

Elsevier required licence: © 2022.

This manuscript version is made available
Under the CC-BY-NC-ND 4.0 license:

<http://creativecommons.org/licenses/by-nc-nd/4.0/>

The definitive publisher version is available online at:

[**https://doi.org/10.1016/j.foreco.2022.120070**](https://doi.org/10.1016/j.foreco.2022.120070)

1 **Title:** Mortality and resprouting responses in forest trees driven more by tree and ecosystem
2 characteristics than drought severity and fire frequency

3
4 **Author information:** Bendall, E. R.^{1,2*}, Bedward, M.¹, Boer, M.³, Clarke, H.^{1,3}, Collins, L.^{4,5,6},
5 Leigh, A.⁷, Bradstock, R. A.¹

6 ¹University of Wollongong, Centre for Environmental Risk Management of Bushfires, Northfields Avenue,
7 Wollongong, New South Wales, Australia 2522

8 ²Fenner School of Environment and Society, Australian National University, Australian Capital Territory,
9 Australia 2600

10 ³Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New South Wales

11 ⁴La Trobe University, Department of Ecology, Environment & Evolution, Bundoora, Victoria, 3086

12 ⁵Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning,
13 Heidelberg, Victoria, 3084

14 ⁶Current address: Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, 506 Burnside
15 Road West, Victoria BC V8Z 1M5, Canada

16 ⁷University of Technology Sydney, School of Life Sciences, Broadway, New South Wales

17 ORCID

18 L. Collins <https://orcid.org/0000-0001-8059-0925>

19 R. Bradstock <https://orcid.org/0000-0002-6904-2394>

20
21
22 ***Corresponding author:** Eli R. Bendall, email: eli.r.bendall@gmail.com, phone: +61 431 683
23 944, address: 18 Morven Road, Leura, NSW, Australia, 2780

32 **Abstract**

33 Increases in tree mortality linked to drought and fires have been reported across a range of
34 forests globally over the last few decades. Forests that resprout epicormically/aerially should
35 be the most resistant and resilient to changes in fire regime, yet they may be at risk of increased
36 mortality, demographic shifts and changes to species composition due to the compounding
37 effects of drought and fire. Despite this, the synergistic effects of drought and fire frequency
38 on resprouters has received less attention than for obligate seeder tree species. Our study
39 examined the effects of drought severity and fire frequency on the fire resistance of eucalypts
40 (i.e., including *Eucalyptus*, *Angophora* and *Corymbia*) that can resprout epicormically.
41 Following large-scale wildfires and drought in 2013, we conducted field surveys of temperate
42 eucalypt forests in the Sydney Basin Bioregion, focusing on two major *Eucalyptus* forest
43 assemblages: dry ridgetops and wet gullies. We measured tree size, previous fire damage (i.e.,
44 fire scars), bark type, mortality and resprouting position (e.g., canopy, stem, base) of
45 reproductive-age trees. We used a Bayesian modelling approach to derive bounded estimates
46 of response probabilities for trees sampled in each combination of drought severity
47 (mild/moderate versus severe) and fire frequency (low versus high), as well as bounded
48 estimates of differences between trees with and without fire scars, different bark types and
49 drought/fire histories. Eucalypt populations in both vegetation types were resilient to increases
50 in mortality and changes in resprouting position under severe drought and frequent fire, and
51 mortality and resprouting position varied substantially with tree size, fire scar presence/absence
52 and among bark types. Tree mortality and changes in resprouting position were considerably
53 more likely in smaller trees with fire scars. Species with non-compact bark (e.g., fibrous,
54 stringy, rough) were less resilient to lowering in resprouting position, e.g., from canopy to stem.
55 Populations dominated by species that have small stem diameters, thin/non-compact bark and

56 previous fire damage are likely at elevated risk of mortality and changes in resprouting position
57 under future climate change.

58

59 **Keywords:** climate change, drought effects, *Eucalyptus*, fire effects, resprouting, temperate
60 forest, tree bark, tree mortality

61

62 **1.1 Introduction**

63 Climate and fire are major determinants of ecosystem structure, function and evolution at the
64 global scale (Bond & van Wilgen 1996; Bowman *et al.* 2009; Keeley *et al.* 2011). Tree
65 mortality linked to drought and fires has been increasingly reported for a range of vegetation
66 types globally (Allen *et al.* 2010; Brando *et al.* 2014; Clark *et al.* 2016). Mass tree mortality
67 associated with extreme drought or altered fire regimes may destabilize forest ecosystems and
68 potentially lead to conversion of forest to a non-forest state (Bowman *et al.* 2013; Brando *et al.*
69 2014; Allen, Breshears & McDowell 2015). Drought is a key driver of large fire occurrence in
70 forest ecosystems (Andrade *et al.* 2019; Cerano-Paredes *et al.* 2019; Silva Junior *et al.* 2019),
71 with periods of severe drought often coupled with increased fire size, area burned and fire
72 severity (Abatzoglou *et al.* 2018; Clarke *et al.* 2020; Parks & Abatzoglou 2020). The nature of
73 the interactive effects of drought and fire on tree mortality (e.g., antagonistic, additive or
74 synergistic) will have important implications for the stability of forest ecosystems under future
75 climate change (Stephens *et al.* 2018; Coop *et al.* 2020; Nolan *et al.* 2021).

76 Trees survive in drought- and fire-prone landscapes via a combination of resilience (i.e.,
77 regenerative) and resistance (i.e., structural/protective) traits that ultimately shape vegetation
78 structure and species distributions (Clarke *et al.* 2013; Pausas *et al.* 2016). Vegetative
79 resprouting is a key resilience trait in disturbance-prone ecosystems (Bellingham and Sparrow,
80 2000), enabling plants to produce new foliage following disturbances that cause partial or full

81 defoliation (Pausas *et al.* 2016; Pausas & Keeley 2017). Plants are often grouped as either
82 resprouters or non-resprouters, although among resprouters there is variability in resprouting
83 location (Nicolle 2006; Burrows 2013; Clarke *et al.* 2013). Many species resprout exclusively
84 from buds buried below-ground (i.e., basal resprouters), while some arborescent species that
85 experience frequent canopy disturbing fire can resprout from aerial buds (i.e., epicormic
86 resprouters) (Clarke *et al.* 2013; Pausas & Keeley 2017; Pausas *et al.* 2018). Forests dominated
87 by epicormic resprouters recover canopy cover quickly following high severity fire (e.g. within
88 10–20 years, Vivian *et al.* 2008, Haslem *et al.* 2016; Collins *et al.* 2021b) and are generally
89 considered resilient to disturbance (Catry *et al.* 2013; Matusick *et al.* 2016).

90 Thick, protective bark is a resistance trait that shields the cambium and epicormic buds
91 from lethal temperatures during fire (Lawes *et al.* 2011b; Wesolowski, Adams & Pfautsch
92 2014; Pausas 2015). Investment in protective bark to increase survival probability of stems is
93 likely to be a trade-off with growth rate and overall-size (Jackson, Adams & Jackson 1999).
94 For example, trees that grow in open-forest conditions that experience frequent fire may invest
95 relatively more into thick protective bark than trees that grow in closed-forest conditions, where
96 fire may be infrequent (Jackson, Adams & Jackson 1999). However, there may be wide
97 variability in bark thickness patterns within a vegetation type, owing to interspecific
98 differences, trade-offs between growth, form and the multiple functions of bark in protecting
99 against fire, pathogens and moisture loss (Poorter *et al.* 2014). Bark thickness decreases with
100 decreasing stem size (Lawes *et al.* 2011a), making small stems and thin canopy branches more
101 vulnerable to mortality during fire than large stems and thick branches (Hoffmann & Solbrig
102 2003; Hoffman *et al.* 2009; Trouvé, Osborne & Baker 2021). Thus, eucalypts with relatively
103 thin bark on either the main stem or canopy branches are likely more vulnerable to mortality
104 or were less resilient to lowering in resprouting position on the stem via increased topkill, i.e.,

105 the extent to which above-ground components are killed during fire (Hoffman *et al.* 2009;
106 Lawes *et al.* 2011a; Denham *et al.* 2016).

107 Forests dominated by trees capable of epicormic resprouting typically experience low
108 rates of fire-related mortality (e.g. 2–15%, Vivian *et al.* 2008; Catry *et al.* 2013) or stem
109 mortality (i.e. topkill), allowing the overstorey to maintain stable biomass even under high fire
110 frequencies (e.g. mean inter-fire intervals of 5–10 years, Gordon *et al.* 2018; Collins *et al.*
111 2019). However, higher mortality rates (e.g. 20–35%) have been reported following more
112 extreme conditions (e.g. prolonged extreme drought preceding high severity fire; Trouvé,
113 Osborne & Baker 2021). Consecutive high severity short-interval fires can also increase
114 mortality, alter resprouting dynamics and shift population structure (Fairman *et al.* 2017;
115 Fairman, Bennett & Nitschke 2019; Collins 2020). For example, the stem diameter (DBH) at
116 which trees become increasingly likely to revert to basal resprouting may increase with the
117 number of fires, e.g., from 15 cm (one fire) to 22 cm (two fires; Fairman *et al.* 2019).
118 Additionally, high severity fire can reduce the likelihood of successful epicormic resprouting,
119 causing topkill (Catry *et al.* 2013; Collins 2020), though degree of topkill varies as a function
120 of species and stem size (Trouvé, Osborne & Baker 2021). Further, species that are more
121 sensitive to the effects of high severity fire, such as those found in wet gullies, may be relatively
122 more susceptible to topkill or mortality among larger size-classes than species with greater
123 resilience to fire, such as those found on exposed ridgetops (Trouvé, Osborne & Baker 2021).

124 Stem collapse is a major cause of stem mortality in resprouting forests (Whitford &
125 Williams 2001; Gibbons, Cunningham & Lindenmayer 2008). Basal ‘fire scars’, whereby the
126 cambium is killed by fire and begins to erode stem integrity, can make trees more vulnerable
127 to stem collapse during future fires and storms (Lawes *et al.* 2013; Silvério *et al.* 2019; Collins
128 2020). Variation in bark thickness/density among species may influence susceptibility to fire
129 scar formation/stem collapse during and following fire (Gibbons *et al.* 2000b; Gibbons *et al.*

130 2000a; Collins *et al.* 2012; Collins 2020). Increased fire frequency in resprouting forests may
131 accelerate the development of fire scars (Wardell-Johnson 2000; Collins *et al.* 2012), resulting
132 in the loss of large stems (Fairman *et al.* 2017).

133 With the expected future increases in concurrent drought and fire (IPCC 2021), several
134 mechanisms could result in major structural and compositional changes to resprouting forests.
135 For example, drought may increase fire severity and area burned via changes to soil moisture
136 and fuel dynamics, leading to increased tree mortality (Van Nieuwstadt 2005; Fredriksson,
137 Danielsen & Swenson 2006; Xiao & Zhuang 2007). Pre-fire drought may also increase the
138 susceptibility of trees to mortality during fire, via drought-induced physiological changes, such
139 as reduced xylem conductivity, increased branch cavitation and starvation of carbohydrates
140 needed for post-fire resprouting (van Mantgem *et al.* 2013; Jacobsen *et al.* 2016; Matusick *et*
141 *al.* 2016). Forests may also experience increased mortality, decreased recruitment and inhibited
142 resprouting if antecedent drought/fire has a compounding effect on resistance and resilience
143 traits (Allen *et al.* 2010; Enright *et al.* 2015; Clark *et al.* 2016). Developing a comprehensive
144 understanding of coupled drought-fire effects on forest trees will facilitate better prediction of
145 the likely responses of forests to global change.

146 Temperate forests cover a diverse range of climates and are periodically subjected to
147 drought and fire (van Mantgem & Stephenson 2007; Stevens-Rumann *et al.* 2018). Trees from
148 the genera *Angophora*, *Corymbia* and *Eucalyptus*, referred to as ‘eucalypts’, dominate
149 temperate forests across southeastern Australia and are generally resilient to fire, with most
150 species possessing the capacity to resprout epicormically following canopy defoliating fires
151 (Nicolle 2006; Burrows 2013). Eucalypts exhibit diverse physiological responses to drought
152 (Merchant *et al.* 2006; Merchant *et al.* 2007). Substantial stem mortality (e.g. 26%) and crown
153 mortality (e.g. >70%) can occur in temperate eucalypt forests following extended periods of
154 low rainfall (Matusick *et al.* 2013), though mortality rates may be variable among eucalypt

155 species (Ruthrof, Matusick & Hardy 2015). Drought can also result in structural changes, such
156 as loss of canopy foliage, akin to fire-driven disturbance in some eucalypt communities
157 (Ruthrof, Matusick & Hardy 2015; Matusick *et al.* 2016; Walden *et al.* 2019).

