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Wildfire refugia in forests: Severe fire weather and drought mute the influence of topography and fuel age

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8 **Wildfire refugia in forests: severe fire weather and drought mute the influence of**
9 **topography and fuel age**

10 **Running title:** Weather and drought determine fire refugia11 **Authors:** Collins, L.^{1,2,3}, Bennett, A.F.^{1,2,3}, Leonard, S.W.J.^{1,3,4}, Penman, T.D.⁵12 ¹ Department of Ecology, Environment & Evolution, La Trobe University, Bundoora,
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21 Australia22 **Corresponding author:** Luke Collins, tel +61 3 9479 3982, email: l.collins3@latrobe.edu.au23 **Keywords:** drought, eucalypt forests, fire refuge, fire weather, temperate forest, wildfire

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24 **Paper type:** Primary Research

25 **Abstract**

26 Wildfire refugia (unburnt patches within large wildfires) are important for the persistence of
27 fire-sensitive species across forested landscapes globally. A key challenge is to identify the
28 factors that determine the distribution of fire refugia across space and time. In particular,
29 determining the relative influence of climatic and landscape factors is important in order to
30 understand likely changes in the distribution of wildfire refugia under future climates. Here,
31 we examine the relative effect of weather (i.e. fire weather, drought severity) and landscape
32 features (i.e. topography, fuel age, vegetation type) on the occurrence of fire refugia across 26
33 large wildfires in south-eastern Australia. Fire weather and drought severity were the primary
34 drivers of the occurrence of fire refugia, moderating the effect of landscape attributes.
35 Unburnt patches rarely occurred under 'severe' fire weather, irrespective of drought severity,
36 topography, fuels or vegetation community. The influence of drought severity and landscape
37 factors played out most strongly under 'moderate' fire weather. In mesic forests, fire refugia
38 were linked to variables that affect fuel moisture, whereby the occurrence of unburnt patches
39 decreased with increasing drought conditions and were associated with more mesic
40 topographic locations (i.e. gullies, pole-facing aspects) and vegetation communities (i.e.
41 rainforest). In dry forest, the occurrence of refugia was responsive to fuel age, being
42 associated with recently burnt areas (<5 years since fire). Overall, these results show that
43 increased severity of fire weather and increased drought conditions, both predicted under
44 future climate scenarios, are likely to lead to a reduction of wildfire refugia across forests of
45 southern Australia. Protection of topographic areas able to provide long-term fire refugia will
46 be an important step towards maintaining the ecological integrity of forests under future
47 climate change.

48

49 **Introduction**

50 Wildfires are a recurrent disturbance across forest ecosystems globally (Archibald *et al.*,
51 2013). They influence a range of ecosystem properties including the distribution of plants and
52 animals, nutrient cycling, carbon emission and sequestration, erosion and water quality
53 (Bowman *et al.*, 2009, Bradstock *et al.*, 2012). Wildfires in temperate forests typically

54 display spatial heterogeneity in fire severity (i.e. the consumption of organic matter; Keeley,
55 2009), which is driven by complex interactions between weather, fuels and topography (e.g.
56 Bradstock *et al.*, 2010, Clarke *et al.*, 2014). Fire severity and the spatial patterns of severity
57 classes (e.g. patch size, configuration) have important implications for ecosystem response
58 (Bennett *et al.*, 2017, Chia *et al.*, 2015, Doerr *et al.*, 2006, Smucker *et al.*, 2005). Unburnt
59 patches within large wildfires, here termed ‘fire refugia’, facilitate the persistence of fire-
60 sensitive plants and animals in forest ecosystems globally (Meddens *et al.*, 2018b, Robinson
61 *et al.*, 2013). Fire refugia can enhance survival during a fire event, support the persistence of
62 individuals and populations in the post-fire environment, and promote the re-establishment of
63 populations in the long-term (Robinson *et al.*, 2013). Furthermore, areas that consistently
64 remain unburnt over many fire events, here termed ‘persistent fire refugia’, preserve unique
65 or high value habitat, increase ecosystem heterogeneity and beta-diversity across landscapes,
66 and are important carbon stores (Meddens *et al.*, 2018b, Robinson *et al.*, 2013).

67 Fire spread depends on three main factors: sufficient fuel biomass; whether fuels are
68 available to burn (i.e. fuel moisture); and fire weather conditions that facilitate fire
69 propagation (Bradstock, 2010, Moritz *et al.*, 2012). The biomass of surface and near-surface
70 fuels are particularly important for fire spread (Catchpole, 2002), though active fire spread in
71 canopy fuels can occur in some ecosystems (e.g. conifer forests; van Wagner, 1977). Fuel
72 ignitability and rate of spread decrease with increasing fuel moisture (Cheney *et al.*, 2012),
73 leading to negative associations between fuel moisture levels and area burned in ecosystems
74 where fuel biomass is not limiting (Abatzoglou & Williams, 2016, Nolan *et al.*, 2016). Fire
75 weather conditions affect the ignitability of material (e.g. temperature, humidity), and flame
76 length and ember propagation (e.g. wind speed), all of which determine the likelihood that
77 fire will cross fuel gaps (Sullivan *et al.*, 2012, Zylstra *et al.*, 2016).

78 Landscape characteristics (e.g. topography, fuel age) influence forest fire behaviour through
79 their effect on fuel loads, fuel moisture and interactions with fire weather (e.g. wind speed
80 and direction; Catchpole, 2002, Sullivan *et al.*, 2012), though the latter can be somewhat
81 stochastic in nature (e.g. Sharples *et al.*, 2012). Topographically induced variability in fuel
82 moisture is consistently identified as a driver of spatial heterogeneity in forest fire severity
83 (Bradstock *et al.*, 2010, Krawchuk *et al.*, 2016). For example, sheltered topographic locations
84 (e.g. gullies, valleys) and poleward facing aspects typically have higher levels of fine-fuel
85 moisture than ridges and equatorial facing aspects (Nyman *et al.*, 2015, Slijepcevic *et al.*,

86 2018) and, as such, are often found to provide wildfire refugia (Berry *et al.*, 2015, Leonard *et al.*, 2014, Wood *et al.*, 2011). Recent fires can reduce the flammability of surface fuels by
87 decreasing fuel mass and continuity (Catchpole, 2002, Fernandes & Botelho, 2003), reducing
88 fire severity and increasing the likelihood of unburnt patches (Bradstock *et al.*, 2010, Collins
89 *et al.*, 2007, Leonard *et al.*, 2014).

91 Fire weather and drought can moderate the effects of fuel and topography on fire behaviour
92 (Clarke *et al.*, 2014, Littell *et al.*, 2016). Extreme fire weather (strong winds, high
93 temperature, low humidity) can allow fire to overcome fuel gaps, reducing the effect of fuel
94 discontinuity on fire spread (Zylstra *et al.*, 2016), as well as facilitating fire spread into sites
95 that would otherwise be unlikely to burn due to topography or vegetation type (Krawchuk *et al.*,
96 2016, Leonard *et al.*, 2014). Drought conditions can increase the connectivity of dry fuels
97 across the landscape, by desiccating fuels in mesic gullies and poleward-facing slopes
98 (Caccamo *et al.*, 2012), removing these barriers to fire spread. Drought also increases litter
99 production (Duursma *et al.*, 2016, Pook, 1986) and can cause partial or whole plant mortality
100 (Collins *et al.*, 2018a, Ruthrof *et al.*, 2016), thereby increasing surface fuel loads and the
101 amount of dead elevated fuel (Ruthrof *et al.*, 2016). Drought-related 'pulse' inputs of fuel
102 have the potential to offset fuel limitations in recently burnt areas. The occurrence of fire
103 refugia may therefore depend on the interplay between weather (i.e. fire weather, drought
104 severity) and landscape factors (e.g. topography and fuels) (Krawchuk *et al.*, 2016, Leonard
105 *et al.*, 2014, Román-Cuesta *et al.*, 2009).

106 Studies investigating the interactive effects of weather and landscape on fire severity and fire
107 refugia often use fire weather indices that combine drought severity and fire weather in such
108 a way that short and long term weather effects cannot be disentangled (e.g. Clarke *et al.*,
109 2014, Collins *et al.*, 2014, Krawchuk *et al.*, 2016). Isolating the relative effects of drought
110 severity and fire weather is important, because the two processes have different rates of
111 occurrence and affect landscape flammability at different temporal scales. For example, in
112 Australian temperate forests, droughts occur sporadically (Bradstock, 2010), but have lasting
113 effects on landscape flammability (months to years) (Caccamo *et al.*, 2012, Ruthrof *et al.*,
114 2016); whereas severe to extreme fire weather events can occur multiple times over a fire
115 season (Bradstock, 2010), but only affect landscape flammability and potential fire behaviour
116 at hourly time scales (Sullivan *et al.*, 2012).

117 Anthropogenic climate change is predicted to increase the frequency, intensity and duration
118 of drought (CSIRO and Bureau of Meteorology, 2015, IPCC, 2014), and the severity of fire
119 weather during the wildfire season (Bedia *et al.*, 2014, Clarke & Evans, 2018), across many
120 fire-prone forested regions globally. Extreme fire weather and drought are positively
121 associated with the occurrence of large wildfires (Barbero *et al.*, 2014, Bradstock *et al.*, 2009)
122 and the area burnt by high severity fire (e.g. Reilly *et al.*, 2017). It is not clear how future
123 changes to climate and fire regimes will affect the persistence of topographic fire refugia or
124 the availability of transient refugia associated with past burns (Meddens *et al.*, 2018b).

125 This study assesses the relative effect of weather (fire weather, drought severity) and
126 landscape (topography, fuel age, vegetation) factors on the occurrence of unburnt patches,
127 with a focus on the potential moderating effect of top-down drivers. Specifically we ask: (i)
128 what are the relative effects of fire weather, drought severity, topography, fuels and
129 vegetation on the occurrence of fire refugia?; (ii) can fire weather and drought severity
130 override the effect of topography, fuels and vegetation on fire refugia?, and (iii) are the
131 drivers of fire refugia different in dry and mesic forest types?

132 **Materials and Methods**

133 *Study area*

134 The study focused on 18 large wildfires and 2 wildfire complexes (median size: 18,111 ha;
135 range: 1,700 - 1,061,000 ha) that occurred in coastal areas and ranges (< 1,400 m elevation)
136 of the state of Victoria, south eastern Australia (Fig. 1). The wildfire complexes considered
137 included 8 discrete fire events (described below), resulting in 26 fires in total. The fires were
138 selected because they were large (>1,000 ha), had reliable fire severity mapping, and fire
139 weather conditions could be assigned to sections of the burnt area based on recorded
140 progression data, written accounts and remotely sensed fire detection (i.e. hotspots) data
141 (<http://sentinel.ga.gov.au>, accessed 17 January 2019). The fires occurred between 2005 and
142 2016, a period characterised by extensive wildfire activity in south-eastern Australia
143 (Fairman *et al.*, 2016). Most fires occurred in summer months (December to February), with
144 two fires igniting in Autumn. The cumulative area burnt by the study fires was ~1.8 million
145 ha, which represents 81% of the area burnt within the study area between 2005 and 2016
146 (Fig. 1). Five fires (including the fire complexes) were very large, exceeding 85 000 ha and
147 reaching between 45 km to 150 km in length (Fig. 1). The duration of the study fires ranged

148 from several days to several months, hence weather conditions experienced during the fires
149 were typically variable. The distribution of the fires across space and time allowed for a
150 diverse range of climatic conditions to be sampled in the dataset (Appendix S1).

