In comparison, mean tree mortalities for the four large size
321 intervals (20 – 30, 30 – 50, 50 – 70, ≥ 70 cm dbh) ranged from 24 to 46% at High severity
322 sites, 5 to 12% at Low severity sites, and 10 to 24% at Unburnt sites (Figure 1).

323 3.2 *Fire effects on medium-term eucalypt seedling regeneration*

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

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

332 3.3 *Fire effects on new eucalypt establishment*

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

343 Very few of all small live eucalypt stems either originated from basal resprouts (sub-
344 class ‘stem as basal resprout’; 1.3%), or supported a live basal resprout (3.1%) five years after
345 the 2009 wildfire. These proportions were not influenced by 2009 wildfire severity class, or
346 by time since fire prior to 2009 (data not shown). Similarly, the percentage of small dead
347 eucalypt stems that originated from basal resprouts was universally small (1.8%), and very
348 few supported live basal resprouts (6.6%) irrespective of wildfire severity class or of time
349 since fire (data not shown). Few basal resprouts and lack of fire effects on resprouting
350 frequency were also evident in the medium-sized stem class (10 – 20 cm dbh; data not
351 shown). That is, very few medium eucalypt stems clearly originated from basal resprouts (live
352 1.3%; dead 3.2%), or supported live basal resprouts five years after the 2009 wildfire (live
353 4.4%; dead 5.4%).

354 *3.4 Most important explanatory variables*

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

366 CBI was also included as a significant explanatory variable in models of small eucalypt
367 percentage mortalities (negative association), although number of years since the preceding

368 fire was ranked higher (negative; Table 3), which was consistent with significantly greater
369 mean mortalities at Recently burnt than Long unburnt sites in this size class (Figure 3). In
370 addition, another measure of wildfire severity, percentage number of large stems that were
371 charred (TCHAR), was a significant explanatory variable of percentage mortalities of
372 medium-sized eucalypts, of small live eucalypt densities, and of live eucalypt seedling
373 densities (all positive associations; Table 3).

374 **4. Discussion**

375 *4.1 Increased medium-term tree mortality with increased wildfire severity*

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

391 Greater percentage mortalities of medium- than large-sized stems was consistent with
392 findings elsewhere that smaller eucalypts lack sufficient bark thickness or crown height to
393 survive high-intensity fire (Gill & Ashton, 1968; Wilkinson & Jennings, 1993; Lawes *et al.*,
394 2001). We recorded almost complete medium-term mortality of medium-sized eucalypt stems
395 after high-severity wildfire (93%), representing the near loss of an entire cohort of stems. This
396 indicates potential for a decrease in the woody complexity of mixed-species eucalypt stands
397 after high-severity wildfire. Such demographic legacies could also influence stand recovery
398 after the next fire, for example, the development of bottlenecks in the transition from juvenile
399 to mature tree stages, akin to those in savannahs where smaller stems are killed by a
400 subsequent fire before they have a chance to be recruited into the large size classes (Bond *et*
401 *al.*, 2012).

402 The 'Black Saturday' wildfires occurred towards the end of an extended drought in
403 which southeast Australia recorded the driest 7- to 11-year periods on record (Bureau of
404 Meteorology, 2012). Thus, chronic 'hydraulic deterioration' (Anderegg *et al.*, 2013)
405 associated with this drought might have contributed to relatively high baseline mortalities at
406 our Unburnt sites (*cf.* Bennett *et al.*, 2013), leading to unusually high mortalities at our High
407 severity sites. This is consistent with atypically high post-fire mortalities confounded by
408 antecedent drought in a recent study in the dry eucalypt forests of Tasmania (Prior *et al.*,
409 2016). Nonetheless, we suggest that our findings will be increasingly relevant to fire/ climate
410 interactions in the near future given predictions of more frequent high-severity wildfires
411 (Clarke *et al.*, 2011; King *et al.*, 2013), and of more frequent severe droughts (CSIRO &
412 Bureau of Meteorology, 2015) in southern Australia under climate change projections.