158 Topography is an important driver of vegetation heterogeneity in temperate forests via
159 its effects on resource gradients, such as soil nutrients and moisture (McColl 1969), and on fire
160 behavior (Bradstock *et al.* 2010; Collins *et al.* 2019a). In the temperate forests of southeastern
161 Australia, ridgetop environments are generally dry with low nutrient availability, while gully
162 environments retain higher levels of moisture and soil nutrients (McColl 1969). Consequently,
163 gully environments display greater resistance to canopy defoliating fires (Bradstock *et al.* 2010)
164 and are more likely to provide unburnt refugia than adjacent ridgetops (Collins *et al.* 2019a).
165 However, increasing drought severity may reduce the resistance of gully environments to
166 wildfire (e.g., Collins *et al.* 2019a). Gullies typically support taller growth with dense
167 understories of soft-leaved plants and a higher proportion of fire-sensitive species generally
168 found in wet-sclerophyll forest (WSF) communities, whereas ridgetops are typically dominated
169 by small-medium sized trees and sclerophyllous shrubs, indicative of dry-sclerophyll forest
170 (DSF; Keith and Benson 1988). Thus, gullies may buffer vegetation from the effects of drought
171 and fire by providing refugia within topographically complex landscapes.

172 Our study investigated the effects of antecedent drought, fire frequency and tree
173 characteristics (size, basal fire scars, bark type) on the stem resistance of trees in forests
174 dominated by epicormic resprouters, across two contrasting vegetation types (DSF, WSF).
175 Specifically, this study focused on reproductive-age trees, the cohort that have had sufficient
176 time to develop traits related to fire resistance (e.g., thick bark, tall canopies). We asked
177 whether severe drought and frequent fire: (i) increased the likelihood of mortality above
178 typically expected levels (e.g., 2–15%; Vivian *et al.* 2008; Catry *et al.* 2013) or levels at the
179 upper extreme (e.g., 20–35%; Trouvé, Osborne & Baker 2021) described in other studies of

180 eucalypts and (ii) altered the expected resprouting position, i.e., from canopy branches to either
181 the stem or stem-base. We also asked whether mortality and resprouting position changed as a
182 function tree-size, bark type (i.e., compact, hard bark versus loose, fibrous bark) and previous
183 fire damage, and assessed the importance of these factors relative to drought severity and fire
184 frequency. We independently assessed these responses for two contrasting vegetation types to
185 gain insight into community-level responses to coupled drought-fire effects.

186

187 **2.1 Material and methods**

188 *2.1.1 Study area*

189 The study took place within the Sydney Basin bioregion of south-eastern Australia
190 (approximate centre = 150.76743, -33.58654; Fig. 1). Topography across the bioregion is
191 highly heterogeneous, consisting of coastal escarpments and steeply dissected terrain.
192 Elevation ranges from sea level to over 1200 m in the more mountainous areas located along
193 the western edge of the bioregion. Soils are mainly of low fertility, derived from sandstone and
194 shale parent material (DPI 2017). Temperature and rainfall vary across the bioregion as
195 function of both altitude and distance from coast. The mean minimum temperature of the
196 coolest month ranges between approximately 2–8°C and mean maximum temperature of the
197 warmest month ranges between 25–32°C, while rainfall ranges between approximately 600
198 mm–1500 mm (e.g. stations 063292, 061397, 068052, 062100, 066062,
199 <http://www.bom.gov.au/climate/data/>, 23/12/2021). DSF dominates ridgetops and WSF
200 dominates gullies, with most forested land occurring within the National Park estate (see
201 Supporting Information 1 for details on vegetation types).

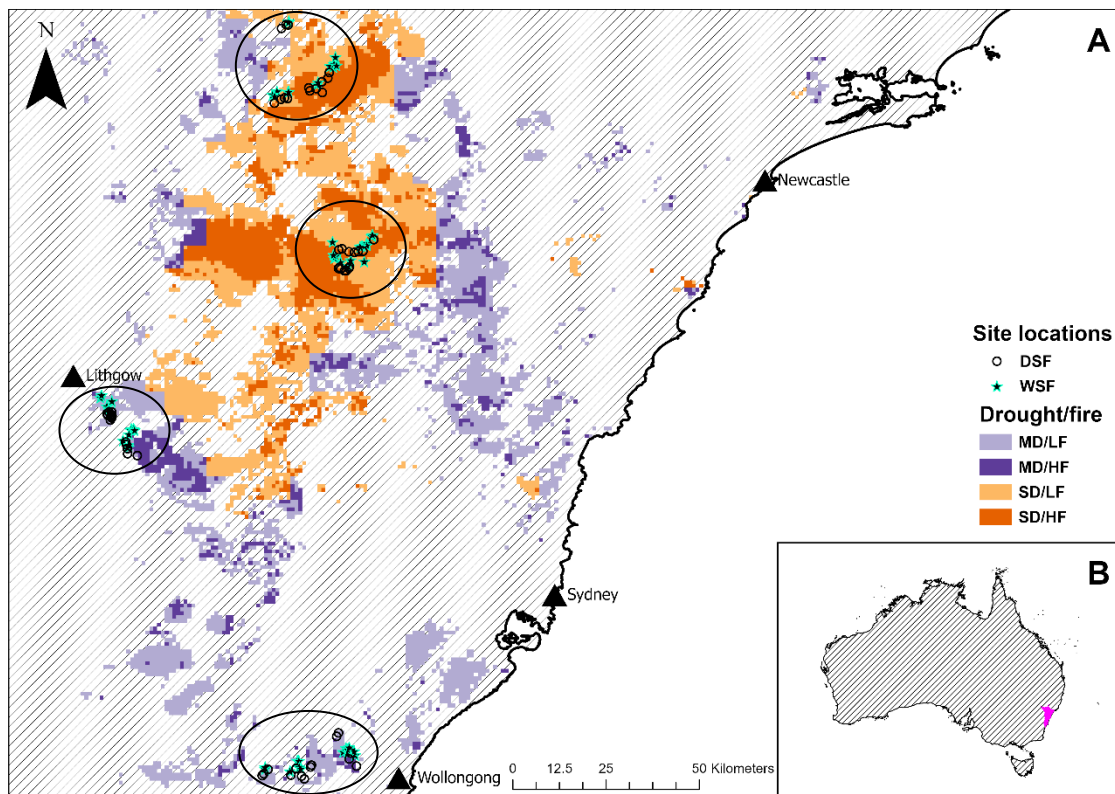
202 Fire regimes in DSF and WSF communities consists of a combination of mixed severity
203 wildfires and low to moderate severity prescribed burns (NPWS 2004; Bradstock *et al.* 2010;
204 Collins *et al.* 2021a). Typical fire intervals range between 5–20 years in DSF and 20–100 years

205 in WSF (Murphy *et al.* 2013). Fires occurring at very short intervals (<5 years) in these forests
206 are likely to result in changes to vegetation composition and structure (Arno & Allison-Bunnell
207 2002; Lewis *et al.* 2012; Cawson *et al.* 2017). Forests within the Sydney basin have been
208 subjected to several major wildfire seasons in the past 30 years (i.e., 1993/94, 2001–03,
209 2006/07, 2013/14 and 2019/20), with large areas of forest being reburned by wildfires within
210 this period. Since reliable fire history records began in the 1970s, most DSF and WSF in the
211 study region have burned 1–3 times, with a smaller proportion (~10%) burning in excess of
212 three times (Hammill, Tasker & Barker 2013).

213

214 *2.1.2 Fire history*

215 The study focused on four areas that were most recently burnt by large wildfires in October
216 2013 (Fig. 1). We selected areas where the most recent fire occurred between October 2013 to
217 February 2014 to control for the potentially confounding effects of fire frequency and time
218 since fire. The fires targeted in our study occurred in four different sub-regions across the
219 Sydney Basin, with two sub-regions experiencing mild/moderate drought (MD) and two
220 experiencing severe drought (SD; Fig. 1). Antecedent fire frequency was calculated as the
221 number of fires in the 20-year period that occurred between 1993 and 2013 and was categorized
222 as low frequency (1–2 fires; LF) or high frequency (3 or more fires; HF). Fire history data were
223 obtained from the New South Wales National Parks and Wildlife Service (NPWS 2016).



225 **Figure 1.** Composite image of the study region showing site locations (DSF = circles; WSF = stars),
 226 pre-fire drought severity and fire frequency combinations (coloured shading) within the Sydney Basin
 227 bioregion (panel a). Panel B shows location of Sydney Basin bioregion (magenta shading) within context
 228 of Australia. Pre-fire drought severity was determined by calculating 6-monthly SPEI for October 2013.
 229 Fire frequency was calculated between June 1993–January 2014 (low ≤ 2 fires; high ≥ 3 fires). Black
 230 ellipses highlight sites locations within each sub-region. Coloured shading also represents extent of
 231 fires during the 2013/14 fire season. MD = mild/moderate drought; SD = severe drought; LF = low fire
 232 frequency; HF = high fire frequency (see [2.1.3 Drought severity](#) for details on drought severity classes).
 233

234 2.1.3 Drought severity

235 Drought severity was quantified by using the Standardized Precipitation-Evapotranspiration
 236 Index (SPEI, Vicente-Serrano *et al.* 2010). SPEI is an index of the climatic water balance
 237 (precipitation minus potential evapotranspiration based on 30 years of gridded monthly weather
 238 data) expressed as the number of standard deviation units from average values based on the
 239 previous 30 years. Negative SPEI values indicate increased water deficit relative to long-term
 240 conditions, while positive values indicate surplus water availability relative to long-term
 241 conditions. We calculated SPEI at a 6-monthly time scale, which is sufficient for detecting
 242 drought stress in temperate eucalypt forests (Pook 1986; Pook, Gill & Moore 1997). Slette *et*

243 *al.* (2019) suggest SPEI values between -1 and +1 can be treated as falling within the range of
244 normal climatic variability, while values below -1 represent progressively more severe drought
245 conditions; however, values at or below -0.5 have been considered to be representative of
246 drought conditions in temperate Australia (Ma *et al.* 2015). We partitioned sub-regions in our
247 study into either mild/moderate drought (MD; SPEI = 0 to -1.4) or severe drought (SD; SPEI
248 = < -1.4). This threshold was chosen as it divided the study area into two approximately equal-
249 sized and climatically coherent regions, each containing substantial DSF and WSF populations.
250 For example, values below -1.4 were restricted to typically drier, warmer areas at lower
251 elevation in the north-west of the study region while values above -1.4 occurred along the
252 coastal fringe and in cooler areas with higher elevation (Fig. 1).

253 In the six months preceding the 2013/14 fire season, drought severity varied
254 considerably within the study region, with fires in the northern sub-regions burning under
255 severe drought and fires in the southern sub-regions burning under mild/moderate drought (Fig.
256 1). Most areas returned to low drought/normal conditions in the six months following October
257 2013. For each sub-region, SPEI was calculated at 0.05° x 0.05° resolution for the 6-month
258 period prior to and after the 2013 fire. Field sites were only placed in areas where post-fire
259 SPEI had returned to normal/near normal. Thus, we restricted our sampling to those areas with
260 substantial variability in pre-fire drought severity and minimal variation in post-fire drought
261 conditions. Climatic data used to calculate SPEI was obtained from the SILO database (SILO
262 2019). SPEI was calculated using the 'SPEI' package in R (Vicente-Serrano *et al.* 2010).

263

264 2.1.4 Study design

265 The study design incorporated drought severity (mild/moderate; severe), fire frequency (low:
266 1–2 fires; high: 3 or more fires) and vegetation type (DSF; WSF) in a fully factorial manner.
267 111 sites were evenly distributed across the four sub-regions (27–28 sites per sub-region; 13-

268 14 sites per treatment) in order to obtain sufficient spatial variability in drought severity (Fig.
269 1). Sub-regions occupied narrow bounds of mean annual temperature and rainfall (e.g., $\pm 2^{\circ}\text{C}$
270 and 200 mm across sites within each sub-region). All DSF sites were last burnt in 2013/14 at
271 moderate-high severity, with a high amount of scorching and consumption of canopy foliage
272 (canopy 70–100% burnt; severity classes 3-5, Hammill & Bradstock 2006), whereas all WSF
273 sites were last burnt in 2013/14 at low-moderate severity, with a mix of unburnt and scorched
274 canopy foliage (canopy <70% burnt; severity classes 1-2, Hammill & Bradstock 2006). Our
275 study did not consider the severity of antecedent fires when quantifying fire frequency, as this
276 data was not available; thus, it is unclear whether trees were subjected to multiple high severity
277 fire events prior to the fires in the 2013/2014 fire season. The topography of the study region
278 limited the prevalence of high severity fires in gullies (Bradstock *et al.* 2010) so fire severity
279 could not be matched between vegetation types. Instead, we contrasted the ‘common’ fire
280 severity patterns between vegetation types, e.g., high severity in DSF and low/moderate
281 severity in WSF (Bradstock *et al.* 2010).