151 The study region falls within the temperate climatic zone, with average daily maximum
152 summer temperature ranging between 16°C and 30°C and average daily minimum winter
153 temperature ranging between -5°C and 9°C. Mean annual precipitation ranges from 500 mm
154 to 2200 mm across the study region, with precipitation in excess of 1000 mm being confined
155 to mountainous areas of the Great Dividing Range and some coastal areas in the east and the
156 south (Appendix S2). The eastern parts of the study region are characterised by uniform
157 annual rainfall, whereas the central and western parts experience slightly higher rainfall (e.g.
158 one-third of annual rainfall) in the winter months (www.bom.gov.au, accessed 2nd January
159 2019). This region experienced an intense and prolonged drought between 2000 – 2010 (i.e.
160 the Millennium Drought), the worst on record since 1900 (see Ma *et al.*, 2015).

161 Vegetation across the study fires is predominantly forest, with some intermixed patches of
162 woodland, shrubland and grassland (Cheal, 2010). Temperate forest communities of southern
163 Australia are broadly classified as ‘Open-forests’, ‘Tall open-forests’ or ‘Closed forests’ (i.e.
164 rainforest), based on canopy cover and height (Gill & Catling, 2002). Open-forests and tall
165 open-forests are dominated by genera from the Myrtaceae family - *Eucalyptus*, *Corymbia* and
166 *Angophora* (i.e. eucalypts) - and have a canopy cover of 30 – 70%, whereas closed forests are
167 dominated by non-eucalypts (e.g. *Nothofagus cunninghamii*) with canopy cover exceeding
168 70% (Gill & Catling, 2002). Open-forests are 10 – 30 m tall, with an open shrub layer and a
169 ground stratum consisting of herbs, grasses and ferns (Cheal, 2010, Gill & Catling, 2002).
170 Tall open-forests are 30 - 100 m tall, with an understorey comprised of tall shrubs or small
171 trees and a mesic lower stratum consisting of tree and ground ferns, palms, cycads, herbs and
172 grasses (Cheal, 2010, Gill & Catling, 2002). Closed forests are greater than 10 m tall and
173 have lower stratum dominated by ferns, lianes and mesic herbs (Gill & Catling, 2002). Open-
174 forests are widespread across southern Australia, with tall-open forests and closed forests
175 being confined to more mesic and fertile parts of the landscape (Cheal, 2010, Gill & Catling,
176 2002). Inter-fire intervals typically are 5 – 20 years in open-forests, 20 – >100 years in tall-
177 open forests and >100 years in closed forests (Gill & Catling, 2002, Murphy *et al.*, 2013).

178 *Mapping wildfire refugia*

179 A spatial map of wildfire severity was created for each wildfire at a 30 m spatial resolution
180 using Landsat imagery. Google Earth Engine (Gorelick *et al.*, 2017) was used to acquire and
181 process Landsat images into classified severity maps. Five fire severity classes were mapped,
182 following classification protocols used by the Department of Environment, Land, Water and
183 Planning, Victoria (DELWP) (McCarthy *et al.*, 2017): these were tree crown consumed,
184 crown scorched, crown partially scorched, crown unburnt (i.e. ground burn only), and
185 unburnt vegetation. Classification of Landsat imagery was undertaken by using a Random
186 Forest classification approach described by Collins *et al.* (2018b), which produces an
187 accurate classification (~92% accuracy) of fire severity in Australian temperate forests.
188 Random Forest classification has been found to identify unburnt vegetation with >90%
189 classification accuracy in both Australian eucalypt forests (Collins *et al.*, 2018b) and North
190 American conifer forests (Meddens *et al.*, 2016), outperforming (>10% increase in
191 classification accuracy) common classification approaches using only the pre- and post-fire
192 differenced Normalised Burn Ratio. Fourteen of the fires examined in this study were used in
193 the Random Forest training dataset created by Collins *et al.* (2018b) and therefore are known
194 to have a high level of classification accuracy. Fire severity maps were reclassified within the
195 fire perimeter to a binary classification i.e. burnt (0) or unburnt (1, i.e. refugium).

196 *Climatic and landscape variables*

197 The McArthur Forest Fire Danger Index (FFDI) was used to measure fire danger across the
198 study fires. The FFDI combines temperature, relative humidity, wind speed and a drought
199 factor to derive a single index of fire danger for Australian forests (Gill *et al.*, 1987). The
200 FFDI has been shown to be correlated with fire spread, intensity and severity in eucalypt
201 forests, whereby high values of FFDI equate to more extreme fire behaviour (Penman *et al.*,
202 2013, Storey *et al.*, 2016). Operationally, FFDI has been broken into six classes (FFDI range
203 is presented in parentheses) that are related to the likelihood of suppression success: (i) Low
204 (0 – 12); High (13 – 25); Very high (26 – 49); Severe (50 – 74); Extreme (75 – 99); and (vi)
205 Catastrophic (≥ 100). Terrain and vegetation have a strong influence on fire behaviour under
206 lower FFDI (e.g. < 35). However, under higher FFDI (FFDI > 49) the influence of landscape
207 factors on fire behaviour diminishes, with rapid rates of fire spread and extensive canopy-
208 consuming fires occurring (Price & Bradstock, 2012, Storey *et al.*, 2016).

209 Fire weather conditions were classified as either ‘severe’ (SEV) or ‘moderate’ (MOD) based
210 on FFDI and observed fire behaviour. An objective of our study was to separate the effects of
211 drought and fire weather, so we standardised the drought factor in the FFDI calculations by
212 assuming the worst drought conditions possible (i.e. drought factor = 10). This assumption is
213 valid as large wildfires typically occur in Australian forests only when drought factor is very
214 high (≥ 8) (Bradstock *et al.*, 2009). SEV fire weather days were those with a maximum FFDI
215 ≥ 49 , which occurs during periods of high temperatures ($> 35^{\circ}\text{C}$), low relative humidity ($<$
216 20%) and strong westerly to north westerly winds ($> 30 \text{ km h}^{-1}$ with gusts $> 50 \text{ km h}^{-1}$)
217 (Appendix S1). SEV fire weather typically occurs between midday and early evening and
218 rarely occurs over consecutive days. MOD fire weather was defined as periods with a
219 maximum FFDI ≤ 35 , which were characterised by temperatures $< 30^{\circ}\text{C}$, relative humidity $>$
220 25% , wind speeds $< 30 \text{ km h}^{-1}$ with gusts $< 50 \text{ km h}^{-1}$ (Appendix S1). MOD fire weather
221 conditions occur for days to months in succession. We did not target intermediate FFDI (i.e.
222 $35 - 49$) because expansive patches that burned under these conditions were uncommon,
223 owing to low rates of fire spread and the rarity of consecutive days experiencing intermediate
224 FFDI. We note that ‘moderate’ and ‘severe’ fire weather used in our study do not strictly
225 equate to FFDI classes that are used for operational purposes in Australia.

226 Digitised fire progression data (source: DELWP) and Sentinel Hotspots data
227 (<http://sentinel.ga.gov.au>, accessed 17 January 2019) were used to assign the date of burning,
228 in some cases to the hour, to areas within the final fire perimeter. Digitised fire progression
229 polygons were created by DELWP by using a combination of aerial thermal imagery and
230 observations collected during firefighting operations. Each progression polygon had a date
231 and time stamp. Sentinel Hotspots data were used to check the reliability of the digitised fire
232 progression data. Hotspots data consisted of a point layer of thermal hotspots associated with
233 active fires, derived from a number of satellites, including the Moderate Resolution Imaging
234 Spectroradiometer (MODIS) and Visible Infrared Imaging Radiometer Suite (VIIRS)
235 satellites. Hotspots data were overlaid on the progression data and areas of agreement were
236 identified and used in the analysis.

237 FFDI was calculated at 30-minute timescales for the duration of a fire using weather data
238 acquired from the closest Bureau of Meteorology weather station (www.bom.gov.au).
239 Maximum FFDI was assigned to each progression polygon using the 30-minute weather
240 observations (Appendix S3). Areas that burnt under SEV and MOD weather conditions were

241 then identified and digitised into homogeneous weather classes in ArcMAP (V10.5.1, ESRI).
242 Weather stations were typically widely dispersed across the study area (~30 km – 90 km
243 separation), so observations of fire behaviour (i.e. rate of spread and fire severity) were used
244 to support the SEV weather classification i.e. large patches (>1 ha) of tree crown
245 consumption and average rates of spread exceeding 1000 m hr⁻¹ in forest vegetation.

246 Fires within fire complexes were considered as discrete events in situations where the
247 ignitions were far apart (>~10 km) and fires burnt independently for several days. Due to the
248 high number of ignitions (>20) in the largest fire complex (the 2007 Great Divide Fire; ~1
249 million ha), it was difficult to assign burnt areas to individual fires after they began merging.
250 Therefore, this fire complex was split into six fire regions that were geographically distinct
251 and largely affected by different fires. Two fires were recognised in the Goongerah fire
252 complex. Thus, a total of 26 fires originating from independent ignitions were examined
253 across the study. Fourteen of these fires contained areas burnt under SEV weather conditions
254 and 23 of the fires had areas burnt under MOD weather conditions.

255 Drought severity was measured for each wildfire by using the Standardised Precipitation
256 Evapotranspiration Index (SPEI). The SPEI is a standardised measure of the difference
257 between precipitation (water input) and evapotranspiration (water loss) over a defined
258 window of time. SPEI values of zero equate to the long-term median, whereas increasingly
259 negative values represent increasing water deficit and increasingly positive values represent
260 increasing water availability (<http://spei.csic.es/>). SPEI values below -0.5 have been
261 considered as drought conditions in temperate regions of Australia (Ma *et al.*, 2015). We
262 calculated SPEI over three and six month windows, as this timeframe is sufficient for the
263 drying of forest fuels to levels that can facilitate large wildfires (Caccamo *et al.*, 2012, Nolan
264 *et al.*, 2016), and in the case of the latter, to stress eucalypts sufficiently to cause high rates of
265 litterfall (Pook, 1986). SPEI was calculated at a 5 km x 5 km resolution using monthly
266 precipitation and potential evapotranspiration data (1911 – 2016) from the Australian Bureau
267 of Meteorology Australian Water Resources Assessment Landscape model
268 (<http://www.bom.gov.au/water/landscape>, accessed 23rd January 2017). Potential
269 evapotranspiration was calculated using the Penman equation (Penman, 1948). Due to the
270 monthly resolution of the SPEI dataset, the SPEI values used for each fire included rainfall
271 and evaporation data from the month in which the fire ignited. The R package ‘SPEI’ was
272 used to calculate SPEI for the gridded data (Beguería & Vicente-Serrano, 2017).