413 How increased site-level mortalities after high-severity wildfire will influence mortality
414 patterns at broader landscape scales remains unclear. Just c. 15% of the area of the Kilmore
415 East-Murrindindi fire complex in mixed-species eucalypt forest was classified as High

416 severity, compared with nearly two-thirds as Medium severity (Table 1). Limited field
417 assessments shortly after the fire recorded tree mortalities in Medium-severity plots that were
418 about half those in High-severity plots (Benyon & Lane, 2013; Nolan *et al.*, 2014), suggesting
419 that there would be high mean percentage survival over the entire area of mixed-species
420 eucalypt forest. However, a comprehensive field assessment of the fire complex concluded
421 that unburnt patches within the fire boundary were rare, particularly where mixed-species
422 eucalypt forests were burnt by high-severity wildfire (Leonard *et al.*, 2014). This indicates a
423 potential for large contiguous areas (> c. 1000 ha) of increased tree mortality after high-
424 severity wildfires in these forest landscapes.

425 4.2 *New stem recruitment dominated by seedlings rather than basal resprouts*

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

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

457 4.3 *Effects of recent prescribed fire on medium-term mortality and regeneration*

458 Our study indicated that recent prescribed fire had limited impact on site-level
459 resistance, but had the potential to decrease site-level resilience (*sensu* Enright *et al.*, 2014) of
460 mixed-species eucalypt forests to wildfire. That is, while there were no effects on medium and
461 large stem mortalities, recent prescribed fire was associated with greater mortalities of small
462 stems, and with decreases in live seedling densities after low-severity wildfire (an effect
463 masked by the prolific regeneration after high-severity wildfire). Both of these effects are
464 consistent with previous findings of increased mortalities of small eucalypts with more

465 frequent fire, even low-intensity prescribed fire (Abbott & Loneragan, 1984; Bennett *et al.*,
466 2013; Collins *et al.*, 2014). That is, shorter intervals associated with more frequent fires
467 provide insufficient time for new seedlings that regenerated after one fire to establish
468 sufficient protective mechanisms (bark thickness, crown height) to survive the next, and/or for
469 small stems that survived the preceding fire to recover adequate bark thickness to escape
470 cambial death from the next fire (Lawes *et al.*, 2001; Bennett *et al.*, 2013). As such, there
471 were no indications that recent prescribed fires mitigated wildfire effects on tree dynamics at
472 the site level. This does not discount the potential for prescribed fires to mitigate wildfire
473 effects at the landscape level by reducing the extent of high-severity wildfires (most likely
474 under moderate fire weather; Price & Bradstock, 2012), and increasing the likelihood of
475 unburnt patches (Leonard *et al.*, 2014). However, low encounter rates with recent prescribed
476 fire areas (c. 9%; Table 1) arguably decreased the potential for landscape-scale mitigation of
477 the 'Black Saturday' wildfires.

478 **5. Conclusions and management implications**

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

484 High percentage mortalities of small stems coupled with unreliable basal resprouting,
485 highlighted the importance of seedling recruitment to fill size gaps in these resprouter forests.
486 A binary response of seedling recruitment with (predominantly) epicormic resprouting of
487 mature stems also fits general understanding that these forest types can persist under a range
488 of fire conditions (Gill, 1997). However, over-reliance on seedling recruitment could increase

489 vulnerability to subsequent fires, particularly if a warmer drier future climate decreases
490 seedling establishment and growth rates (Enright *et al.*, 2015). Potential feedback
491 mechanisms associated with more open forest structures can include changes in understorey
492 composition, fuel distribution, and associated flammability (Dobrowski *et al.*, 2015; Holz *et*
493 *al.*, 2015; Coppoletta *et al.*, 2016), although such feedbacks remain under-examined in
494 eucalypt forests (Fairman *et al.*, 2016). Other knowledge gaps include understanding the
495 effects of compounded disturbances on tree mortality and regeneration in temperate forests,
496 particularly the recent succession of short-interval wildfires in southeast Australia (Fairman *et*
497 *al.*, 2016), and of potential stabilizing processes that both mitigate and compensate for tree
498 mortality after severe wildfire (Lloret *et al.*, 2012).