282 All data were collected between February 2018 and July 2018. A 50 m x 20 m plot was
283 established at each site. DSF plots were confined to the top of ridges along contours, whereas
284 WSF plots were confined to gully bottoms or lower slopes, adjacent to creeks along contours
285 (see Supporting Information 1 for examples of typical sites). Plot aspect varied between sites
286 to minimize aspect bias. Plots were selected randomly within a few kilometers of access roads
287 and within the treatment levels identified in a GIS. Plots were placed at least 50 m from roads
288 and trails to avoid edge effects and at least 300–500 m apart to reduce spatial autocorrelation.

289

290 2.1.5 Field methods

291 Larger mature trees >20 cm diameter at breast height over bark (DBH) were identified (i.e., by
292 species and bark type, Supporting Information 1) and individually measured within the 50 x 20

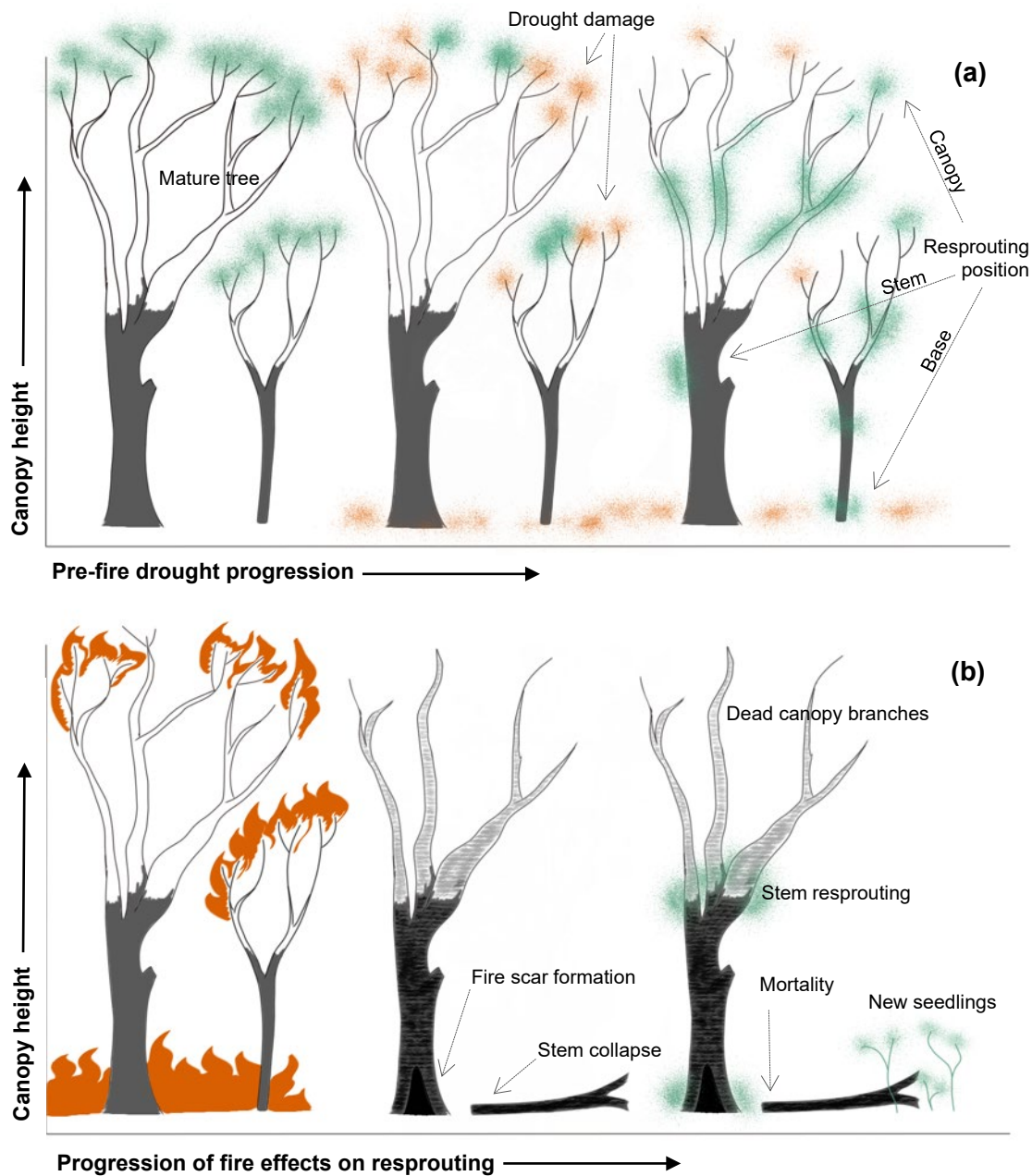
293 m plot. Smaller mature trees 10–20 cm DBH were identified and measured on a 50 m x 10 m
294 sub-plot located on the lower half of the main plot (Supporting Information 1). We will address
295 trees <10 cm DBH (reproductively immature trees) in a related paper. The variable plot-sizes
296 were designed to ensure representative sample sizes were collected (McElhinny *et al.* 2005;
297 McElhinny, Gibbons & Brack 2006). Species were identified using the keys provided by
298 Klaphake (2012) and Brooker and Kleinig (1999). When stems were closely-spaced a 1000
299 mm x 4 mm steel rod was used to probe between stems to determine whether they were
300 connected by a sub-surface lignotuber.

301 For each stem we measured DBH, height, whether alive or dead, resprouting position
302 and fire scar presence. DBH was measured over bark at 1.3 m above the ground on the uphill
303 side of the tree. Mortality was defined as a dead standing tree (i.e., no observable live foliage),
304 or log and associated stump representing a whole tree which had died due to the most recent
305 fire (Fig. 2). Stumps and logs were measured if they met the following criteria: (a) determined
306 to be a product of the most recent fire by being allocated a decay state of ‘1’ or less (wood hard
307 and intact, see Gordon *et al.* 2018; Roxburgh *et al.* 2006); (b) had most likely fallen due to fire
308 scar formation and collapse, evidenced by a fire scar at the break point, rather than wind-felled.
309 Resprouting position was defined as the highest position on a tree at which resprouting was
310 observed, classified as follows: *base* = all pre-fire stems killed during most recent fire and
311 resprouting only observed within 30 cm of the tree base; *stem* = no live foliage observed on
312 secondary and tertiary branches, but successful epicormic resprouting from main stems and/or
313 primary branches, and; *canopy* = live foliage observed on secondary/tertiary branches, possibly
314 accompanied by epicormic and basal resprouting (Fig. 2; see Supporting Information 1 for
315 further examples). For some taller WSF trees, a resprouting response was not elicited, because
316 the fire was not intense enough to cause canopy scorch. These trees were grouped with trees
317 that had resprouted from the canopy and classed as *canopy/unaffected*. Bark thickness was

318 measured on both north and south sides of trees using a 50 mm bark gauge (Haglof Barktax,
319 Sweden). The maximum height of dead branches (pre-fire) and maximum height of live foliage
320 (post-fire) was measured using an angle-compensated laser rangefinder (Nikon Forestry Pro
321 500, Japan). Fire scar presence/absence was recorded for all trees (see Supporting Information
322 1 for fire scar examples). We measured all fire scars present before and/or created by the
323 2013/14 fires. We recorded over 40 *Eucalyptus* species across the sites, with only a handful
324 occurring across all drought and fire combinations. Bark thickness patterns were consistent
325 among bark types (see Supporting Information 2). Thus, we aggregated species by bark type
326 (i.e. rough, fibrous, hard, smooth, stringy) for analysis and this was determined according to
327 bark texture and the height of persistent bark on the main stem (Collins 2019; Boland et al.
328 2006). Five bark type categories were identified: rough, fibrous, hard, smooth and stringy (see
329 Supporting Information 1 for details on bark characteristics).

330

331



333 **Figure 2.** Diagram showing categories of pre-fire drought effects (panel a) and fire effects (panel b) on
 334 trees. Panel a shows drought damage followed by initial resprouting response. Panel b shows potential
 335 fire effects on forest trees: dead canopy branches and change in maximum height of resprouting
 336 position from canopy to stem, fire scar formation, stem collapse, mortality and seedling recruitment.
 337

338 *2.1.6 Data analysis*

339 We used a Bayesian modelling approach to derive bounded estimates of response probabilities
 340 for trees sampled in each combination of drought severity (mild/moderate versus severe) and
 341 fire frequency (low versus high), as well as bounded estimates of differences between trees

342 with and without fire scars, different bark types and drought/fire histories. We included DBH
343 as a smooth term (in the sense of generalized additive modelling; Wood 2017) in all models to
344 account for the non-linear relationship between tree diameter and resprouting response
345 (Fairman, Bennett, Nitschke 2019). We modelled DSF and WSF independently due to
346 confounding by fire severity. Separate models were fitted for two response variables: (a) the
347 probability of mortality for each tree:

$$348 \quad (1) \text{ mortality} \sim s(\text{DBH}) + \text{drought severity} * \text{fire frequency} + \text{fire scar presence} + \\ 349 \quad \text{bark type}$$

350 and; (b) the probability of membership in each resprouting position class for trees that survived
351 fire:

$$352 \quad (2) \text{ resprouting position} \sim s(\text{DBH}) + \text{drought severity} * \text{fire frequency} + \text{fire scar presence} + \\ 353 \quad \text{bark type}$$

354 A weighting term was included to account for the different plot sizes within each size
355 class of trees and logs that were recorded, e.g. $\text{mortality} \mid \text{weights} \sim$. Models were fitted using
356 Markov Chain Monte Carlo (MCMC) as implemented in the ‘brms’ package for R version
357 3.5.0 (Bürkner 2017 , R Core Team 2019). Missing data for bark type (e.g. charred logs with
358 no bark; n = 146) was imputed via multiple imputation using the MICE algorithm implemented
359 in the R package MICE (van Buuren & Groothuis-Oudshoorn 2011).

360 Mortality was modelled as a Bernoulli-distributed variable while resprouting position
361 was modelled as an ordinal variable. For each model, we sampled four Markov chains, each
362 consisting of 5000 model iterations. We assessed model convergence using the Gelman-Rubin
363 diagnostic (Gelman and Rubin 1992) and checked for acceptable levels of serial
364 autocorrelation. Separate Markov chains for each model were then combined into a matrix of
365 samples from the joint posterior distribution of model parameters, which we subsequently used
366 to derive predictions of probabilities among the treatments (Kruschke 2015; Suzuki 2019). We

367 then used the matrix of posterior samples from the model to calculate posterior difference
368 distributions for selected contrasts. Where applicable these calculations are referred to in the
369 results as ‘calculated mean difference’, i.e. the mean value of summarised difference
370 calculations. Credible intervals were calculated as highest posterior density intervals (HPDI),
371 in order to display the central 50% of model predictions and lower/upper 95% bounds of model
372 predictions. The term ‘intermediate size’ or similar is used throughout the results and
373 accompanied in the first instance by a range of DBH values. Note that this value inherently
374 varies between vegetation types. The data and R scripts used to generate the results are provided
375 online in a data repository (<https://github.com/erb418/EB.C-h2.scripts>) and secondary results
376 summaries can be found in Supporting Information 2.

377

378 **3.1 Results**

379 We recorded 3060 individual trees. On average there were 27.5 ± 13.5 trees per site across the
380 112 sites. The average mortality rate was 28.8% per site, with greater mortality being recorded
381 on ridges (DSF = 32.8%) versus gullies (WSF = 24.7%). The average incidence of fire scars
382 was 46.2% trees per site, with greater incidence of fire scars being recorded on ridges (DSF =
383 49.6%) versus gullies (WSF = 42.8%).