273 Three measures of terrain were considered in this study, namely slope, aspect and
274 topographic position (Table 1), as they have been found to be influential in determining fire
275 severity and refugia patterns in Australian forests (Collins *et al.*, 2014, Leonard *et al.*, 2014,
276 Penman *et al.*, 2007). A 30 m digital elevation model (DEM) acquired from Geoscience
277 Australia (<http://www.ga.gov.au/>) was used to calculate the topographic indices. The DEM
278 was derived from the North American Space Agency Shuttle Radar Topography Mission
279 (<https://www2.jpl.nasa.gov/srtm/>) and converted to a smoothed ground surface DEM by
280 Geoscience Australia. Slope and aspect were calculated using the ‘terrain’ function in the
281 ‘raster’ package in R. Slope and aspect calculations considered all eight pixels directly
282 adjacent to the focal pixel. Aspect was recalculated as the aspect relative to north (ASPN),
283 using the following equation:

$$284 \quad \text{If Aspect} \leq 180: \text{ASPN} = \text{Aspect} \quad \text{Equation 1}$$

$$285 \quad \text{If Aspect} > 180: \text{ASPN} = 360 - \text{Aspect}$$

286 whereby ASPN ranges from 0° (north facing) to 180° (south facing). We used north as the
287 reference aspect as there are large differences in surface fuel moisture between north (driest)
288 and south (wettest) facing slopes, but little difference between east and west (intermediate
289 moisture) facing slopes (Nyman *et al.*, 2015). A Topographic Position Index (TPI) was
290 calculated as the difference between the elevation of a focal pixel and the mean elevation of
291 the surrounding pixels within a defined sampling window. A sampling window of 33 x 33
292 pixels (990 m x 990 m) was used for these calculations, which was deemed to be a suitable
293 scale for characterising topographic position across the study region (Bradstock *et al.*, 2010,
294 Price & Bradstock, 2012). TPI was calculated in R using the ‘focal’ function in the ‘raster’
295 package.

296 The biomass and spatial arrangement (i.e. horizontal and vertical connectivity) of fine fuels is
297 influential in determining fire behaviour and flammability in forest ecosystems (Cheney *et al.*
298 *et al.*, 2012, Zylstra *et al.*, 2016). Three variables representing fuel characteristics were
299 considered: namely, forest type, time since the previous fire (TSF), and time since the most
300 recent timber harvesting event (TSH) (Table 1). Fuel biomass, arrangement and structure
301 vary across broad forest types in temperate regions of Australia (McColl-Gausden &
302 Penman, 2019, Thomas *et al.*, 2014). Vegetation communities were initially categorised into
303 five groups based on vegetation structure and site productivity (Ecological Vegetation

304 Divisions are in parenthesis; Cheal, 2010): i) Dry open-forests (infertile soils; EVD 3 & 7); ii)
305 Dry open-forest (fertile soils; EVD 8 & 9); iii) Tall-open moist forest (fertile soils; EVD 10 &
306 11); iv) Tall-open mist forest (fertile soils; EVD 12) and v) Closed forest (fertile soils; EVD
307 13) (Cheal, 2010). The vegetation groups were assigned as either ‘Dry Forest’ or ‘Mesic
308 Forest’ based on the seasonal period that the vegetation is flammable. Dry forests include the
309 two dry open-forest vegetation groups (EVDs 3, 7, 8 and 9) which are considered potentially
310 flammable from spring to autumn (Cheal, 2010). Mesic forest includes the mesic tall-open
311 forest and closed forest groups (EVDs 10, 11, 12 and 13) which generally are flammable only
312 in summer during periods of water deficit and high – catastrophic FFDI (Cheal, 2010). The
313 distinction between the two forest types was based on the perceived sensitivity of fire
314 behaviour to drought, whereby the occurrence of unburnt patches is likely to be more
315 sensitive to drought in mesic forest than in dry forest (Duff *et al.*, 2018). The dry forest types
316 are dominated by eucalypt species that recover rapidly by resprouting following wildfire
317 (within ~10 – 20 years). Mesic forests are dominated by resprouter and/or obligate seeder
318 eucalypts (e.g. *Eucalyptus regnans*) (i.e. Tall-open forest) or rainforest species (i.e. Closed
319 forest) (Cheal, 2010).

320 Time since previous fire (TSF) and time since timber harvesting (TSH) were used in the
321 analysis as they are related to fuel mass, leaf litter connectivity and vegetation structure
322 (Cawson *et al.*, 2018, Zylstra, 2018). TSF was calculated by using a spatial dataset of fire
323 history perimeters, which included fires recorded between 1903 and 2017. Systematic
324 digitisation of fire perimeters has occurred only from 1970 onwards in Victoria: prior to
325 1970, only wildfires of significance were mapped. We calculated TSF up until 1903, because
326 of the long time frame required for the regeneration of mist and closed forests (Mackey *et al.*,
327 2002). We consider that the omission of some fires prior to 1970 will have little impact on the
328 study, because a) fires affecting mesic forests prior to 1970 typically were recorded in the fire
329 history (e.g. 1939 Black Friday fire), and b) most dry forests sampled (~63%) had
330 experienced fire since 1970 (excluding the study fires). TSH was calculated using a spatial
331 dataset of timber harvesting operations (1960 onwards) (Table 1). Spatial data layers of forest
332 type, TSF and TSH were obtained from DELWP
333 (<https://services.land.vic.gov.au/SpatialDatamart/>).

334 *Data sampling*

335 We used a point-based sampling approach to sample fire refugia and environmental and
336 climatic variables. Fire refugia were recorded as a binary response i.e. whether a pixel at the
337 sampling point was burnt (0) or unburnt (1, i.e. refugium). Fire severity patterns show spatial
338 dependence due to the propagation of fire across the landscape (Bradstock *et al.*, 2010,
339 Collins *et al.*, 2014). Spatial variation in fire severity patterns is strongly influenced by
340 topographic position (e.g. ridges vs gullies) (Bradstock *et al.*, 2010, Leonard *et al.*, 2014). We
341 defined a minimum distance between sampling points based on spatial dependence of the
342 topographic position index (TPI) across the sampled landscapes. TPI was sampled across
343 each fire weather polygon by using a grid of points with 100 m spacing. Semi-variograms
344 were then produced for each fire to identify the scale of dependence, up to a distance of 2000
345 m. A sampling distance of 400 m was determined to be appropriate (Appendix S4), consistent
346 with sampling distances used in previous point-scale analyses of fire severity (e.g. Price &
347 Bradstock, 2012).

348 Sample points were confined to patches (>2.25 ha) of native forest and were not located
349 within 50 m of non-native or non-forest vegetation, within 30 m of major sealed roads, and
350 within 90 m of major power line easements. Examination of fire severity maps suggest that
351 small unsealed roads (typically <8 m wide) had no effect on severity patterns mapped at 30 m
352 resolution using Landsat imagery (LC pers. obs.). Sampling also was excluded from locations
353 within 250 m of the perimeter of mapped fire weather zones to account for spatial inaccuracy
354 in the digitisation of fire perimeters (~10 - 100 m; Price & Bradstock, 2010). Climatic,
355 topographic, fuel and refugia data were extracted for each sample point by using the 'extract'
356 function in the 'raster' package in R.

357 *Data analysis and spatial modelling*

358 Examination of the gridded point sample revealed that unburnt patches rarely occurred under
359 SEV fire weather (n = 68; <1% of the data points), suggesting that fire weather determines
360 the influence environmental variables have on fire refugia. The low frequency of refugia
361 under SEV weather limited our capacity to model the effect of the full suite of environmental
362 predictors using binary regression approaches (van der Ploeg *et al.*, 2014). Consequently, the
363 analysis was broken up to first assess the effect of fire weather on the availability of unburnt
364 forest within fire perimeters, then to examine the effect of drought, topography and fuels on

365 the occurrence of fire refugia under the contrasting weather conditions (i.e. MOD vs SEV)
366 using the point data.

367 Fire severity maps were used to quantify the area of unburnt forest under MOD and SEV fire
368 weather and to test the effect of fire weather on the availability of refugia. The percentage of
369 unburnt pixels within each fire weather polygon was calculated as a measure of refugia
370 availability. Calculations were separated by forest type (i.e. dry vs mesic), to account for
371 differences in flammability across broad vegetation groupings. A linear mixed effect model
372 was used to examine the interaction between weather and forest type on the availability of
373 refugia. The analysis excluded forest types if the total area of the forest type within a fire
374 weather polygon was less than 100 ha. The size restriction was imposed to ensure results
375 were not overly influenced by small fires. The fire year and fire identifier were included as
376 random effects, with fires being nested within years. A natural log transformation ($\log_n + 0.1$)
377 was applied to the data to meet the assumptions of homogeneity of variance and normality of
378 residuals.

379 Generalised additive mixed models (GAMMs) with a binomial distribution were used to
380 examine the empirical relationships between the occurrence of fire refugia and associated
381 climatic and environmental predictors by using the gridded point sample. This analysis was
382 undertaken separately for the SEV and MOD weather classes. GAMMs were used as they
383 allow for non-linear relationships to be modelled between response and predictor variables,
384 through a smoothing function (Zuur *et al.*, 2009). For the smoothed terms in the models, we
385 allowed up to 4 degrees of freedom for additive effects and up to 6 degrees of freedom for
386 interactions to produce biologically meaningful relationships and to avoid overfitting the
387 data. A 'fire year' identifier was included in all models as a random effect to account for the
388 nesting of sample points within time.

389 The SEV and MOD datasets were assessed for spatial autocorrelation by fitting a null model
390 and assessing spatial dependency in the model residuals using a spatial variogram. There was
391 evidence of spatial autocorrelation up to a distance of ~1200 m. A spatially lagged response
392 variable (SLRV) (Haining, 2003) was derived to account for spatial dependency in fire
393 severity. Values of one to five were assigned to the ordinal fire severity classes (lowest to
394 highest). The SLRV was calculated as the sum of the fire severity scores transformed using
395 an inverse-distance weighting:

396

$$SLRV_i = \frac{\sum_j (W_{ij} \times Y_j)}{\sum_j (W_{ij})} \quad \text{Equation 2}$$

397 where i and j are the focal and neighbouring points respectively, W is the inverse distance
398 between i and j and Y is fire severity. We used a 1200 m radius to calculate the SLRV. A low
399 value of SLRV is indicative of predominantly low severity fire in the surrounding
400 neighbourhood, whereas a high SLRV is indicative of high severity fire in the surrounding
401 neighbourhood.