499 Options for management to mitigate wildfire effects on tree mortality in mixed-species
500 eucalypt forests will rely on decreasing the incidence and extent of high-severity wildfire
501 however possible, including through wildfire suppression and effective prescribed fire
502 programs (Fernandes & Botelho, 2003; Boer *et al.*, 2009; Cheney, 2010). However, extensive
503 use of prescribed fires will need careful consideration of the fire intervals required to maintain
504 new cohorts of eucalypt stems, including intervals close to the minimum tolerable fire interval
505 for these forests (c. 15 years; Cheal, 2010), and/ or a diversity of intervals within any given
506 landscape as non-burnt patches within prescribed fire boundaries or using a mosaic of
507 prescribed fire intervals at broader scales (Burrows, 2008). If tree mortality is increased in
508 extent by, for example, two wildfires in quick succession, management options might need to
509 include re-seeding the dominant eucalypts in mixed-species forests in a manner akin to the
510 fire-sensitive ‘ash-type’ eucalypt forests dominated by obligate seeder trees (Bassett *et al.*,
511 2015b). That is, rather than assuming perpetual resistance and resilience to fire, our study
512 highlights the need to carefully monitor tree population dynamics in even the most fire-

513 tolerant forests, particularly in light of the many emerging threats to forest health posed by
514 changing disturbance and climate regimes (Millar & Stephenson, 2015).

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Figure Captions

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

796 **Fig. 2** Densities of live and dead eucalypt seedlings by combinations of 2009 wildfire
797 severity class and time since fire (TSF: left grey bars, Recently burnt: <10 years since
798 prescribed fire prior to 2009; right white bars, Long unburnt: >30 years since any fire prior to
799 2009). Values (provided for clarity) are the mean densities five years after the wildfire
800 (fourth-root back-transformed) at 7 sites, with 95% confidence intervals. Significant effects of
801 severity (S: High severity HS, Low severity LS, Unburnt UB), and severity by TSF
802 interactions are indicated by asterisks (* $P < 0.05$, *** $P < 0.001$).

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

809 (TSF: Recently Burnt RB, Long unburnt LUB) are indicated by asterisks (* $P < 0.05$, *** $P <$
810 0.001).