384

385 ***3.1.1 Dry sclerophyll forest***

386 *3.1.2 Mortality*

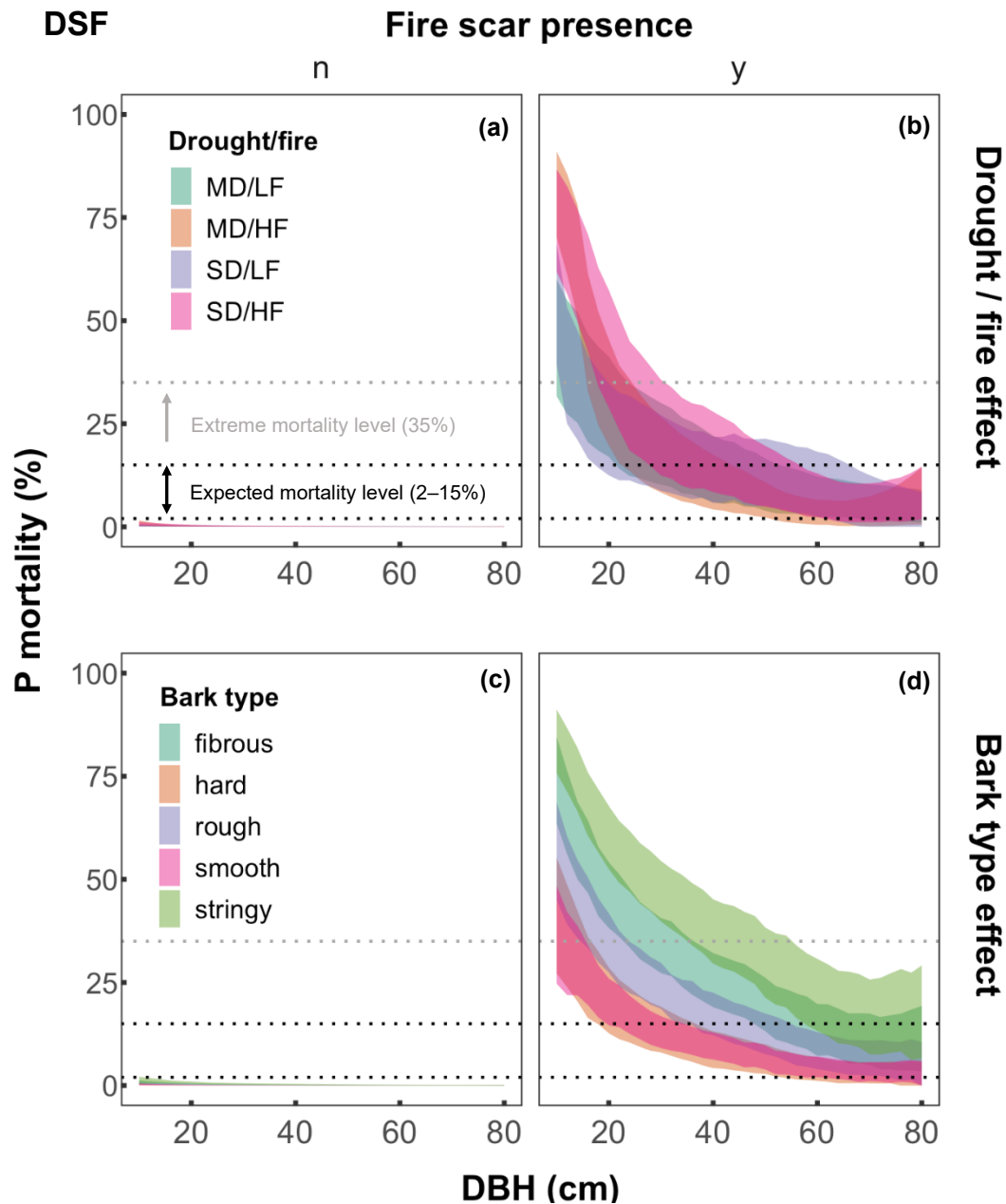
387 Trees without fire scars in DSF communities were very unlikely to be dead and the probability
388 of mortality was below the lower bound of the expected level of mortality of 2%, regardless of
389 DBH, drought/fire combination or bark type (Fig. **3a**). When trees had a fire scar, the
390 probability of mortality increased as DBH decreased (Fig. **3b, d**). Trees with fire scars were
391 more likely to exceed the upper bound of the expected level of mortality as DBH decreased

392 below 45–55 cm (Fig. **3b, d**), and more likely to exceed the extreme mortality level when DBH
393 decreased below 20–30 cm, with the maximum mean probability of mortality being 41–74%
394 in the smallest stems (Fig. **3b, d**).

395 Mortality was more likely for small trees (<20 cm DBH) with fire scars exposed to high
396 fire frequency compared to low fire frequency (Fig. **3b, d**). Fire frequency had little effect on
397 mortality for trees above ~30 cm DBH (Fig. **3b**). The mean diameter at which mortality
398 exceeded the upper expected threshold was ~10 cm greater under high fire frequency, relative
399 to low frequency (Fig. **3b**). Drought severity had little effect on the probability of mortality
400 (Fig. **3a, b**).

401 When DBH was less than 50 cm, there were moderate to substantial differences in the
402 probability of mortality for trees with fire scars compared to trees without fire scars (Fig. **3b,**
403 **d**). For trees of intermediate size (25–35 cm) with fire scars, stringy bark was the most likely
404 bark type to experience mortality, followed by fibrous bark, rough bark then hard and smooth
405 bark, which had similarly low probabilities (Fig. **3d**).

406



408 **Figure 3.** The effect of DBH (x-axis), drought severity/fire frequency combination (panels a, b), fire scar
 409 presence (left/right panels; n = no scar; y = scar present) and bark type (panels c, d) on the probability
 410 of mortality for trees 10–80 cm DBH in dry sclerophyll forest (DSF) of the Sydney Basin. Drought/fire
 411 combinations are notated as follows: MD = moderate drought; SD = severe drought; LF = low fire
 412 frequency; HF = high fire frequency. Coloured ribbons represent 50% credible intervals; dotted lines
 413 represent the expected (black) and extreme (grey) levels of mortality described in other studies of
 414 eucalypts (2-35%; Vivian et al. 2008; Catry et al. 2013; Trouvé, Osborne & Baker 2021).
 415

416

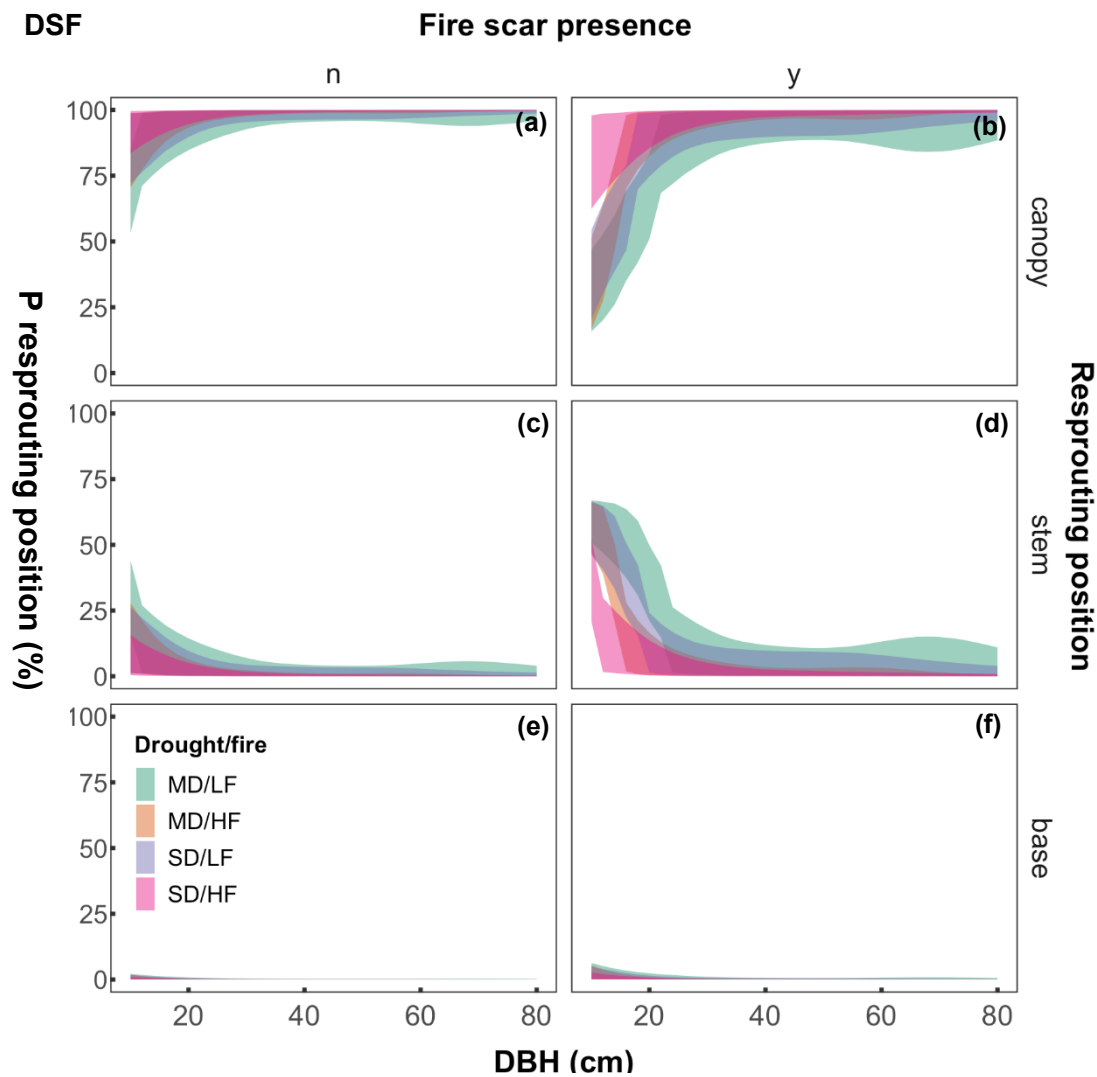
417

418 3.1.3 Resprouting position

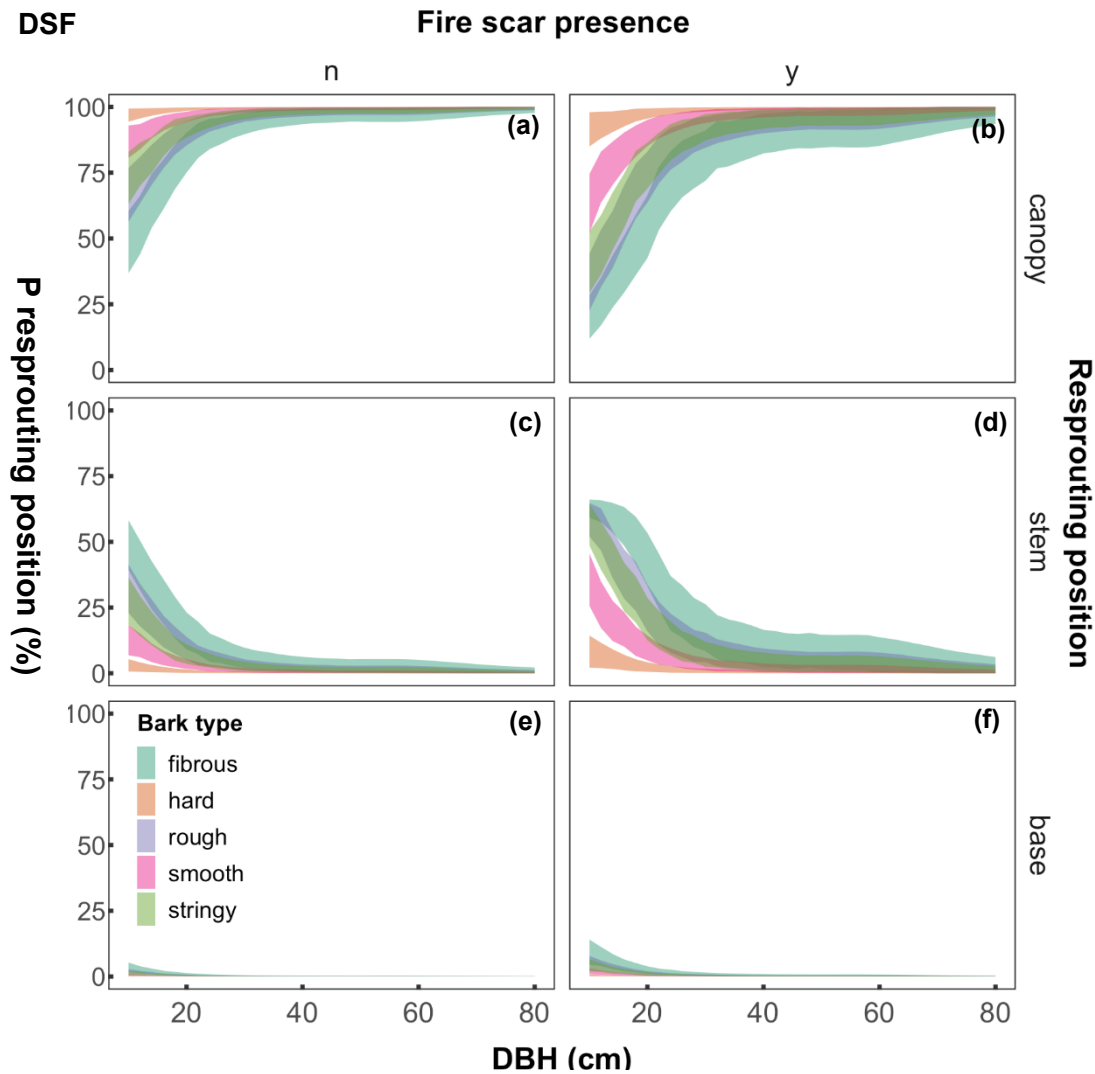
419 Trees in the DSF community typically resprouted from the *canopy* branches, across the range
420 of DBH values, drought/fire combinations, bark types and fire scar classes (mean probabilities:
421 32–99%), followed by *stem* (mean probabilities: 1–56%), with *base* very unlikely to be the sole
422 resprouting position (mean probabilities: 0–11.4%; Figs 4, 5). The probability of *stem*
423 resprouting increased as DBH decreased below 25–35 cm across all combinations of drought
424 severity and fire frequency, bark types and fire scar classes (Figs 4c, d, 5c, d), with
425 corresponding reductions in *canopy* resprouting (Figs 4a, b, 5a, b). At smaller DBH values
426 (10–15 cm), trees without fire scars were on average 7–25% more likely to be *canopy*
427 resprouters than trees with fire scars, depending on bark type (Figs 4a, 5a). Small trees (10–15
428 cm DBH) with fire scars were 10–25% more likely to be *stem* resprouters than trees without
429 fire scars (Figs 4c, 5c).