402 Data analysis for MOD fire weather was undertaken separately for the dry and mesic forests,
403 respectively, as we expected diverging effects of SPEI, topography and fuels on refugia
404 across forest type (i.e. dry forests will be sensitive to variables affecting fuel biomass whereas
405 mesic forests will be sensitive to variables influencing fuel moisture). For each forest type we
406 initially fitted a 'baseline' GAMM that included the SLRV, SPEI, TPI, ASPN, slope, TSF,
407 TSH and vegetation community as additive effects. The three and six month SPEI were
408 compared when fitting the initial baseline models. The six month SPEI produced a better fit
409 to the data and was therefore used for the analysis. Two-way interactions involving SPEI and
410 landscape variables (TPI, ASPN, slope and TSF) were then assessed to determine whether
411 drought was moderating the effect of landscape on the occurrence of refugia. The interaction
412 between TSH and SPEI and vegetation community and SPEI were not assessed due to
413 insufficient replication across the gradient of SPEI. Each two-way interaction was added
414 individually to the baseline GAMM to test whether drought was modifying the effect of
415 topography and TSF on the occurrence of refugia. Each two-way interaction was assessed
416 independently to avoid overfitting of models. Models containing a two-way interaction were
417 compared to the baseline GAMM using AIC (Burnham & Anderson, 2002). If the addition
418 of the interaction resulted in considerable improvement to the model (i.e. > 4 AIC point
419 reduction) (Burnham & Anderson, 2002), the interaction was added to the final model. We
420 used a conservative AIC cut-off because preliminary analysis found that smaller
421 improvements in AIC were not leading to ecologically meaningful relationships. Model
422 predictions were then made to visualise the relationships between SPEI, topography, TSF and
423 TSH.

424 Analysis of the SEV fire weather data focused on the effects of SPEI, topographic variables,
425 fuels and vegetation type in isolation, owing to the limited number of sample points occurring
426 in fire refugia. GAMMs included one environmental predictor and the SLRV as additive

427 effects. Akaike Information Criterion (AIC) was used to compare models to the ‘null’ model
428 containing only the SLRV (Burnham & Anderson, 2002). Variables that resulted in
429 considerable improvement to model performance (i.e. > 4 AIC point reduction) relative to the
430 intercept only model were considered meaningful (Burnham & Anderson, 2002).

431 Data analysis was undertaken in R v3.4.1. Linear mixed effect models were fitted using the
432 ‘nlme’ package (Pinheiro *et al.*, 2017). GAMMs were fitted using the ‘gamm4’ package
433 (Wood & Scheipl, 2016).

434 **Results**

435 A total of 23, 211 data points were sampled, of which 55% (n = 12, 673) burnt under
436 ‘moderate’ (MOD) fire weather conditions. SPEI showed considerable variability across the
437 study fires, ranging between -2.5 (extreme drought) to 0.5 (above average water availability)
438 (Fig. 2, Appendix S5). Dry forests were present across all 26 fires and mesic forests were
439 present in all but two (Appendix S5). The proportion of points that were unburnt was slightly
440 higher in mesic forest (7.7%) than dry forest (4.8%). However, within mesic forest there were
441 large differences in the availability of fire refugia across different communities, with
442 proportionally more unburnt points occurring in closed forest (36.6%) and tall-open mist
443 forest (13.5%) than tall-open moist forest (5.7%). Mesic forests tended to occur in lower
444 topographic positions (i.e. gullies and lower slopes) and on south-facing aspects, compared
445 with dry forests (Fig. 2). The TSF distribution was skewed towards lower values in dry forest,
446 more so than in mesic forests (Fig. 2).

447 Fire weather had an overriding effect on the availability of unburnt forest, with refugia
448 making up 1.5% of mapped areas that were burnt during ‘severe’ fire weather (SEV) and
449 9.8% of areas burnt during ‘moderate’ fire weather (MOD). There was a significant
450 interaction between weather and forest type on the availability of refugia ($F_{1,37} = 4.72$; $p =$
451 0.04), whereby the effect of forest type played out under MOD weather, but not SEV weather
452 (Fig. 3a). Under MOD weather, proportionally more mesic forest remained unburnt than dry
453 forest (11.2% vs 8.5%), whereas under SEV weather there was no difference between the
454 vegetation types (1.1% vs 1.8%) (Fig. 3a). It was evident from the visual examination of fire
455 severity maps that the underlying effects of vegetation and landscape on fire severity were
456 less influential under SEV than MOD weather (e.g. Fig. 3b). GAMMs testing the effects of
457 environmental variables during SEV fire weather were no better than the null model (Δ AIC

458 <4; Appendix S6), indicating that SPEI and landscape factors were not an important
459 influence on the occurrence of fire refugia during severe - extreme fire weather events.

460 SPEI values were spread across the range of landscape predictor values (i.e. TPI, slope,
461 aspect, TSF and TSH) for MOD fire weather (Appendix S7), indicating that the dataset was
462 suitable for investigating the proposed two-way interactions between landscape factors and
463 SPEI. The full additive model performed substantially better than the null model in both
464 forest types (Table 2). The inclusion of the interaction between SPEI and TSF resulted in
465 substantial improvement ($\Delta AIC = 13.3$) of model performance in dry forest (Table 2). No
466 other interactions led to model improvements in the dry forest type ($\Delta AIC < 4$; Table 2).
467 None of the SPEI by landscape interactions resulted in substantial improvement of model
468 performance in mesic forest ($\Delta AIC < 4$; Table 2).

469 Occurrence of refugia in the dry and mesic forest types showed differences in sensitivity to
470 climate, topography and TSF, as predicted. In mesic forests, fire refugia were significantly
471 influenced ($p < 0.05$) by variables related to moisture availability, including vegetation
472 community, SPEI, TPI and aspect. The probability of the occurrence of refugia decreased
473 with decreasing values of SPEI (Fig. 4a), indicating reduced probability of unburnt forest
474 with increasing drought severity. Refugia were more likely to occur in moist topographic
475 locations including gullies and on lower slopes (i.e. low values of TPI) (Fig. 4b) and on pole-
476 facing aspects (i.e. high values of ASPN) (Fig. 4c). However, their probability of occurrence
477 was generally low (Prob. < 0.10) at low values of SPEI (< -1.5), irrespective of TPI and
478 ASPN (Fig. 5). There were differences in the likelihood of the occurrence of refugia across
479 the vegetation communities within the mesic forest type, whereby their occurrence increased
480 across a gradient of ecosystem moisture availability (i.e. Closed forest $>$ Mist forest $>$ Moist
481 forest) (Fig. 4). TSH had a significant effect on the occurrence of refugia in mesic forests,
482 whereby recently harvested areas (TSH $<$ 30 years) had a higher likelihood of remaining
483 unburnt than long unharvested areas (TSH $>$ 30 years) ($\Delta Prob. \sim 0.08$; Appendix S8). TSF
484 and slope did not affect the occurrence of refugia in mesic forests ($p > 0.05$).

485 Unburnt patches in dry forest were largely insensitive to changes in climate, topography and
486 fuels (Fig. 4). The likelihood of the occurrence of refugia was highest (Prob. = 0.08) in
487 recently burnt areas (TSF $<$ 5 years), decreasing over the first 10 years following fire, before
488 levelling off (Fig. 4d). The effect of TSF was dependent upon SPEI, whereby the influence of
489 recent fire (i.e. TSF $<$ 10 years) decreased as SPEI decreased (Fig. 6), though this effect was

490 small and may not be ecologically meaningful. Recently harvested areas had a slightly higher
491 likelihood ($\Delta\text{Prob.} \sim 0.02$) of remaining unburnt than long unharvested areas (Appendix S8).
492 Topographic variables (TPI, Aspect, Slope) and vegetation community did not affect the
493 occurrence of fire refugia in dry forests ($p > 0.05$).

494 The spatially lagged response variable (SLRV) was highly significant ($p < 0.001$) in GAMMs
495 for both forest types. Occurrence of refugia was greatest when there was predominantly low
496 severity fire in the surrounding landscape (i.e. low values of SLRV).

497 **Discussion**

498 This research provides unique insight into the interactive effects of top-down (i.e. weather,
499 climate) and bottom-up (i.e. landscape) factors on the occurrence of unburnt patches (fire
500 refugia), during wildfire. We assessed the relative influence of fire weather and drought
501 severity on the occurrence of wildfire refugia, through the use of fire severity maps from 18
502 large wildfires and 2 fire complexes, collectively burning over 1.8 million ha in area between
503 2005 and 2016. Top-down factors (i.e. fire weather, drought severity) were of primary
504 importance, with landscape factors such as topography and fuel age having secondary effects.
505 Notably, severe to catastrophic fire weather (i.e. SEV weather) markedly muted the effects of
506 drought and landscape factors on the occurrence of fire refugia, such that unburnt patches
507 were rare ($\sim 1.5\%$ of the landscape); consistent with recent findings from other temperate
508 forest ecosystems (e.g. Krawchuk *et al.*, 2016). These results suggest that projected increases
509 in severe fire weather events (Clarke & Evans, 2018, CSIRO and Bureau of Meteorology,
510 2015) will reduce the influence of landscape factors on the occurrence of unburnt patches
511 within fires, potentially reducing the availability of persistent fire refugia associated with
512 protected topographic locations (i.e. gullies and south-facing slopes in mesic forests; Mackey
513 *et al.*, 2002).

514 Fire weather has an overriding effect on forest fire severity patterns and the pattern of
515 occurrence of fire refugia across a range of ecosystems in Australia (Berry *et al.*, 2015,
516 Clarke *et al.*, 2014, Price & Bradstock, 2012), North America (Krawchuk *et al.*, 2016) and
517 Europe (Román-Cuesta *et al.*, 2009). The absence of clear landscape effects (e.g. topographic
518 position) on the occurrence of unburnt forest under severe to catastrophic fire weather was
519 surprising, as previous research from eucalypt forest ecosystems has consistently found
520 significant effects of topography and fuel age on the occurrence of low-severity understorey

521 fires (including unburnt patches) under these weather conditions (e.g. Bradstock *et al.*, 2010,
522 Clarke *et al.*, 2014, Collins *et al.*, 2014). This suggests that under severe to catastrophic fire
523 weather conditions, landscape factors modify fire behaviour (i.e. fire severity) but do not
524 necessarily inhibit its spread into less flammable parts of the landscape (e.g. deep gullies,
525 closed forests, young fuels). However, under the worst fire weather conditions, such as those
526 experienced during the 2009 Black Saturday fires in Victoria (i.e. temperature > 40°C, RH <
527 10%, wind speed > 50 km h⁻¹), landscape features will have little influence on fire severity
528 patterns in eucalypt forests (Leonard *et al.*, 2014, Price & Bradstock, 2012). It is likely that
529 the extreme drought conditions over much of the study period (Ma *et al.*, 2015) enhanced the
530 effect of fire weather by muting landscape effects on fuel properties (i.e. biomass and
531 connectivity, moisture; see discussion below).