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Figure 1

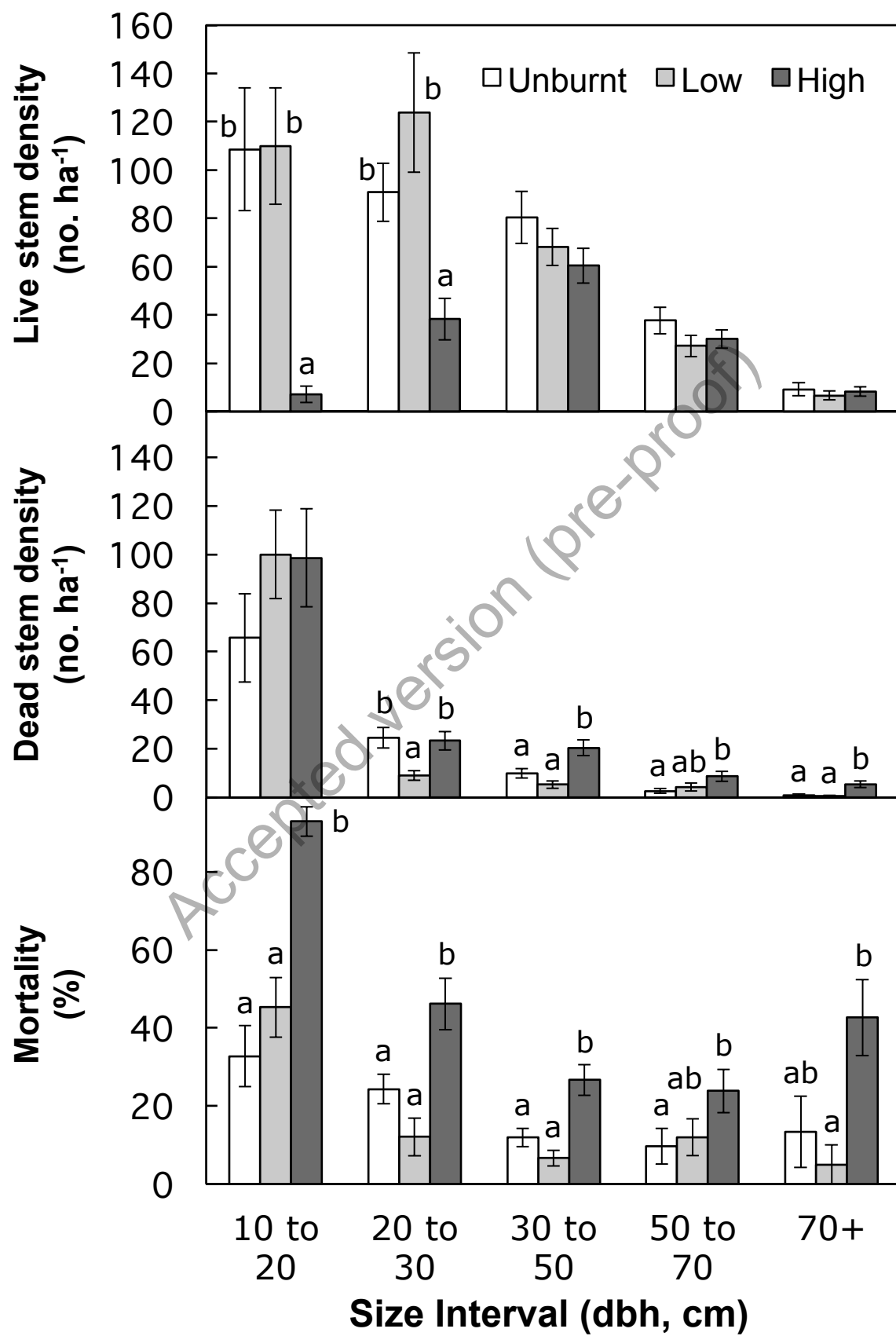


Figure 2

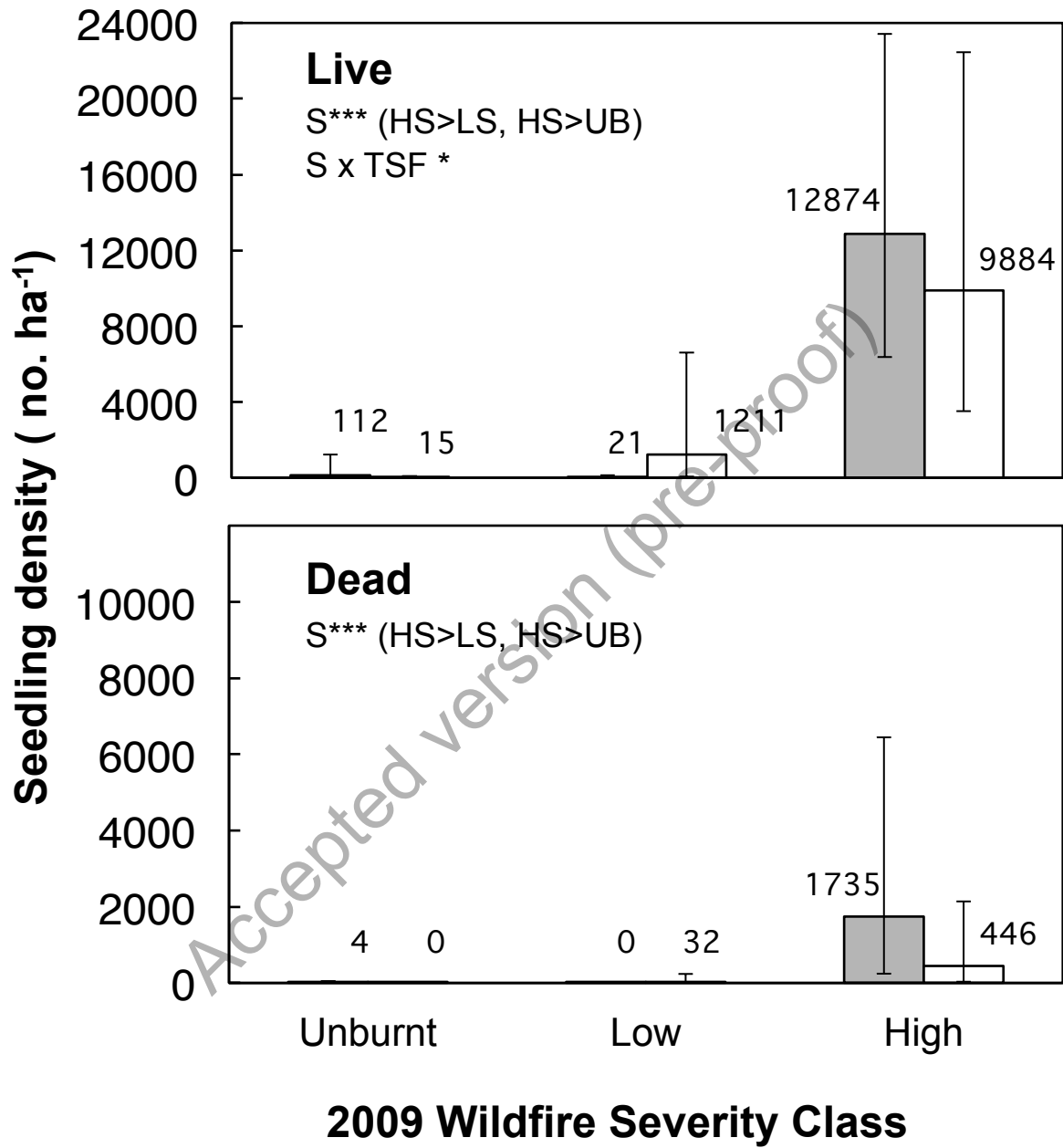


Figure 3

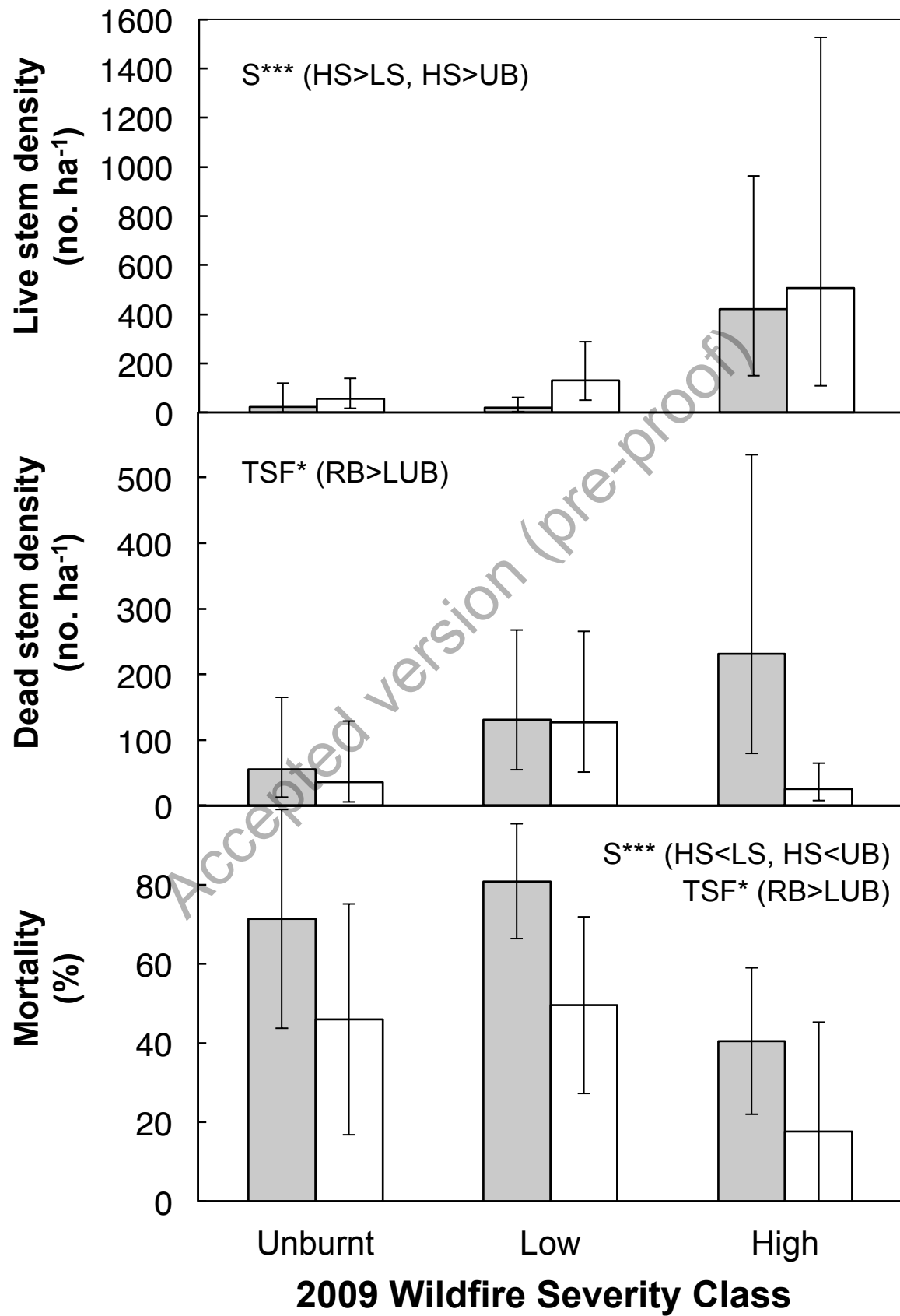


Table 1

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).

Wildfire severity class ^b	Time since fire prior to 2009				Total
	<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')	
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).

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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 (0.00)	-RAINDQ (0.03)			14*
Mortality (%)	+CBI (0.00)	-NORTH (0.02)	+TEMP_MEAN (0.02)		24
Medium eucalypt stems (10 – <20 cm dbh)					
Live density (no ha ⁻¹)	-CBI (0.00)	+EAST (0.02)	+SLOPE (0.03)		55
Mortality (%)	+CBI (0.00)	-EAST (0.00)	-SLOPE (0.00)	+TCHAR (0.00)	61
Small eucalypt stems (2.5 – <10 cm dbh)					
Live density (no ha ⁻¹)	+CBI (0.00)	-SLOPE (0.00)	+TCHAR (0.01)		19
Mortality (%)	-LASTFIREYR (0.00)	-CBI (0.00)	+EAST (0.01)	-TEMP_MEAN (0.02)	22
Eucalypt seedlings (<2.5 cm diameter)					
Live density (no ha ⁻¹)	+CBI (0.00)	-EAST (0.01)	+TCHAR (0.02)		39*

^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.