430 Fire frequency and drought generally had a negligible effect on resprouting position.
431 The exception was small trees (10–20 cm) with fire scars, which were 7–15% more likely to
432 be *canopy* resprouters if they had experienced severe drought and high fire frequency (Figs 4b,
433 5b).

434 *Stem* and *base* resprouting was most common in small trees (10–15 cm DBH) with fire
435 scars and fibrous bark (Fig 5d, 5f). *Base or stem* resprouting was less likely in trees with rough
436 bark (mean probabilities for *base/stem*: 6.5 / 47.7%), stringy bark (mean probabilities for
437 *base/stem*: 5.4 / 44%), smooth bark (mean probabilities for *base/stem*: 2.6 / 29.8%), with hard
438 bark trees having the lowest probability (range/mean probabilities for *base/stem*: <1 / 13.8%;
439 Fig. 5d, f).



441 **Figure 4.** The effect of DBH (x-axis), drought severity/fire frequency combination (coloured ribbons)
 442 and fire scar presence (left/right panels; n = no scar; y = scar present) on the probability of membership
 443 in each resprouting position category (canopy = complete resprouting; stem = stem resprouting only,
 444 death of canopy; base = basal resprouting only, death of stem and canopy) for trees 10–80 cm DBH in
 445 dry sclerophyll forest (DSF) of the Sydney Basin. Drought/fire combinations are notated as follows: MD
 446 = moderate drought; SD = severe drought; LF = low fire frequency; HF = high fire frequency; rows
 447 represent resprouting position. Coloured ribbons represent 50% credible intervals; dotted black lines
 448 represent the expected levels of mortality (2–15%).
 449



451 **Figure 5.** The effect of DBH (x-axis), bark type (coloured ribbons) and fire scar presence (left/right
 452 panels; n = no scar; y = scar present) on the probability of membership in each resprouting position
 453 category (canopy = complete resprouting; stem = stem resprouting only, death of canopy; base = basal
 454 resprouting only, death of stem and canopy) for trees 10–80 cm DBH in dry sclerophyll forest (DSF) of
 455 the Sydney Basin. Rows represent resprouting position. Coloured ribbons represent 50% credible
 456 intervals; dotted black lines represent the expected levels of mortality (2–15%).
 457

458 3.2.1 *Wet sclerophyll forest*

459 3.2.2 *Mortality*

460 Trees without fire scars in WSF communities were very unlikely to be dead and the probability
 461 of mortality was below the upper bound of the expected level of mortality of 15%, regardless
 462 of DBH, drought, fire frequency or bark type (Fig. 6a). When trees had a fire scar the
 463 probability of mortality increased as DBH decreased (Fig. 6b, d). Trees with fire scars were

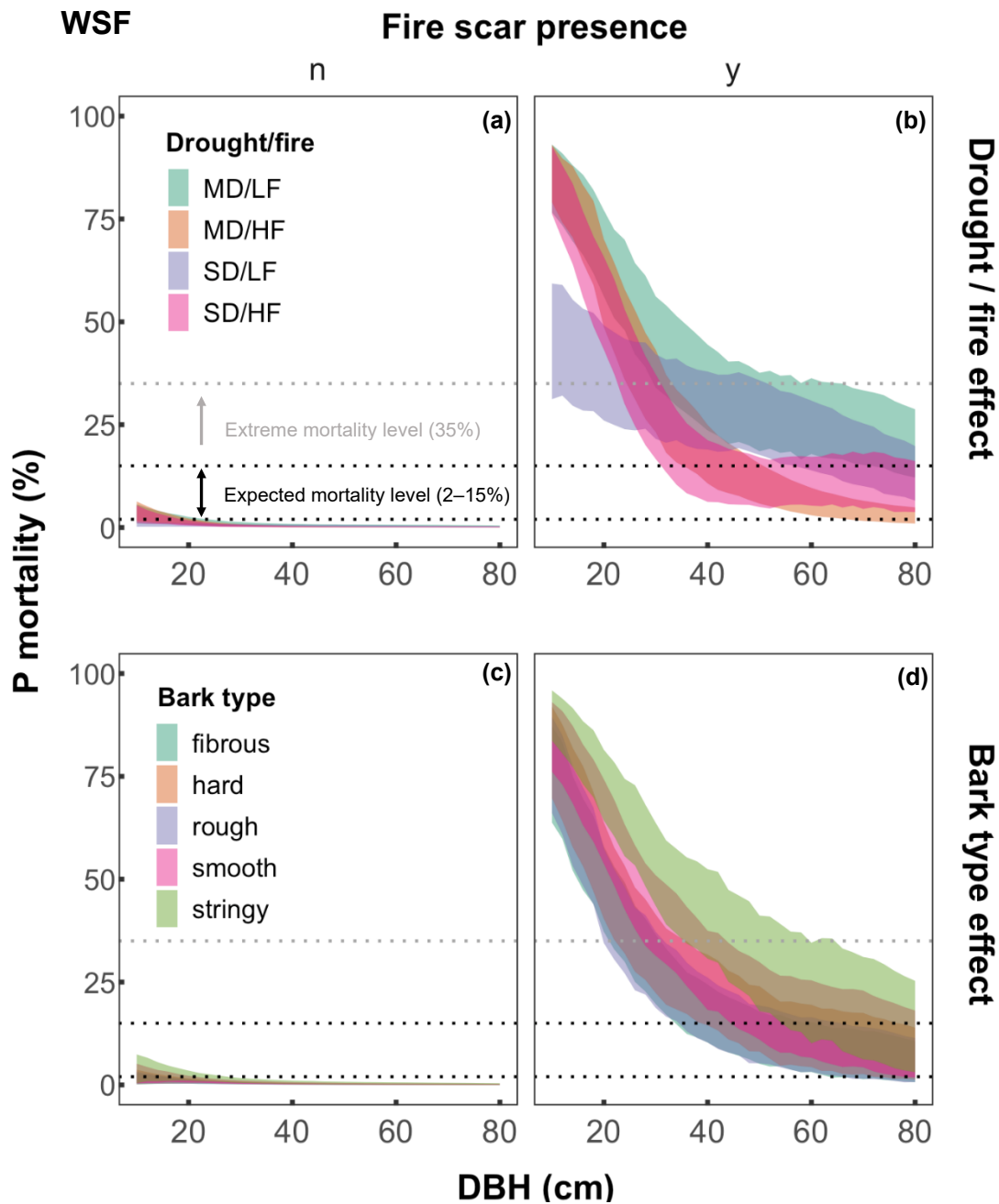
464 more likely to exceed upper bound of the expected level of mortality as DBH decreased below
465 45–55 cm (Fig. **6b, d**), and more likely to exceed the extreme mortality level when DBH
466 decreased below 25–35 cm (Fig. **6b, d**), with the maximum probability of mortality being 37–
467 84% in the smallest stems (i.e., 10 cm; Fig. **6b, d**). Trees that experienced low fire frequency
468 remained mostly above the expected level of mortality regardless of DBH (Fig. **6b**).

469 Mortality was more likely for small trees (<20 cm DBH) with fire scars exposed to high
470 fire frequency compared to low fire frequency when drought was severe (calculated mean
471 difference across bark types 25–31%; Fig. **6b, d**). At intermediate DBH (e.g., 40–41 cm) there
472 was little difference in the probability of mortality for trees with fire scars due to drought
473 severity (calculated mean difference <5%). However, trees that experienced low fire frequency
474 compared to high fire frequency were 10–17% more likely to die (Fig. **6b**).

475 At intermediate DBH there were substantial differences in mortality for trees with fire
476 scars compared to trees without fire scars (calculated mean difference of 15–50%; Fig. **6b, d**).
477 For trees of intermediate size, stringy barks had highest mortality (mean probability: 41.3%),
478 followed by trees with smooth bark (mean probability: 32.4%), hard bark (mean probability:
479 26.9%), rough bark (mean probability: 26.9%), and fibrous bark (mean probability: 22.1%;
480 Fig. **6b**), although there was overlap of 50% credible intervals among bark types.

481

482



484 **Figure 6.** The effect of DBH (x-axis), drought severity/fire frequency combination (panels a, b), fire scar
 485 presence (left/right panels; n = no scar; y = scar present) and bark type (panels c, d) on the probability
 486 of mortality for trees 10–80 cm DBH in wet sclerophyll forest (WSF) of the Sydney Basin. Drought/fire
 487 combinations are notated as follows: MD = moderate drought; SD = severe drought; LF = low fire
 488 frequency; HF = high fire frequency. Coloured ribbons represent 50% credible intervals; dotted lines
 489 represent the expected (black) and extreme (grey) levels of mortality described in other studies of
 490 eucalypts (2–35%; Vivian et al. 2008; Catry et al. 2013; Trouvé, Osborne & Baker 2021).
 491
 492
 493

494

495 3.2.3 Resprouting position

496 Trees in the WSF community typically resprouted from the *canopy* branches or were *unaffected*
497 by disturbance, across the range of DBH values, drought/fire combinations, bark types and fire
498 scar classes (range of mean probabilities: 69–100%) followed by *stem* (range of mean
499 probabilities: 0–23%) with *base* very unlikely (range of mean probabilities: 0–7%). The
500 probability of *stem* resprouting increased as DBH decreased below 25–35 cm.
501 Correspondingly, probability of *canopy/unaffected*, i.e., the expected response, decreased
502 below 25–35 cm DBH. At minimum DBH values (10 cm) trees without fire scars were 4–18%
503 more likely to be *canopy* resprouters or *unaffected* than trees with fire scars, i.e., somewhat
504 more likely to conform to the expected response. Small trees (10–15 cm DBH) with fire scars
505 were 3–12% more likely to be *stem* resprouters than trees without fire scars (see Supporting
506 Information 2 for more details on WSF response).

507 When small trees had a fire scar they were 18–31% more likely to be *canopy* resprouters
508 or *unaffected* if they had experienced severe drought and low fire frequency. However, the
509 magnitude of differences between all drought/fire combinations was generally less than 2% for
510 average sized trees (~40 cm DBH). Rough barked trees were most likely to be *stem* resprouters
511 (mean probability: 23%), followed by fibrous bark trees (mean probability: 17%). Trees with
512 other bark types had low probabilities of *stem* resprouting (mean probabilities: 10–12%; see
513 Supporting Information 2 for more details on WSF response).

514

515 4.1 Discussion

516 In this large-scale field study investigating two key temperate forest types, we found that the
517 effect of fire on the mortality and resprouting position of reproductive-age eucalypts was
518 primarily determined by tree characteristics (i.e., size, bark type and previous fire damage),
519 with pre-fire drought and fire frequency having little effect on stem resistance (mortality) and

520 resilience (resprouting). This finding aligns with work from similar forests subjected to high
521 severity fires (Collins 2020; Trouvé, Osborne & Baker 2021) and indicates that variations in
522 short-term drought history do not greatly affect mortality rates or resprouting responses
523 following fire in the study area. In contrast, fire-related mortality in forests in other global
524 regions can be as high as 89% for obligate-seeders (e.g. coniferous species, *Catry et al.* 2010)
525 and the effects of coupled drought and fire can result in mortality levels of 40–80% in tropical
526 forests dominated by basal resprouters (Brando *et al.* 2014). The probability of mortality varied
527 considerably with bark type in our study and so it is plausible that regional patterns of bark
528 types may have masked other effects such as drought (e.g. see Nolan *et al.* 2020b).