532 Drought severity (i.e. SPEI) had a stronger influence on the occurrence of fire refugia in
533 mesic forests than dry forests, due to the slower rates of fuel desiccation in wetter more
534 productive forests (e.g. Duff *et al.*, 2018). Mesic forests have greater foliage cover (Ellis &
535 Hatton, 2008) relative to dry forests, and are often located in gullies and on poleward-facing
536 aspects (Fig. 2), allowing them to retain higher fuel moisture under most weather conditions
537 (e.g. Slijepcevic *et al.*, 2018). Consequently, the threshold of drying required for a mesic
538 forest to burn is greater than that of a dry forest (Duff *et al.*, 2018, Slijepcevic *et al.*, 2018).
539 Drought severity experienced during the study wildfires typically exceeded the drying
540 threshold for dry forests, due to the intense drought conditions over much of the study period
541 (Ma *et al.*, 2015). The threshold of drying for wetter forest types (e.g. tall-open mist forest
542 and closed forest) appears to fall within our sampling range (e.g. SPEI = ~ -1) (Fig. 4), which
543 would explain why there was a greater effect of SPEI on the occurrence of unburnt patches in
544 the mesic forest types.

545 Topographic variables (TPI, slope, aspect) had a greater effect on fire refugia in mesic forests
546 than dry forest (Fig. 4), likely due to differences between forest types in the desiccation rate
547 of fine fuels. Slijepcevic *et al.* (2018) found that during dry summer and autumn periods,
548 differences in moisture of surface litter fuels across topographic gradients (position and
549 aspect) were more evident in mesic than dry eucalypt forests. Sampling bias towards drought
550 conditions may have inhibited our ability to detect significant interactions between
551 topographic variables and SPEI in dry forest, as SPEI levels may have already exceeded the
552 threshold at which fuels in moist topographic locations in these forest types become

553 'flammable' (Caccamo *et al.*, 2012, Slijepcevic *et al.*, 2018, Stambaugh *et al.*, 2007).
554 However, as mesic eucalypt forests typically burn only during very dry conditions (Duff *et*
555 *al.*, 2018), sampling bias is not likely to have been an issue.

556 Time since previous fire had differential effects on fire refugia across forest types and the
557 gradient of drought severity. In dry forests, the likelihood of the occurrence of fire refugia
558 was greatest in young sites (<5 years since fire), decreasing rapidly over the first decade
559 following fire, likely due to rapid regeneration of vegetation (Caccamo *et al.*, 2014, Haslem
560 *et al.*, 2016) and accumulation of fuels (Thomas *et al.*, 2014). Dry forests are considered fuel
561 limited in relation to fire in the early stages of regeneration, with fuel moisture becoming the
562 limiting factor as surface fine fuels re-accumulate and shrubs regenerate (Bradstock, 2010).
563 We found a weak trend that suggests that under intense drought (e.g. SPEI < -1.5), the
564 limiting effect of recent fire in dry forest lessened. Drought increases the rate of canopy
565 litterfall and the curing of herbaceous plants in eucalypt forests and woodlands (Collins *et al.*,
566 2018a, Duursma *et al.*, 2016, Pook, 1986), which may provide an input of fine fuel sufficient
567 to mitigate the effects of recent fire. There was no effect of time since fire on the occurrence
568 of unburnt patches in mesic forests, which suggests fuel does not limit fire occurrence in
569 these forests. The fuel hazard in mesic forests is often high soon after fire (< 10 years), thus
570 fire behaviour is limited by fuel moisture rather than fuel age (Cawson *et al.*, 2018, Huston,
571 2003, McColl-Gausden & Penman, 2019).

572 Unburnt patches within fire scars are considered important in facilitating the survival,
573 persistence and recolonisation of a range of plants and animals (e.g. Banks *et al.*, 2017,
574 Landesmann & Morales, 2018, Robinson *et al.*, 2014). However, the definition of what
575 constitutes fire refugia is scale- and context- dependent (see Robinson *et al.*, 2013), hence our
576 analysis will undoubtedly underestimate the availability of fire refugia. For example, patches
577 affected by low severity (understorey) fire may provide refugial habitat for arboreal species
578 that require unburnt canopy foliage for persistence (e.g. the greater glider, *Petauroides*
579 *volans*) (Chia *et al.*, 2015). Furthermore, low severity fires often include small unburnt
580 patches at the sub-Landsat pixel scale (McCarthy *et al.*, 2017, Penman *et al.*, 2007), that may
581 be sufficient to facilitate the survival and persistence of fire-sensitive plants and animals
582 (Banks *et al.*, 2011, Ooi *et al.*, 2006, Whelan *et al.*, 2002). Landscape features that are not
583 flammable, such as rock outcrops, can also provide a 'permanent' source of fire refugia for
584 some species (Bradstock *et al.*, 2005).

586 Research on the effect of a changing climate on spatial patterns in forest fire severity and fire
587 refugia has predominantly occurred in the western regions of North America (e.g. Meddens *et al.*
588 *et al.*, 2018a, Reilly *et al.*, 2017). Despite temporal trends of increasing fire size and occurrence,
589 driven by greater fuel aridity (Abatzoglou & Williams, 2016), analysis of Landsat-derived
590 fire severity maps have shown no concurrent reduction in the proportion of the unburnt area
591 within fire perimeters in recent decades (Kolden *et al.*, 2015b, Meddens *et al.*, 2018a).
592 However, detection of temporal trends in fire severity patterns using Landsat-derived fire
593 history databases is problematic at present, as the decadal time scale over which fires are
594 recorded (i.e. 1980s - present; Kolden *et al.*, 2015b) are equivalent to, or shorter than, fire
595 return intervals in many ecosystems (i.e. decades to centuries; Agee, 1993, Murphy *et al.*,
596 2013). Modelling approaches incorporating climatic variables have found weak but
597 significant negative relationships between the availability of unburnt patches and increasing
598 summer drought in North American forests (Kolden *et al.*, 2015a), which is consistent with
599 the findings of our study.

600 Persistent fire refugia are associated with parts of the landscape that, over the long-term,
601 experience longer fire-return intervals, or reduced fire severity, than the surrounding matrix
602 (Robinson *et al.*, 2013). Topographic fire refugia are important for fire-sensitive vegetation
603 communities and biota in temperate forests of southern Australia (Collins *et al.*, 2012,
604 Mackey *et al.*, 2002, Wood *et al.*, 2011) and more broadly across the globe (e.g. Camp *et al.*,
605 1997). For example, in Australia, closed forest and mist forest communities, which support a
606 range of fire-sensitive plants (e.g. *Nothofagus cunninghamii*, *Eucalyptus regnans*) and
607 animals (e.g. *Gymnobelideus leadbeateri*), often persist in deeply incised gullies and
608 poleward-facing slopes within a landscape of fire-prone dry eucalypt forest (Mackey *et al.*,
609 2002, Wood *et al.*, 2011). However, under conditions of intense drought and severe fire
610 weather, fires have a high likelihood of encroaching into these areas (Fig. 5). Projected
611 increases in drought frequency (CSIRO and Bureau of Meteorology, 2015, IPCC, 2014) and
612 severity of fire weather (Bedia *et al.*, 2014, Clarke & Evans, 2018), are likely to shorten fire-
613 return intervals in topographic fire refugia. Consequently, we anticipate that a reduction in
614 the number and extent of such persistent refugia is likely across temperate regions of southern
615 Australia under a drier and warmer climate.

616 Targeted efforts to protect persistent fire refugia may be required in the future in order to
617 preserve the value of these ecologically important landscape features (Meddens *et al.*,
618 2018b). Could fuel management be used to protect persistent fire refugia from the effects of
619 wildfire (Morelli *et al.*, 2016)? Prescribed burning is routinely used to reduce wildfire risk for
620 built assets at the wildland-urban interface: it reduces fuels and thereby increases the
621 likelihood of wildfire suppression (Fernandes & Botelho, 2003, Penman *et al.*, 2011). Our
622 results suggest there is scope to use prescribed burning in dry eucalypt forests to reduce fuel
623 hazard and stop fires before they reach adjacent refugial habitats (Fig. 6); but this may be
624 limited for two main reasons. First, persistent refugia are likely to burn only under extreme
625 drought and fire weather conditions, when fuel age has little effect on fire spread in dry forest
626 communities. Second, regular application of prescribed burning (e.g. 5 year intervals) would
627 be required to achieve effective fuel reduction (Penman *et al.*, 2011). The shortening of inter-
628 fire intervals can have negative effects on habitat components, biota and carbon stocks in
629 eucalypt forests (Collins *et al.*, 2019, Collins *et al.*, 2012, Gill & Catling, 2002). Further
630 work is required to evaluate the relative ecological benefits of protecting refugia by regular
631 prescribed burning compared with the potential ecological and financial costs of an
632 increasing fire frequency across landscapes.

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639

640 **References**

641 Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire
642 across western US forests. *Proceedings of the National Academy of Sciences*, **113**,
643 11770-11775.

644 Agee JK (1993) *Fire Ecology of Pacific Northwest Forests*, Island Press, Washington.

- 645 Archibald S, Lehmann CER, Gómez-Dans JL, Bradstock RA (2013) Defining pyromes and
646 global syndromes of fire regimes. *Proceedings of the National Academy of Sciences*,
647 **110**, 6442-6447.
- 648 Banks SC, Dujardin M, McBurney L, Blair D, Barker M, Lindenmayer DB (2011) Starting
649 points for small mammal population recovery after wildfire: recolonisation or residual
650 populations? *Oikos*, **120**, 26-37.
- 651 Banks SC, McBurney L, Blair D, Davies ID, Lindenmayer DB (2017) Where do animals
652 come from during post-fire population recovery? Implications for ecological and
653 genetic patterns in post-fire landscapes. *Ecography*, **40**, 1325-1338.
- 654 Barbero R, Abatzoglou JT, Steel EA, K Larkin N (2014) Modeling very large-fire
655 occurrences over the continental United States from weather and climate forcing.
656 *Environmental Research Letters*, **9**, 124009.
- 657 Bedia J, Herrera S, Camia A, Moreno JM, Gutiérrez JM (2014) Forest fire danger projections
658 in the Mediterranean using ENSEMBLES regional climate change scenarios. *Climatic*
659 *Change*, **122**, 185-199.
- 660 Beguería S, Vicente-Serrano SM (2017) SPEI: Calculation of the Standardised Precipitation-
661 Evapotranspiration Index. R package version 1.7. [https://CRAN.R-](https://CRAN.R-project.org/package=SPEI)
662 [project.org/package=SPEI](https://CRAN.R-project.org/package=SPEI).
- 663 Bennett LT, Bruce MJ, Machunter J, Kohout M, Krishnaraj SJ, Aponte C (2017) Assessing
664 fire impacts on the carbon stability of fire-tolerant forests. *Ecological Applications*,
665 **27**, 2497-2513.
- 666 Berry LE, Driscoll DA, Stein JA, Blanchard W, Banks SC, Bradstock RA, Lindenmayer DB
667 (2015) Identifying the location of fire refuges in wet forest ecosystems. *Ecological*
668 *Applications*, **25**, 2337-2348.