529 Fire scar presence and DBH were the most influential predictors of mortality and
530 resprouting position in trees of both forest types (Figs 3, 4). Almost all dead trees (98.7%) in
531 our study had a fire scar (see Supporting Information 2), compared to 56.4% of live trees,
532 highlighting the importance of fire scar presence on mortality. However, there was substantial
533 variation in the magnitude of the DBH effect on mortality for trees with fire scars, and on
534 resprouting more generally, as a function of bark type. Interestingly, the pattern was not
535 consistent across our two forest types. For dry sclerophyll species, hard and smooth bark, the
536 more compact bark types, provided greater resistance to mortality, while fibrous and rough
537 bark provided greater resistance for wet sclerophyll species, highlighting potential species-
538 level differences within bark types and between vegetation types. Variation in topkill and
539 mortality response is known to be related to bark type and stem size among eucalypt species
540 (Nolan *et al.* 2020b; Trouvé, Osborne & Baker 2021). In contrast to the effects of bark type on
541 whether or not a tree died from fire, the influence of bark type on resprouting position provides
542 insights for the future of trees that survived. Thinner, non-compact bark types (fibrous, stringy,
543 rough; see Supporting Information 2 for details on bark thickness) were less resilient to
544 lowering in resprouting position from *canopy* to *stem* or *base*, consistent with work elsewhere

545 (Lawes *et al.* 2011b; Brando *et al.* 2012; Collins 2020). This phenomenon was consistent
546 between vegetation types, but amplified for smaller trees on ridgetops (dry sclerophyll) and
547 diminished for larger trees in gullies (wet sclerophyll), suggesting that interactions between
548 topographically moderated soil water availability and fire severity, basal damage and bark
549 morphology will determine stem and branch resistance and syndromes of resilience via
550 resprouting. Finally, although species-level analysis was beyond the scope of this study,
551 inherent species effects may also exist (see Trouvé *et al.* 2021). For example, drought-induced
552 canopy damage can vary between co-occurring myrtaceous species in eucalypt dominated
553 forests (Fensham *et al.* 2014). There is also evidence that species in our study may have been
554 more prone to drought-induced canopy damage than others (see Li *et al.* 2018), leading to
555 changes in the maximum height of resprouting position. Successful canopy resprouting was
556 negatively affected by the presence of fire scars, providing support for the proposal that basal
557 damage is a driver of topkill (Whitford & Williams 2001; Gibbons, Cunningham &
558 Lindenmayer 2008; Collins 2020).

559

560 *4.1.1 Biological mechanisms underlying mortality & resprouting responses*

561 The mortality and damage of stems and branches will be determined by the exposure of living
562 tissues to lethal temperatures during fire (Wesolowski, Adams & Pfautsch 2014). Bark is an
563 important insulator against the effects of fire (Pausas 2015) and the observed effects of stem
564 size and bark type in our study reflect this: small trees were more likely to be killed, as found
565 elsewhere (Catry *et al.* 2013; Bennett *et al.* 2016; Denham *et al.* 2016) and the likelihood of
566 mortality varied substantially across bark type (Figs 3, 6). The reduced likelihood of mortality
567 with increasing stem size may be explained by accumulation of bark thickness with stem
568 size/age. Bark thickness increases with increasing stem diameter (Lawes *et al.* 2013), providing
569 larger trees with greater protection from lethal temperatures during fire (Wesolowski, Adams

570 & Pfautsch 2014). The differences across bark types observed in our study therefore likely
571 reflect a combination of bark thickness/density and age among species (Wesolowski, Adams
572 & Pfautsch 2014).

573 Our finding that species with non-compact bark types (fibrous, stringy, rough) with fire
574 scars were generally more likely to be killed by fire than those with compact bark types (hard,
575 smooth), supports the proposition that resistance traits influence mortality trends in forested
576 landscapes (Gibbons, Cunningham & Lindenmayer 2008; Brando *et al.* 2012; Collins 2020).
577 Dense, thick bark may confer greater resistance to fire scarring and stem mortality than lower-
578 density, fibrous bark types in eucalypts (Collins 2020). Conversely, thick bark with low density
579 is also known to provide greater resistance to mortality than thick bark with high density (Nolan
580 *et al.* 2020b). Complex interactions between bark density and water content are likely to drive
581 variability in stem insulation across species (Lawes *et al.* 2011b; Wesolowski, Adams &
582 Pfautsch 2014; Nolan *et al.* 2020b). Heat transfer from the outer bark to the cambium is the
583 key mechanism influencing cambium necrosis (Wesolowski *et al.* 2014) and thus fire scar
584 formation. Fire scars may impair hydraulic function by reducing sapwood area and limiting the
585 volume of water that can be transported to foliage and growth buds in the crown, thereby
586 increasing the risk of resprouting failure and stem collapse (Whitford & Williams 2001).

587 Aside from the characteristics of trees, their vegetation community and associated
588 topographic position in the landscape influence resilience to fire. Mature wet sclerophyll forest
589 trees in gullies displayed a high degree of canopy resistance to fire, with most trees having low
590 levels of branch mortality. Gullies typically retain higher fuel moisture than adjacent ridgetops
591 due to accumulation of soil water and lower insolation produced by topographic relief and high
592 foliage cover (Nyman *et al.* 2015). In addition, trees in gullies typically have higher relative
593 crown height compared with trees in ridges (Supporting Information 2), reducing the likelihood
594 of canopy scorch or consumption during fire (Bradstock *et al.* 2010; Zylstra 2018). Therefore,

595 ecosystem resilience to drought and fire is likely higher in WSF than DSF due to the moderation
596 of topoclimatic conditions and severity of disturbance.

597

598 4.1.2 Consequences for resprouting

599 While canopy cover in most resprouting eucalypt forests recovers relatively quickly from high-
600 severity fire (generally 10–20 years, Vivian *et al.* 2008, Haslem *et al.* 2016; Collins *et al.*
601 2021b), it has been proposed that multiple high severity fires in quick succession could lead to
602 longer-term structural or demographic changes, through mortality and a shift from epicormic
603 to basal resprouting (Fairman, Bennett & Nitschke 2019). In our study, smaller dry sclerophyll
604 trees on ridgetops were most likely to be *stem* resprouters (up to 56.2%, Fig. 5). This indicates
605 that the ‘escape size’ (Fairman *et al.* 2019), which refers to the stem size above which trees are
606 at least 50% likely to resprout epicormically, for trees in Sydney sandstone forests is <10 cm
607 DBH. This threshold is considerably lower than in other eucalypt forests (e.g., 20 cm DBH;
608 Fairman *et al.* 2019), suggesting that forests of the study region are comparatively more
609 resilient than eucalypt forests studied elsewhere. However, there was considerable variation in
610 understory composition in our study (see Supporting Information 1), and it is not clear how
611 pre-fire shrub density/fuel structure may have influenced fire intensity and thus our results.
612 Nonetheless, smaller trees on ridgetops had 10–25% greater mortality under high fire frequency
613 compared to low fire frequency, and therefore remain vulnerable in our study region. For larger
614 trees, the influence of drought and fire on mortality and resprouting position were generally
615 reduced compared to smaller trees.

616 Populations dominated by species that have: (1) previous fire damage; (2) small stem
617 diameters (e.g., due to poor-soils or other growth-limiting factors); (3) thin, non-compact bark;
618 and (4) experience high fire frequency could be less resilient to lowering in resprouting
619 position—and thus community state-changes—given severe drought and fire conditions. Also,

620 species vary in their response to conditions leading up to fire, in turn influencing their fire
621 response. For example, *Eucalyptus piperita* is particularly susceptible to branch death during
622 severe drought (Li *et al.* 2018), demonstrating potential for further variation in post-
623 drought/post-fire topkill rates among species. Thus, while ecosystem conversion appears
624 unlikely, these intra-specific differences in stem resistance may lead to compositional changes
625 with important ecological implications. Future studies that focus on these ‘at-risk’ eucalypt
626 populations may be able to detect changes that are otherwise masked by high species diversity
627 and site variability.

628

629 *4.1.3 Potential future changes to forests*

630 It is predicted that ecosystem-conversion, e.g., forest to non-forest, may be driven by climate-
631 change and extreme disturbance regimes (Bowman *et al.* 2013; Fairman, Nitschke & Bennett
632 2016). Our findings indicate that severe drought and frequent fire at levels experienced at the
633 time of our study are unlikely to result in major structural changes—such as the loss of mature
634 trees—in the eucalypt forests of the Sydney region. Mortality was not elevated for mature trees
635 under severe drought and high fire frequency compared to less severe conditions, which is
636 broadly consistent with predictions (Bowman *et al.* 2013) and findings elsewhere (Catry *et al.*
637 2013). However, the smaller trees on ridgetops had an increased chance of mortality under high
638 fire frequency and were also more likely to revert to *stem* or *base* resprouting. It is important
639 to interpret our findings in the context of recent trends of increased fire frequency and drought
640 intensity over the last 20 years. This work was conducted prior to the unprecedented 2019/20
641 bushfires (Boer *et al.* 2020; Collins *et al.* 2021), which swept through our study area and are
642 generally accepted to have been exacerbated by chronic drought on top of record-breaking
643 temperatures (Nolan *et al.* 2020a; Abram *et al.* 2021). During this event, interactions between
644 extreme drought and heat led to complete canopy defoliation of some resprouting eucalypt

645 forests, which was followed by severe fires of unprecedented scale (Nolan *et al.* 2021). The
646 consequences of such conditions on tree mortality and forest structure may be known for a
647 number of years (Nolan *et al.* 2021).

648 Understorey fires and canopy fires have contrasting effects on the response of
649 epicormic resprouters to fire, whereby eucalypt forests display high resistance to low severity
650 fire (Watson, French & Collins 2020), but must resprout in response to high severity fire
651 (Collins 2020). Generally, rates of tree topkill increase with fire severity (Denham *et al.* 2016;
652 Trouvé, Osborne & Baker 2021). Our study did not consider the severity of fires when
653 quantifying fire frequency; thus, it is unclear whether trees were subjected to multiple high
654 severity fire events that stimulated a resprouting response. Contrasting both low and high fire
655 severity across fire frequency classes could shed also further light on the role of fire severity
656 in mortality and resprouting processes for forests in our study region. Additionally, assessing
657 the impacts of consecutive droughts and fires on specific species of interest, e.g. those found
658 in marginal areas, as previously outlined, may give deeper insight into the future trajectories
659 of plant communities.

660 We suggest that Sydney sandstone forests may be at the upper end of overstorey
661 resilience and may provide a baseline for other comparative studies. However, it is important
662 to interpret our findings in the context of recent global trends of increasing drought and
663 associated mega-fires (Kirchmeier-Young *et al.* 2019; Boer, Resco de Dios & Bradstock 2020;
664 Collins *et al.* 2021a). Our study was conducted prior to the unprecedented 2019/20 fires, which
665 burnt more than one-fifth of the temperate eucalypt forest biome (Boer *et al.* 2020) and much
666 of our study area. Continued intensification of disturbance regimes may alter the way these
667 forests respond in future. To better understand the environmental conditions and vegetation
668 characteristics that promote mortality and changes to resprouting position in forests, an
669 integrated approach inclusive of landscape variables such as drought, fire and topography,

670 population level phenomena, including demographic bottlenecks and distribution of bark types,
671 and species attributes, such as the structure of fuels at the base of the tree, is needed.

672

673 **Acknowledgements**

674 Pritt Paartalu, who provided valuable comments on the manuscript. Volunteers who assisted in
675 the collection of data in the field: Jeremy Bendall, Graham Bendall, Max Bedward, Marie-
676 Claire Demers, Rhys Wyber, Edward Hack, Kerensa Cleaver, Dee Mould, James Barker, Jack
677 Dirk, Allison Broad. Agencies that facilitated access to field sites: New South Wales National
678 Parks and Wildlife Service, Sydney Water, Blue Mountains City Council, Lithgow City
679 Council.

680

681 **Funding**

682 This research did not receive any specific grant from funding agencies in the public,
683 commercial, or not-for-profit sectors.

684

685 **Author's contributions**

686 Eli Bendall, Ross Bradstock, Luke Collins and Andrea Leigh conceived the ideas; Eli
687 Bendall, Ross Bradstock, Luke Collins and Andrea Leigh designed the methodology; Eli
688 Bendall collected the data; Eli Bendall and Michael Bedward analysed the data; Eli Bendall
689 led the writing of the manuscript; Ross Bradstock, Luke Collins, Michael Bedward, Andrea
690 Leigh, Matthias Boer and Hamish Clarke contributed to the writing of the manuscript; Eli
691 Bendall prepared the Supporting Information. All authors contributed critically to the drafts
692 and gave final approval for publication.

693

694 **Statement on inclusion**

695 Our study included scientists from institutions across Australia, representing a broad
696 knowledge base of experts within their fields. We consulted extensively with relevant land
697 management agencies at the field work stage of the project.

698

699 **Conflict of interest**

700 The authors declare that they have no conflict of interest, financial or otherwise, that could
701 have influenced this paper.

702

703 **Data availability statement**

704 All data and R scripts used to manage data, analyse data and generate figures are provided
705 online in a data repository (<https://github.com/erb418/EB.C-h2.scripts>).

706

707 **References**

708 Abatzoglou, J.T., Williams, A.P., Boschetti, L., Zubkova, M. & Kolden, C.A. (2018) Global
709 patterns of interannual climate-fire relationships. *Glob Chang Biol*, **24**, 5164-5175.

710 Abram, N.J., Henley, B.J., Sen Gupta, A., Lippmann, T.J.R., Clarke, H., Dowdy, A.J., Sharples,
711 J.J., Nolan, R.H., Zhang, T., Wooster, M.J., Wurtzel, J.B., Meissner, K.J., Pitman, A.J., Ukkola,
712 A.M., Murphy, B.P., Tapper, N.J. & Boer, M.M. (2021) Connections of climate change and
713 variability to large and extreme forest fires in southeast Australia. *Communications Earth &*
714 *Environment*, **2**.

715 Allen, C.D., Breshears, D.D. & McDowell, N.G. (2015) On underestimation of global
716 vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene.
717 *Ecosphere*, **6**, 1-55.

718 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M.,
719 Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang,

720 Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N.
721 (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate
722 change risks for forests. *Forest Ecology and Management*, **259**, 660-684.

723 Andrade, C.F., Duarte, J.B., Barbosa, M.L.F., Andrade, M.D., Oliveira, R.O., Delgado, R.C.,
724 Pereira, M.G., Batista, T.S. & Teodoro, P.E. (2019) Fire outbreaks in extreme climate years in
725 the State of Rio de Janeiro, Brazil. *Land Degradation & Development*, **30**, 1379-1389.

726 Arno, S.F. & Allison-Bunnell, S. (2002) *Flames in our forest: disaster or renewal?* Island
727 Press, Washington DC.

728 Bendall, E.R. & Bedward, M. (2020) Chapter 2 scripts. GitHub.

729 Bennett, L.T., Bruce, M.J., MacHunter, J., Kohout, M., Tanase, M.A. & Aponte, C. (2016)
730 Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and
731 recent prescribed fire. *Forest Ecology and Management*, **380**, 107-117.

732 Boer, M.M., Resco de Dios, V. & Bradstock, R.A. (2020) Unprecedented burn area of
733 Australian mega forest fires. *Nature Climate Change*, **10**.

734 Bond, W.J. & van Wilgen, B.W. (1996) *Fire and Plants*. Chapman and Hall, London, United
735 Kingdom.

736 Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A.,
737 D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E.,
738 Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, C., Roos, C.L., Scott, A.C.,
739 Swetnam, T.W., van der Werf, G.R. & Pyne, S.J. (2009) Fire in the Earth System. *Science*,
740 **324**, 481-484.

741 Bowman, D.M.J.S., Murphy, B., Boer, M.M., Bradstock, R., Cary, G.J., Cochrane, M.A.,
742 Fensham, R.J., Krawchuk, M.A., Price, O.F. & Williams, R.J. (2013) Forest fire management,
743 climate change, and the risk of catastrophic carbon losses. *Frontiers in Ecology and the*
744 *Environment*, **11**, 66-68.

745 Bradstock, R.A., Hammill, K.A., Collins, L. & Price, O. (2010) Effects of weather, fuel and
746 terrain on fire severity in topographically diverse landscapes of south-eastern Australia.
747 *Landscape Ecology*, **25**, 607-619.

748 Brando, P.M., Balch, J.K., Nepstad, D.C., Morton, D.C., Putz, F.E., Coe, M.T., Silverio, D.,
749 Macedo, M.N., Davidson, E.A., Nobrega, C.C., Alencar, A. & Soares-Filho, B.S. (2014)
750 Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proc Natl Acad*
751 *Sci U S A*, **111**, 6347-6352.

752 Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. & Putz, F.E.
753 (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size,
754 wood density and fire behavior. *Global Change Biology*, **18**, 630-641.

755 Brooker, M.I.H. & Kleinig, D.A. (1999) *Field Guide to Eucalypts of South-eastern Australia*.
756 Bloomings Books, Hawthorn VIC.

757 Bürkner, P. (2017) brms: An R package for Bayesian Multilevel Models using Stan. *Journal*
758 *of Statistical Software*, **80**, 1-28.

759 Burrows, G.E. (2013) Buds, bushfires and resprouting in the eucalypts. *Australian Journal of*
760 *Botany*, **61**, 331.

761 Catry, F.X., Moreira, F., Tujeira, R. & Silva, J.S. (2013) Post-fire survival and regeneration of
762 *Eucalyptus globulus* in forest plantations in Portugal. *Forest Ecology and Management*, **310**,
763 194-203.

764 Catry, F.X., Rego, F., Moreira, F., Fernandes, P.M. & Pausas, J.G. (2010) Post-fire tree
765 mortality in mixed forests of central Portugal. *Forest Ecology and Management*, **260**, 1184-
766 1192.

767 Cawson, J.G., Duff, T.J., Tolhurst, K.G., Baillie, C.C. & Penman, T.D. (2017) Fuel moisture
768 in Mountain Ash forests with contrasting fire histories. *Forest Ecology and Management*, **400**,
769 568-577.

770 Cerano-Paredes, J., Villanueva-Díaz, J., Vázquez-Selem, L., Cervantes-Martínez, R., Magaña-
771 Rueda, V.O., Constante-García, V., Esquivel-Arriaga, G. & Valdez-Cepeda, R.D. (2019)
772 Climatic influence on fire regime (1700 to 2008) in the Nazas watershed, Durango, Mexico.
773 *Fire Ecology*, **15**.

774 Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A.W.,
775 Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M.,
776 Schwartz, M.W., Waring, K.M. & Zimmermann, N.E. (2016) The impacts of increasing
777 drought on forest dynamics, structure, and biodiversity in the United States. *Glob Chang Biol*,
778 **22**, 2329-2352.

779 Clarke, H., Penman, T., Boer, M., Cary, G.J., Fontaine, J.B., Price, O. & Bradstock, R.A.
780 (2020) The Proximal Drivers of Large Fires: A Pyrogeographic Study. *Frontiers in Earth*
781 *Science*, **8**.

782 Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J.
783 & Knox, K.J. (2013) Resprouting as a key functional trait: how buds, protection and resources
784 drive persistence after fire. *New Phytol*, **197**, 19-35.

785 Collins, L. (2020) Eucalypt forests dominated by epicormic resprouters are resilient to repeated
786 canopy fires. *Journal of Ecology*, **00**, 1-15.

787 Collins, L., Bennett, A.F., Leonard, S.W.J. & Penman, T.D. (2019a) Wildfire refugia in forests:
788 Severe fire weather and drought mute the influence of topography and fuel age. *Glob Chang*
789 *Biol*, **00**, 1-15.

790 Collins, L., Bradstock, R., de Aquino Ximenes, F., Horsey, B. & Sawyer, R. (2019b)
791 Aboveground forest carbon shows different responses to fire frequency in harvested and
792 unharvested forests. *Ecological Applications*, **29**, e01815-01811-e01815-01814.

793 Collins, L., Bradstock, R.A., Clarke, H., Clarke, M.F., Nolan, R.H. & Penman, T.D. (2021a)
794 The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-
795 severity fire. *Environmental Research Letters*, **16**.

796 Collins, L., Bradstock, R.A., Tasker, E.M. & Whelan, R.J. (2012) Can gullies preserve complex
797 forest structure in frequently burnt landscapes? *Biological Conservation*, **153**, 177-186.

798 Collins, L., Hunter, A., McColl-Gausden, S., Penman, T.D. & Zylstra, P. (2021b) The Effect
799 of Antecedent Fire Severity on Reburn Severity and Fuel Structure in a Resprouting Eucalypt
800 Forest in Victoria, Australia. *Forests*, **12**, 450-467.

801 Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M.D.,
802 Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S., Falk, D.A.,
803 Fornwalt, P.J., Fule, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North,
804 M., Parisien, M.A., Prichard, S. & Rodman, K.C. (2020) Wildfire-Driven Forest Conversion
805 in Western North American Landscapes. *Bioscience*, **70**, 659-673.

806 Denham, A.J., Vincent, B.E., Clarke, P.J. & Auld, T.D. (2016) Responses of tree species to a
807 severe fire indicate major structural change to *Eucalyptus–Callitris* forests. *Plant Ecology*, **217**,
808 617-629.

809 DPI, N. (2017) Geoscience Information. pp. Interactive Geological Map of New South Wales.
810 DPI, NSW.

811 Enright, N.J., Fontaine, J.B., Bowman, D.M.J.S., Bradstock, R.A. & Williams, R.J. (2015)
812 Interval squeeze: altered fire regimes and demographic responses interact to threaten woody
813 species persistence as climate changes. *Front Ecol Environ*, **13**, 265-272.

814 Fairman, T.A., Bennett, L.T. & Nitschke, C.R. (2019) Short-interval wildfires increase
815 likelihood of resprouting failure in fire-tolerant trees. *J Environ Manage*, **231**, 59-65.

816 Fairman, T.A., Bennett, L.T., Tupper, S. & Nitschke, C.R. (2017) Frequent wildfires erode tree
817 persistence and alter stand structure and initial composition of a fire-tolerant sub-alpine forest.
818 *Journal of Vegetation Science*, **28**, 1151-1165.

819 Fairman, T.A., Nitschke, C.R. & Bennett, L.T. (2016) Too much, too soon? A review of the
820 effects of increasing wildfire frequency on tree mortality and regeneration in temperate
821 eucalypt forests. *International Journal of Wildland Fire*, **25**, 831-848.

822 Fensham, R.J., Bouchard, D.L., Catterall, C.P. & Dwyer, J.M. (2014) Do local moisture stress
823 responses across tree species reflect dry limits of their geographic ranges? *Austral Ecology*, **39**,
824 612-618.

825 Fredriksson, G.M., Danielsen, L.S. & Swenson, J.E. (2006) Impacts of El Niño related drought
826 and forest fires on sun bear fruit resources in lowland dipterocarp forest of East Borneo.
827 *Biodiversity and Conservation*, **16**, 1823-1838.

828 Gibbons, P., Cunningham, R.B. & Lindenmayer, D.B. (2008) What factors influence the
829 collapse of trees retained on logged sites? *Forest Ecology and Management*, **255**, 62-67.

830 Gibbons, P., Lindenmayer, D.B., Barry, S.C. & Tanton, M.T. (2000a) The effects of slash
831 burning on the mortality and collapse of trees retained on logged sites in south-eastern
832 Australia. *Forest Ecology and Management*, **139**, 51-61.

833 Gibbons, P., Lindenmayer, D.B., Barry, S.C. & Tanton, M.T. (2000b) Hollow formation in
834 eucalypts from temperate forests in southeastern Australia. *Pacific Conservation Biology*, **6**,
835 218-228.

836 Gordon, C.E., Bendall, E.R., Stares, M.G., Collins, L. & Bradstock, R.A. (2018) Aboveground
837 carbon sequestration in dry temperate forests varies with climate not fire regime. *Glob Chang*
838 *Biol*, **24**, 4280-4292.

839 Hammill, K.A. & Bradstock, R.A. (2006) Remote sensing of fire severity in the Blue
840 Mountains: influence of vegetation type and inferring fire intensity. *International Journal of*
841 *Wildland Fire*, **15**, 213-226.

842 Hammill, K.A., Tasker, E.M. & Barker, C. (2013) The Invisible Mosaic: Fire Regimes in One
843 of NSW's Most Iconic Conservation Areas. pp. 13. New South Wales Office of Environment
844 and Heritage, NSW, Australia.

845 Haslem, A., Leonard, S.W.J., Bruce, M.J., Christie, F., Holland, G.J., Kelly, L.T., MacHunter,
846 J., Bennett, A.F., Clarke, M.F. & York, A. (2016) Do multiple fires interact to affect vegetation
847 structure in temperate eucalypt forests? *Ecological Applications*, **26**, 2414-2423.

848 Hoffman, W.A., Adasme, R., Haridasan, M., De Carvalho, M.T., Geiger, E.L., Pereira, M.A.B.,
849 Gotsch, S.G. & Franco, A.C. (2009) Tree topkill, not mortality, governs the dynamics of
850 savanna–forest boundaries under frequent fire in central Brazil. *Ecology*, **90**, 1326-1337.

851 Hoffmann, W.A. & Solbrig, O.T. (2003) The role of topkill in the differential response of
852 savanna woody species to fire. *Forest Ecology and Management*, **180**, 273-286.

853 IPCC (2021) Summary for Policymakers. *Climate Change 2021: The Physical Science Basis.*
854 *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental*
855 *Panel on Climate Change* (eds V. Masson-Delmotte, P. Zhai, A. Pirani, S.L. Connors, C. Péan,
856 S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy,
857 J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu & B. Zhou). Cambridge
858 University Press, In Press.

859 Jackson, J.F., Adams, D.C. & Jackson, U.B. (1999) Allometry of Constitutive Defense: A
860 Model and a Comparative Test with Tree Bark and Fire Regime. *Am Nat*, **153**, 614-632.

861 Jacobsen, A.L., Tobin, M.F., Toschi, H.S., Percolla, M.I. & Pratt, R.B. (2016) Structural
862 determinants of increased susceptibility to dehydration-induced cavitation in post-fire
863 resprouting chaparral shrubs. *Plant Cell Environ*, **39**, 2473-2485.