- 669 Bowman DMJS, Balch JK, Artaxo P *et al.* (2009) Fire in the Earth System. *Science*, **324**,
670 481-484.
- 671 Bradstock RA (2010) A biogeographic model of fire regimes in Australia: current and future
672 implications. *Global Ecology and Biogeography*, **19**, 145-158.
- 673 Bradstock RA, Bedward M, Gill AM, Cohn JS (2005) Which mosaic? A landscape ecological
674 approach for evaluating interactions between fire regimes, habitat and animals.
675 *Wildlife Research*, **32**, 409-423.
- 676 Bradstock RA, Cohn JS, Gill AM, Bedward M, Lucas C (2009) Prediction of the probability
677 of large fires in the Sydney region of south-eastern Australia using fire weather.
678 *International Journal of Wildland Fire*, **18**, 932-943.
- 679 Bradstock RA, Gill AM, Williams RJ (2012) *Flammable Australia: Fire Regimes,*
680 *Biodiversity and Ecosystems in a Changing World*, Collingwood, VIC, CSIRO
681 Publishing.
- 682 Bradstock RA, Hammill KA, Collins L, Price O (2010) Effects of weather, fuel and terrain on
683 fire severity in topographically diverse landscapes of south-eastern Australia.
684 *Landscape Ecology*, **25**, 607–619.
- 685 Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical*
686 *Information-theoretic Approach*, Springer, New York.
- 687 Caccamo G, Bradstock R, Collins L, Penman T, Watson P (2014) Using MODIS data to
688 analyse post-fire vegetation recovery in Australian eucalypt forests. *Journal of Spatial*
689 *Science*, 1-12.
- 690 Caccamo G, Chisholm LA, Bradstock RA, Puotinen ML (2012) Using remotely-sensed fuel
691 connectivity patterns as a tool for fire danger monitoring. *Geophys. Res. Lett.*, **39**,
692 L01302.

- 693 Camp A, Oliver C, Hessburg P, Everett R (1997) Predicting late-successional fire refugia pre-
694 dating European settlement in the Wenatchee Mountains. *Forest Ecology and*
695 *Management*, **95**, 63-77.
- 696 Catchpole W (2002) Fire properties and burn patterns in heterogeneous landscapes. In:
697 *Flammable Australia: Fire Regimes and Biodiversity of a Continent*. (eds Bradstock
698 RA, Williams JE, Gill AM) pp 49-75. Cambridge, Cambridge University Press.
- 699 Cawson JG, Duff TJ, Swan MH, Penman TD (2018) Wildfire in wet sclerophyll forests: the
700 interplay between disturbances and fuel dynamics. *Ecosphere*, **9**, e02211.
- 701 Cheal D (2010) *Growth stages and tolerable fire intervals for Victoria's native vegetation*
702 *data sets: Fire and adaptive management Report No. 84.*, East Melbourne, Victoria,
703 Department of Sustainability and Environment.
- 704 Cheney NP, Gould JS, McCaw WL, Anderson WR (2012) Predicting fire behaviour in dry
705 eucalypt forest in southern Australia. *Forest Ecology and Management*, **280**, 120-131.
- 706 Chia EK, Bassett M, Nimmo DG, Leonard SWJ, Ritchie EG, Clarke MF, Bennett AF (2015)
707 Fire severity and fire-induced landscape heterogeneity affect arboreal mammals in
708 fire-prone forests. *Ecosphere*, **6**, 1-14.
- 709 Clarke H, Evans JP (2018) Exploring the future change space for fire weather in southeast
710 Australia. *Theoretical and Applied Climatology*, 1-13.
- 711 Clarke PJ, Knox KJE, Bradstock RA, Munoz-Robles C, Kumar L (2014) Vegetation, terrain
712 and fire history shape the impact of extreme weather on fire severity and ecosystem
713 response. *Journal of Vegetation Science*, **25**, 1033-1044.
- 714 Collins BM, Kelly M, van Wagtenonk JW, Stephens SL (2007) Spatial patterns of large
715 natural fires in Sierra Nevada wilderness areas. *Landscape Ecology*, **22**, 545-557.

- 716 Collins L, Bradstock R, Ximenes F, Horsey B, Sawyer R, Penman T (2019) Aboveground
717 forest carbon shows different responses to fire frequency in harvested and
718 unharvested forests. *Ecological Applications*, **29**, e01815.
- 719 Collins L, Bradstock RA, Penman TD (2014) Can precipitation influence landscape controls
720 on wildfire severity? A case study within temperate eucalypt forests of south-eastern
721 Australia. *International Journal of Wildland Fire*, **23**, 9-20.
- 722 Collins L, Bradstock RA, Resco de Dios V, Duursma RA, Velasco S, Boer MM (2018a)
723 Understorey productivity in temperate grassy woodland responds to soil water
724 availability but not to elevated [CO₂]. *Global Change Biology*, **24**, 2366–2376.
- 725 Collins L, Bradstock RA, Tasker EM, Whelan RJ (2012) Can gullies preserve complex forest
726 structure in frequently burnt landscapes? *Biological Conservation*, **153**, 177-186.
- 727 Collins L, Griffioen P, Newell G, Mellor A (2018b) The utility of Random Forests for
728 wildfire severity mapping. *Remote Sensing of Environment*, **216**, 374-384.
- 729 CSIRO and Bureau of Meteorology (2015) *Climate Change in Australia Information for*
730 *Australia's Natural Resource Management Regions: Technical Report*, Australia,
731 CSIRO and Bureau of Meteorology,.
- 732 Doerr SH, Shakesby RA, Blake WH, Chafer CJ, Humphreys GS, Wallbrink PJ (2006) Effects
733 of differing wildfire severities on soil wettability and implications for hydrological
734 responses. *Journal of Hydrology*, **319**, 295–311.
- 735 Duff TJ, Cawson JG, Harris S (2018) Dryness thresholds for fire occurrence vary by forest
736 type along an aridity gradient: evidence from Southern Australia. *Landscape Ecology*,
737 **33**, 1369–1383.
- 738 Duursma RA, Gimeno TE, Boer MM, Crous KY, Tjoelker MG, Ellsworth DS (2016) Canopy
739 leaf area of a mature evergreen Eucalyptus woodland does not respond to elevated

740 atmospheric [CO₂] but tracks water availability. *Global Change Biology*, **22**, 1666-
741 1676.

742 Ellis TW, Hatton TJ (2008) Relating leaf area index of natural eucalypt vegetation to climate
743 variables in southern Australia. *Agricultural Water Management*, **95**, 743-747.

744 Fairman TA, Nitschke CR, Bennett LT (2016) Too much, too soon? A review of the effects
745 of increasing wildfire frequency on tree mortality and regeneration in temperate
746 eucalypt forests. *International Journal of Wildland Fire*, **25**, 831-848.

747 Fernandes PM, Botelho HS (2003) A review of prescribed burning effectiveness in fire
748 hazard reduction. *International Journal of Wildland Fire*, **12**, 117-128.

749 Gill AM, Catling PC (2002) Fire regimes and biodiversity of forested landscapes of southern
750 Australia. In: *Flammable Australia: Fire Regimes and Biodiversity of a Continent*.
751 (eds Bradstock RA, Williams JE, Gill AM) pp 351-369. Cambridge, Cambridge
752 University Press.

753 Gill AM, Christian KR, Moore PHR, Forrester RI (1987) Bushfire incidence, fire hazard and
754 fuel reduction burning. *Australian Journal of Ecology*, **12**, 299-306.

755 Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R (2017) Google Earth
756 Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of
757 Environment*, **202**, 18–27.

758 Haining R (2003) *Spatial Data Analysis: Theory and Practice*, Cambridge, Cambridge
759 University Press.

760 Haslem A, Leonard SWJ, Bruce MJ *et al.* (2016) Do multiple fires interact to affect
761 vegetation structure in temperate eucalypt forests? *Ecological Applications*, **26**, 2414-
762 2423.

- 763 Huston M (2003) Understanding the effects of fire and other mortality-causing disturbances
764 on species diversity. In: *Fire in Ecosystems of South-west Western Australia: Impacts
765 and Management*. (eds Abbott I, Burrows N) pp 37-70. Leiden, Backhuys Publishers.
- 766 IPCC (2014) *Climate Change 2014: Mitigation of Climate Change. Contribution of Working
767 Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate
768 Change*, Cambridge, United Kingdom, Cambridge University Press.
- 769 Keeley JE (2009) Fire intensity, fire severity and burn severity: A brief review and suggested
770 usage. *International Journal of Wildland Fire*, **18**, 116-126.
- 771 Kolden CA, Abatzoglou JT, Lutz JA, Cansler CA, Kane JT, Van Wagendonk JW, Key CH
772 (2015a) Climate Contributors to Forest Mosaics: Ecological Persistence Following
773 Wildfire. *Northwest Science*, **89**, 219-238.
- 774 Kolden CA, Smith AMS, Abatzoglou JT (2015b) Limitations and utilisation of Monitoring
775 Trends in Burn Severity products for assessing wildfire severity in the USA.
776 *International Journal of Wildland Fire*, **24**, 1023-1028.
- 777 Krawchuk MA, Haire SL, Coop J, Parisien M-A, Whitman E, Chong G, Miller C (2016)
778 Topographic and fire weather controls of fire refugia in forested ecosystems of
779 northwestern North America. *Ecosphere*, **7**, e01632-n/a.
- 780 Landesmann JB, Morales JM (2018) The importance of fire refugia in the recolonization of a
781 fire-sensitive conifer in northern Patagonia. *Plant Ecology*, **219**, 455-466.
- 782 Leonard SWJ, Bennett AF, Clarke MF (2014) Determinants of the occurrence of unburnt
783 forest patches: Potential biotic refuges within a large, intense wildfire in south-eastern
784 Australia. *Forest Ecology and Management*, **314**, 85-93.

- 785 Littell JS, Peterson DL, Riley KL, Liu Y, Luce CH (2016) A review of the relationships
786 between drought and forest fire in the United States. *Global Change Biology*, **22**,
787 2353-2369.
- 788 Ma X, Huete A, Moran S, Ponce-Campos G, Eamus D (2015) Abrupt shifts in phenology and
789 vegetation productivity under climate extremes. *Journal of Geophysical Research:*
790 *Biogeosciences*, **120**, 2036-2052.
- 791 Mackey B, Lindenmayer D, Gill M, McCarthy M, Lindsay J (2002) *Wildlife, Fire and*
792 *Future Climate: A Forest Ecosystem Analysis*, Collingwood, CSIRO Publishing.
- 793 McCarthy G, Moon K, Smith L (2017) Mapping fire severity and fire extent in forest in
794 Victoria for ecological and fuel outcomes. *Ecological Management & Restoration*, **18**,
795 54-65.
- 796 McColl-Gausden SC, Penman TD (2019) Pathways of change: Predicting the effects of fire
797 on flammability. *Journal of Environmental Management*, **232**, 243-253.
- 798 Meddens AJH, Kolden CA, Lutz JA (2016) Detecting unburned areas within wildfire
799 perimeters using Landsat and ancillary data across the northwestern United States.
800 *Remote Sensing of Environment*, **186**, 275-285.
- 801 Meddens AJH, Kolden CA, Lutz JA, Abatzoglou JT, Hudak AT (2018a) Spatiotemporal
802 patterns of unburned areas within fire perimeters in the northwestern United States
803 from 1984 to 2014. *Ecosphere*, **9**, e02029.
- 804 Meddens AJH, Kolden CA, Lutz JA *et al.* (2018b) Fire Refugia: What Are They, and Why
805 Do They Matter for Global Change? *BioScience*, **68**, 944-954.
- 806 Morelli TL, Daly C, Dobrowski SZ *et al.* (2016) Managing Climate Change Refugia for
807 Climate Adaptation. *PLoS One*, **11**, e0159909.

- 808 Moritz MA, Parisien M-A, Batllori E, Krawchuk MA, Van Dorn J, Ganz DJ, Hayhoe K
809 (2012) Climate change and disruptions to global fire activity. *Ecosphere*, **3**, art49.
- 810 Murphy BP, Bradstock RA, Boer MM *et al.* (2013) Fire regimes of Australia: a
811 pyrogeographic model system. *Journal of Biogeography*, **40**, 1048-1058.
- 812 Nolan RH, Boer MM, Resco de Dios V, Caccamo G, Bradstock RA (2016) Large-scale,
813 dynamic transformations in fuel moisture drive wildfire activity across southeastern
814 Australia. *Geophysical Research Letters*, **43**, 4229-4238.
- 815 Nyman P, Metzen D, Noske PJ, Lane PNJ, Sheridan GJ (2015) Quantifying the effects of
816 topographic aspect on water content and temperature in fine surface fuel. *International*
817 *Journal of Wildland Fire*, **24**, 1129-1142.
- 818 Ooi MKJ, Whelan RJ, Auld TD (2006) Persistence of obligate-seeding species at the
819 population scale: effects of fire intensity, fire patchiness and long fire-free intervals.
820 *International Journal of Wildland Fire*, **15**, 261–269.
- 821 Penman HL (1948) Natural evaporation from open water, bare soil and grass. *Proceedings of*
822 *the Royal Society of London A*, **193**, 120–146.
- 823 Penman TD, Christie FJ, Andersen AN *et al.* (2011) Prescribed burning: how can it work to
824 conserve the things we value? *International Journal of Wildland Fire*, **20**, 721-733.
- 825 Penman TD, Collins L, Price OF, Bradstock RA, Metcalf S, Chong DMO (2013) Examining
826 the relative effects of fire weather, suppression and fuel treatment on fire behaviour –
827 A simulation study. *Journal of Environmental Management*, **131**, 325-333.
- 828 Penman TD, Kavanagh RP, Binns DL, Melick DR (2007) Patchiness of prescribed burns in
829 dry sclerophyll eucalypt forests in south-eastern Australia. *Forest Ecology and*
830 *Management*, **252**, 24–32.

- 831 Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) *nlme: Linear and Nonlinear*
832 *Mixed Effects Models*, R package version 3.1-131, [http://CRAN.R-](http://CRAN.R-project.org/package=nlme)
833 [project.org/package=nlme](http://CRAN.R-project.org/package=nlme).
- 834 Pook E (1986) Canopy dynamics of *Eucalyptus maculata* Hook .IV. Contrasting responses to
835 two severe droughts. Australian Journal of Botany, **34**, 1-14.
- 836 Price OF, Bradstock RA (2010) The effect of fuel age on the spread of fire in sclerophyll
837 forest in the Sydney region of Australia. International Journal of Wildland Fire, **19**,
838 35-45.
- 839 Price OF, Bradstock RA (2012) The efficacy of fuel treatment in mitigating property loss
840 during wildfires: Insights from analysis of the severity of the catastrophic fires in
841 2009 in Victoria, Australia. Journal of Environmental Management, **113**, 146-157.
- 842 Reilly MJ, Dunn CJ, Meigs GW, Spies TA, Kennedy RE, Bailey JD, Briggs K (2017)
843 Contemporary patterns of fire extent and severity in forests of the Pacific Northwest,
844 USA (1985–2010). Ecosphere, **8**, e01695.
- 845 Robinson NM, Leonard SWJ, Bennett AF, Clarke MF (2014) Refuges for birds in fire-prone
846 landscapes: The influence of fire severity and fire history on the distribution of forest
847 birds. Forest Ecology and Management, **318**, 110-121.
- 848 Robinson NM, Leonard SWJ, Ritchie EG *et al.* (2013) REVIEW: Refuges for fauna in fire-
849 prone landscapes: their ecological function and importance. Journal of Applied
850 Ecology, **50**, 1321-1329.
- 851 Román-Cuesta RM, Gracia M, Retana J (2009) Factors influencing the formation of
852 unburned forest islands within the perimeter of a large forest fire. Forest Ecology and
853 Management, **258**, 71-80.

- 854 Ruthrof KX, Fontaine JB, Matusick G, Breshears DD, Law DJ, Powell S, Hardy G (2016)
855 How drought-induced forest die-off alters microclimate and increases fuel loadings
856 and fire potentials. *International Journal of Wildland Fire*, **25**, 819-830.
- 857 Sharples JJ, McRae RHD, Wilkes SR (2012) Wind–terrain effects on the propagation of
858 wildfires in rugged terrain: fire channelling. *International Journal of Wildland Fire*,
859 **21**, 282-296.
- 860 Slijepcevic A, Anderson WR, Matthews S, Anderson DH (2018) An analysis of the effect of
861 aspect and vegetation type on fine fuel moisture content in eucalypt forest.
862 *International Journal of Wildland Fire*, **27**, 190-202.
- 863 Smucker KM, Hutto RL, Steele BM (2005) Changes in bird abundance after wildfire:
864 importance of fire severity and time since fire. *Ecological Applications*, **15**, 1535-
865 1549.
- 866 Stambaugh MC, Guyette RP, Dey DC (2007) *Forest fuels and landscape level fire risk*
867 *assessment of the Ozark Highlands, Missouri*, Knoxville, TN, USDA Forest Service,
868 Southern Research Station.
- 869 Storey M, Price O, Tasker E (2016) The role of weather, past fire and topography in crown
870 fire occurrence in eastern Australia. *International Journal of Wildland Fire*, **25**, 1048-
871 1060.
- 872 Sullivan AL, McCaw WL, Cruz MG, Matthews S, Ellis PF (2012) Fuel, fire weather and fire
873 behaviour in Australian ecosystems. In: *Flammable Australia: Fire Regimes,*
874 *Biodiversity and Ecosystems in a Changing World*. (eds Bradstock RA, Gill AM,
875 Williams RJ). Collingwood, VIC, CSIRO Publishing.
- 876 Thomas PB, Watson PJ, Bradstock RA, Penman TD, Price OF (2014) Modelling surface fine
877 fuel dynamics across climate gradients in eucalypt forests of south-eastern Australia.
878 *Ecography*, **37**, 827-837.

- 879 van der Ploeg T, Austin PC, Steyerberg EW (2014) Modern modelling techniques are data
880 hungry: a simulation study for predicting dichotomous endpoints. *BMC Medical*
881 *Research Methodology*, **14**, 137.
- 882 van Wagner CE (1977) Conditions for the start and spread of crown fire. *Canadian Journal of*
883 *Forest Research*, **7**, 23-34.
- 884 Whelan RJ, Rodgerson L, Dickman CR, Sutherland EF (2002) Critical life cycles of plants
885 and animals: developing a process-based understanding of population changes in fire-
886 prone landscapes. In: *Flammable Australia: The Fire Regimes and Biodiversity of a*
887 *Continent*. (eds Bradstock RA, Williams JE, Gill AM) pp 94–124. Cambridge,
888 Cambridge University Press.
- 889 Wood S, Scheipl F (2016) gamm4: Generalized Additive Mixed Models using 'mgcv' and
890 'lme4'.
- 891 Wood SW, Murphy BP, Bowman DMJS (2011) Firescape ecology: how topography
892 determines the contrasting distribution of fire and rain forest in the south-west of the
893 Tasmanian Wilderness World Heritage Area. *Journal of Biogeography*, **38**, 1807-
894 1820.
- 895 Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed Effects Models and*
896 *Extensions in Ecology with R*, New York, Springer.
- 897 Zylstra P, Bradstock RA, Bedward M *et al.* (2016) Biophysical mechanistic modelling
898 quantifies the effects of plant traits on fire severity: Species, not surface fuel loads,
899 determine flame dimensions in eucalypt forests. *PLoS One*, **11**, e0160715.
- 900 Zylstra PJ (2018) Flammability dynamics in the Australian Alps. *Austral Ecology*, **43**, 578-
901 591.
- 902

904 **Table 1** Climatic and environmental variables considered in the analysis of the occurrence of
 905 fire refugia. Acronyms are provided in parentheses next to the variable name.

Variable	Description
Fire weather (SEV, MOD)	Fire weather was classed as either i) ‘Severe’ (FFDI \geq 49) or ii) ‘Moderate’ (FFDI < 35) fire weather. The range of climatic conditions for these two classes are provided in Appendix S1.
Standardised Precipitation Evapotranspiration Index (SPEI)	Standardised Precipitation Evapotranspiration Index calculated using a 6-month temporal resolution.
Topographic Position Index (TPI)	Topographic Position Index calculated as the difference in elevation between a focal pixel and the mean value of surrounding pixels within a window of 33 x 33 pixels (990 m x 990 m).
Slope	Slope in degrees.
Aspect (ASPN)	Aspect relative to north. Values are on a scale of 0 to 180, with values approaching 0 representing northerly aspects and values approaching 180 representing southerly aspects.
Time since fire (TSF)	Time (years) since the previous fire.
Time since harvesting (TSH)	Time (years) since the most recent timber harvesting event categorised as i) <30 years or ii) \geq 30 years.
Vegetation community (VC)	Five groups based on vegetation structure and site productivity (Ecological Vegetation Divisions are in parentheses; Cheal, 2010): i) Dry open-forests (infertile soils; EVD 3 & 7); ii) Dry open-forest (fertile soils; EVD 8 & 9); iii) Tall-open moist forest (fertile soils; EVD 10 & 11); iv) Tall-open mist forest (fertile soils; EVD 12) and v) Closed forest (fertile soils; EVD 13) (Cheal, 2010).
Forest type (FT)	Forest type grouped as i) Dry Forest or ii) Mesic Forest. Groups were derived based on water availability and the

seasons over which the vegetation communities are potentially flammable (Cheal, 2010). Dry forest included the dry open-forest vegetation communities. Dry forests are flammable from spring to autumn (Cheal, 2010). Mesic forest included Tall-open moist forest, Tall mist forest and Closed-forest vegetation groups. Mesic forest types are generally only flammable in the summer months on high – catastrophic FFDI (Cheal, 2010).