864 Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011) Fire as an
865 evolutionary pressure shaping plant traits. *Trends Plant Sci*, **16**, 406-411.

866 Kirchmeier-Young, M.C., Gillett, N.P., Zwiers, F.W., Cannon, A.J. & Anslow, F.S. (2019)
867 Attribution of the Influence of Human-Induced Climate Change on an Extreme Fire Season.
868 *Earth's Future*, **7**, 2-10.

869 Klaphake, V. (2012) *Eucalypts of the Sydney Region*, Third edn., Byabarra NSW.

870 Lawes, M.J., Adie, H., Russell-Smith, J., Murphy, B. & Midgley, J.J. (2011a) How do small
871 savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark
872 thickness. *Ecosphere*, **2**.

873 Lawes, M.J., Midgley, J.J., Clarke, P.J. & Jones, R. (2013) Costs and benefits of relative bark
874 thickness in relation to fire damage: a savanna/forest contrast. *Journal of Ecology*, **101**, 517-
875 524.

876 Lawes, M.J., Richards, A., Dathe, J. & Midgley, J.J. (2011b) Bark thickness determines fire
877 resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant*
878 *Ecology*, **212**, 2057-2069.

879 Lewis, T., Reif, M., Prendergast, E. & Tran, C. (2012) The effect of long-term repeated burning
880 and fire exclusion on above- and below-ground Blackbutt (*Eucalyptus pilularis*) forest
881 vegetation assemblages. *Austral Ecology*, **37**, 767-778.

882 Li, X., Blackman, C.J., Rymer, P.D., Quintans, D., Duursma, R.A., Choat, B., Medlyn, B.E. &
883 Tissue, D.T. (2018) Xylem embolism measured retrospectively is linked to canopy dieback in
884 natural populations of *Eucalyptus piperita* following drought. *Tree Physiol*, **38**, 1193-1199.

885 Ma, X., Huete, A., Moran, S., Ponce-Campos, G. & Eamus, D. (2015) Abrupt shifts in
886 phenology and vegetation productivity under climate extremes. *Journal of Geophysical*
887 *Research*, **120**, 2036-2052.

888 Matusick, G., Ruthrof, K., Fontaine, J.B. & Hardy, G.E.S.J. (2016) *Eucalyptus* forest shows
889 low structural resistance and resilience to climate change-type drought. *Journal of Vegetation*
890 *Science*, **27**, 493-503.

891 Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B. & Hardy, G.S.J. (2013) Sudden forest
892 canopy collapse corresponding with extreme drought and heat in a mediterranean-type eucalypt
893 forest in southwestern Australia. *European Journal of Forest Research*, **132**, 497-510.

894 McCaw, W.L., Smith, R.H. & Neal, J.E. (1997) Prescribed Burning of Thinning Slash in
895 Regrowth Stands of karri (*Eucalyptus diversicolor*)1. Fire Characteristics, Fuel Consumption
896 and Tree Damage. *International Journal of Wildland Fire*, **7**, 29-40.

897 McColl, J.G. (1969) Soil-plant relationships in a *Eucalyptus* forest on the south coast of New
898 South Wales. *Ecology*, **50**, 354-362.

899 McElhinny, C., Gibbons, P. & Brack, C. (2006) An objective and quantitative methodology for
900 constructing an index of stand structural complexity. *Forest Ecology and Management*, **235**,
901 54-71.

902 McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2005) Forest and woodland stand
903 structural complexity: Its definition and measurement. *Forest Ecology and Management*, **218**,
904 1-24.

905 Merchant, A., Callister, A., Arndt, S., Tausz, M. & Adams, M. (2007) Contrasting
906 physiological responses of six *Eucalyptus* species to water deficit. *Ann Bot*, **100**, 1507-1515.

907 Merchant, A., Tausz, M., Arndt, S.K. & Adams, M.A. (2006) Cyclitols and carbohydrates in
908 leaves and roots of 13 *Eucalyptus* species suggest contrasting physiological responses to water
909 deficit. *Plant Cell Environ*, **29**, 2017-2029.

910 Murphy, B.P., Bradstock, R.A., Boer, M.M., Carter, J., Cary, G.J., Cochrane, M.A., Fensham,
911 R.J., Russell-Smith, J., Williamson, G.J., Bowman, D.M.J.S. & Ladiges, P. (2013) Fire regimes
912 of Australia: a pyrogeographic model system. *Journal of Biogeography*, **40**, 1048-1058.

913 Nicolle, D. (2006) A classification and census of regenerative strategies in the eucalypts
914 (*Angophora*, *Corymbia* and *Eucalyptus*—Myrtaceae), with special reference to the obligate
915 seeders. *Australian Journal of Botany*, **54**, 391.

916 Nolan, R.H., Boer, M.M., Collins, L., Resco de Dios, V., Clarke, H., Jenkins, M., Kenny, B. &
917 Bradstock, R.A. (2020a) Causes and consequences of eastern Australia's 2019-20 season of
918 mega-fires. *Glob Chang Biol*, **26**, 1039-1041.

919 Nolan, R.H., Collins, L., Leigh, A., Ooi, M.K.J., Curran, T.J., Fairman, T.A., Resco de Dios,
920 V. & Bradstock, R. (2021) Limits to post-fire vegetation recovery under climate change. *Plant*
921 *Cell Environ*, 1-19.

922 Nolan, R.H., Rahmani, S., Samson, S.A., Simpson-Southward, H.M., Boer, M.M. & Bradstock,
923 R.A. (2020b) Bark attributes determine variation in fire resistance in resprouting tree species.
924 *Forest Ecology and Management*, **474**, 118385.

925 NPWS (2004) Fire Management Strategy Blue Mountains National Park. pp. 74. New South
926 Wales National Parks and Wildlife Service, NSW, Australia.

927 NPWS (2016) National Parks and Wildlife Service Fire History 2016. (ed. N.D.o.P.a.
928 Environment). NSW DPE.

929 Nyman, P., Metzen, D., Noske, P.J., Lane, P.N.J. & Sheridan, G.J. (2015) Quantifying the
930 effects of topographic aspect on water content and temperature in fine surface fuel.
931 *International Journal of Wildland Fire*, **24**, 1129-1142.

932 Parks, S.A. & Abatzoglou, J.T. (2020) Warmer and Drier Fire Seasons Contribute to Increases
933 in Area Burned at High Severity in Western US Forests From 1985 to 2017. *Geophysical*
934 *Research Letters*, **47**, e2020GL089858.

935 Pausas, J.G. (2015) Bark thickness and fire regime. *Functional Ecology*, **29**, 315-327.

936 Pausas, J.G. & Keeley, J.E. (2017) Epicormic Resprouting in Fire-Prone Ecosystems. *Trends*
937 *Plant Sci*, **22**, 1008-1015.

938 Pausas, J.G., Lamont, B.B., Paula, S., Appezzato-da-Gloria, B. & Fidelis, A. (2018) Unearthing
939 belowground bud banks in fire-prone ecosystems. *New Phytol*, **217**, 1435-1448.

940 Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A., Paula, S.,
941 Kaneakua-Pia, I.N. & Davis, S.D. (2016) Towards understanding resprouting at the global
942 scale. *New Phytol*, **209**, 945-954.

943 Pook, E. (1986) Canopy dynamics of *Eucalyptus maculata* Hook .IV. Contrasting responses to
944 two severe droughts. *Australian Journal of Botany*, **34**, 1-14.

945 Pook, E., Gill, A.M. & Moore, P.H.R. (1997) Long-term Variation of Litter Fall, Canopy Leaf
946 Area and Flowering in a *Eucalyptus maculata* Forest on the South Coast of New South Wales.
947 *Australian Journal of Botany*, **45**, 737-755.

948 Poorter, L., McNeil, A., Hurtado, V.-H., Prins, H.H.T., Putz, F.E. & Kitajima, K. (2014) Bark
949 traits and life-history strategies of tropical dry- and moist forest trees. *Functional Ecology*, **28**,
950 232-242.

951 Roxburgh, S.H., Wood, S., Mackey, B., Woldendorp, G. & Gibbons, P. (2006) Assessing the
952 carbon sequestration potential of managed forests: A case study from temperate Australia.
953 *Journal of Applied Ecology*, **43**, 1149-1159.

954 Ruthrof, K., Matusick, G. & Hardy, G. (2015) Early Differential Responses of Co-dominant
955 Canopy Species to Sudden and Severe Drought in a Mediterranean-climate Type Forest.
956 *Forests*, **6**, 2082-2091.

957 SILO (2019) SILO - Australian Climate Data from 1889 to Yesterday. pp. Gridded climatic
958 data for Australia. Queensland Government, Queensland Government.

959 Silva Junior, C.H.L., Anderson, L.O., Silva, A.L., Almeida, C.T., Dalagnol, R., Pletsch,
960 M.A.J.S., Penha, T.V., Paloschi, R.A. & Aragão, L.E.O.C. (2019) Fire Responses to the 2010
961 and 2015/2016 Amazonian Droughts. *Frontiers in Earth Science*, **7**, 97.

962 Silvério, D.V., Brando, P.M., Bustamante, M.M.C., Putz, F.E., Marra, D.M., Levick, S.R.,
963 Trumbore, S.E. & Edwards, D. (2019) Fire, fragmentation, and windstorms: A recipe for
964 tropical forest degradation. *Journal of Ecology*, **107**, 656-667.

965 Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., North,
966 M.P., Safford, H. & Wayman, R.B. (2018) Drought, Tree Mortality, and Wildfire in Forests
967 Adapted to Frequent Fire. *Bioscience*, **68**, 77-88.

968 Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C.,
969 Morgan, P. & Veblen, T.T. (2018) Evidence for declining forest resilience to wildfires under
970 climate change. *Ecol Lett*, **21**, 243-252.

971 Trouvé, R., Osborne, L. & Baker, P.J. (2021) The effect of species, size, and fire intensity on
972 tree mortality within a catastrophic bushfire complex. *Ecological Applications*, **0**, e02383.

973 van Buuren, S. & Groothuis-Oudshoorn, K. (2011) mice: Multivariate Imputation by Chained
974 Equations in R. *Journal of Statistical Software*, **45**, 1-67.

975 van Mantgem, P.J., Nesmith, J.C., Keifer, M., Knapp, E.E., Flint, A. & Flint, L. (2013) Climatic
976 stress increases forest fire severity across the western United States. *Ecol Lett*, **16**, 1151-1156.

977 van Mantgem, P.J. & Stephenson, N.L. (2007) Apparent climatically induced increase of tree
978 mortality rates in a temperate forest. *Ecol Lett*, **10**, 909-916.

979 Van Nieuwstadt, M.G.L.a.S., D. (2005) Drought, fire and tree survival in a Borneo rain forest,
980 East Kalimantan, Indonesia. *Journal of Ecology*, **93**, 191-201.

981 Vicente-Serrano, S.M., Beguería, S. & López-Moreno, J.I. (2010) A Multiscalar Drought Index
982 Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index.
983 *Journal of Climate*, **23**, 1696-1718.

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

987 Walden, L.L., Fontaine, J.B., Ruthrof, K.X., Matusick, G., Harper, R.J. & Hardy, G. (2019)
988 Carbon consequences of drought differ in forests that resprout. *Glob Chang Biol*, **25**, 1653-
989 1664.

990 Wardell-Johnson, G.W. (2000) Responses of forest eucalypts to moderate and high intensity
991 fire in the Tingle Mosaic, south-western Australia: comparisons between locally endemic and
992 regionally distributed species. *Austral Ecology*, **25**, 409-421.

993 Watson, G.M., French, K. & Collins, L. (2020) Timber harvest and frequent prescribed burning
994 interact to affect the demography of Eucalypt species. *Forest Ecology and Management*, **475**,
995 118463.

996 Wesolowski, A., Adams, M.A. & Pfautsch, S. (2014) Insulation capacity of three bark types of
997 temperate *Eucalyptus* species. *Forest Ecology and Management*, **313**, 224-232.

998 Whitford, K.R. & Williams, D.G. (2001) Survival of jarrah (*Eucalyptus marginata* Sm.) and
999 marri (*Corymbia calophylla* Lindl.) Habitat trees retained after logging. *Forest Ecology and*
1000 *Management*, **146**, 181-197.

1001 Wood, S.N. (2017) *Generalized Additive Models: An Introduction with R, Second Edition*.
1002 Chapman and Hall/CRC, New York.

1003 Xiao, J. & Zhuang, Q. (2007) Drought effects on large fire activity in Canadian and Alaskan
1004 forests. *Environmental Research Letters*, **2**, 044003.

1005 Zylstra, P.J. (2018) Flammability dynamics in the Australian Alps. *Austral Ecology*, **43**, 578-
1006 591.

1007