906

907

908 **Table 2** AIC scores for the models considered in the analysis of the occurrence of refugia
 909 during moderate (MOD) fire weather. The ‘Full additive’ model was used as a baseline
 910 (presented in italics) and contains the following variables:

911 SPEI+TPI+slope+ASPN+TSF+TSH+VEG+SLRV. Interactions that led to an AIC point
 912 reduction of ≥ 4 relative to the ‘Full additive’ model were considered meaningful. The
 913 selected model is presented in bold. The NULL model contains only the SLRV. See Table 1
 914 for full names and definitions of each variable.

Dataset	Model	AIC	Δ AIC	Δ AIC
			(Additive model)	(Best model)
Dry forest	<i>Full additive</i>	2971.45	0.00	13.33
	Full additive + SPEI*TSF	2958.13	-13.33	0.00
	Full additive + SPEI* slope	2977.58	6.13	19.46
	Full additive + SPEI* ASPN	2977.58	6.13	19.46
	Full additive + SPEI*TPI	2977.58	6.13	19.46
	Null	3009.27	37.82	51.15
Mesic forest	Full additive	3047.84	0.00	2.00
	Full additive + SPEI*TSF	3045.84	-2.00	0.00
	Full additive + SPEI*ASPN	3045.84	-2.00	0.00
	Full additive + SPEI*TPI	3046.02	-1.82	0.18

Full additive + SPEI*Slope	3046.37	-1.47	0.53
Null	3107.86	60.02	62.02

915

916 **Figure captions**

917 **Figure 1** The study region in Victoria, Australia, showing the location of the wildfires
 918 examined in this study. The fires examined in the study accounted for 81% of the area burnt
 919 within the study period (see inset).

920 **Figure 2** Violin plots depicting the distribution of standardised precipitation
 921 evapotranspiration index (SPEI), topographic position index (TPI), slope, aspect and time
 922 since fire (TSF) sampled for dry and mesic forest. The grey polygons show the probability
 923 distribution of the data, the white point shows the median, the vertical black box shows the 1st
 924 and 3rd quantiles and the vertical lines show ± 1.5 x the interquartile range.

925 **Figure 3** (a) Mean (\pm S.E.) percent of unburnt forest within the burn perimeter for dry and
 926 mesic forest types under ‘severe’ (SEV) and ‘moderate’ (MOD) fire weather; and (b) an
 927 example of observed pattern of unburnt patches for the Goongerah (south) fire in 2014 under
 928 SEV and MOD weather.

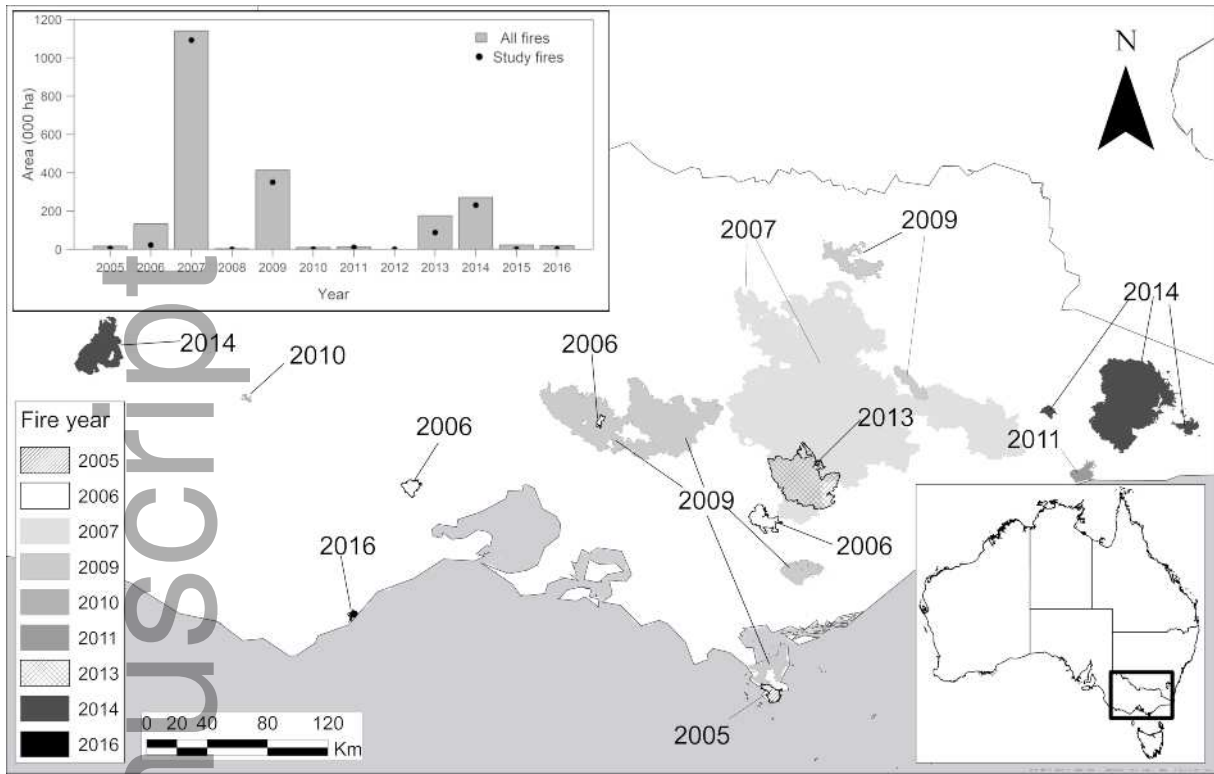
929 **Figure 4** Modelled effects of a) standardised precipitation evapotranspiration index (SPEI),
 930 b) topographic position index (TPI), c) aspect (ASPN) and d) time since fire (TSF) on the
 931 occurrence of fire refugia in dry forest and mesic forests. There were significant differences
 932 between the three mesic forest communities, so each community is plotted separately. Solid
 933 lines are the mean and polygons show the standard error. SPEI was held constant at -0.75 in
 934 plots in which its effect is not depicted. Topographic variables and time since fire (TSF) were
 935 held constant at their mean values in plots where effects are not depicted. Vegetation
 936 community was held constant as Open-forest (fertile soil) for the dry forest type. Time since
 937 harvest (TSH) was held constant at the >30 years category. Predictions for each vegetation
 938 community were capped based on maximum and minimum values in the point dataset,
 939 though plotting regions (x-axis) in b) and d) have been restricted.

940 **Figure 5** The probability of the occurrence of fire refugia in mesic forest (Mist forest) in
 941 response to (a) standardised precipitation evapotranspiration index (SPEI) and topographic

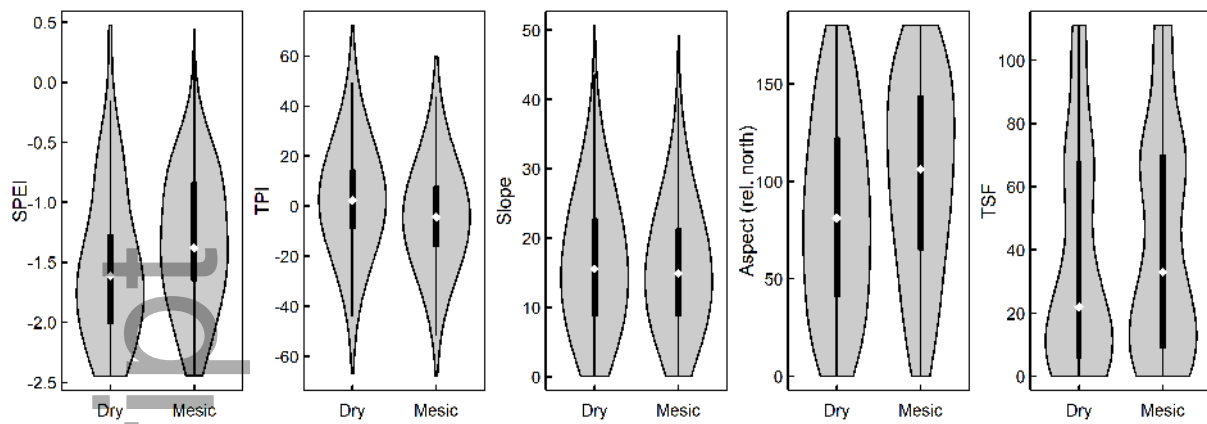
942 position index (TPI) and (b) SPEI and aspect (ASPN). Variables not included in plots were
943 held constant at their mean values, except time since harvest (TSH) which was held constant
944 at the >30 years category.

945 **Figure 6** Interactive effects of time since fire and standardised precipitation
946 evapotranspiration index (SPEI) on the probability of the occurrence of fire refugia in dry
947 forest. Topographic variables were held constant at their mean values, TSH was held constant
948 at the >30 years category and vegetation community was Open-forest (fertile soil).

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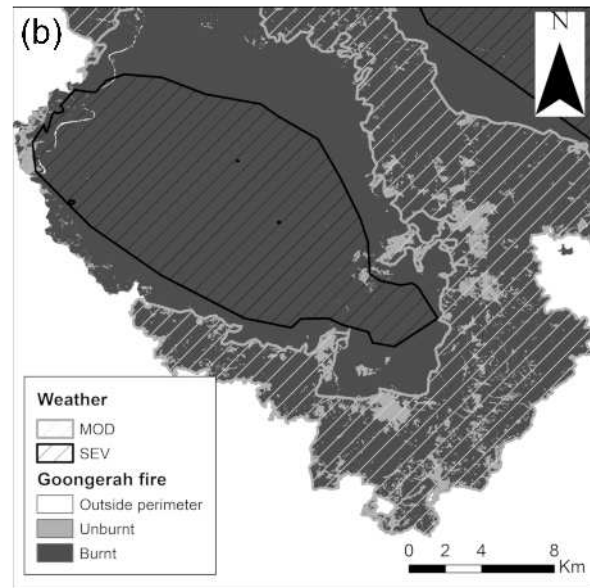
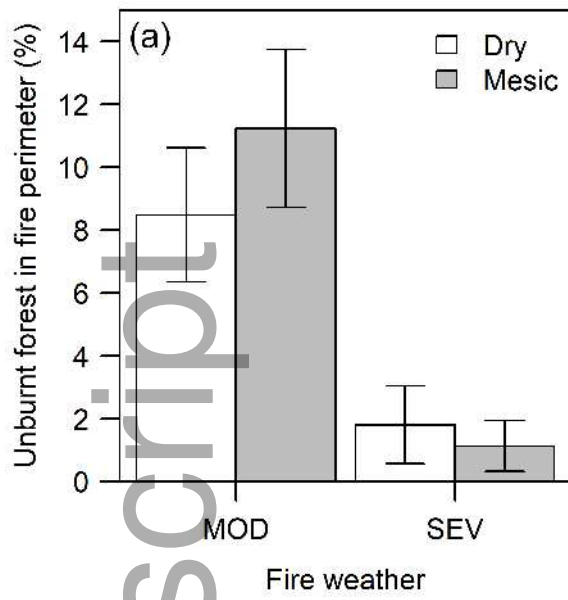


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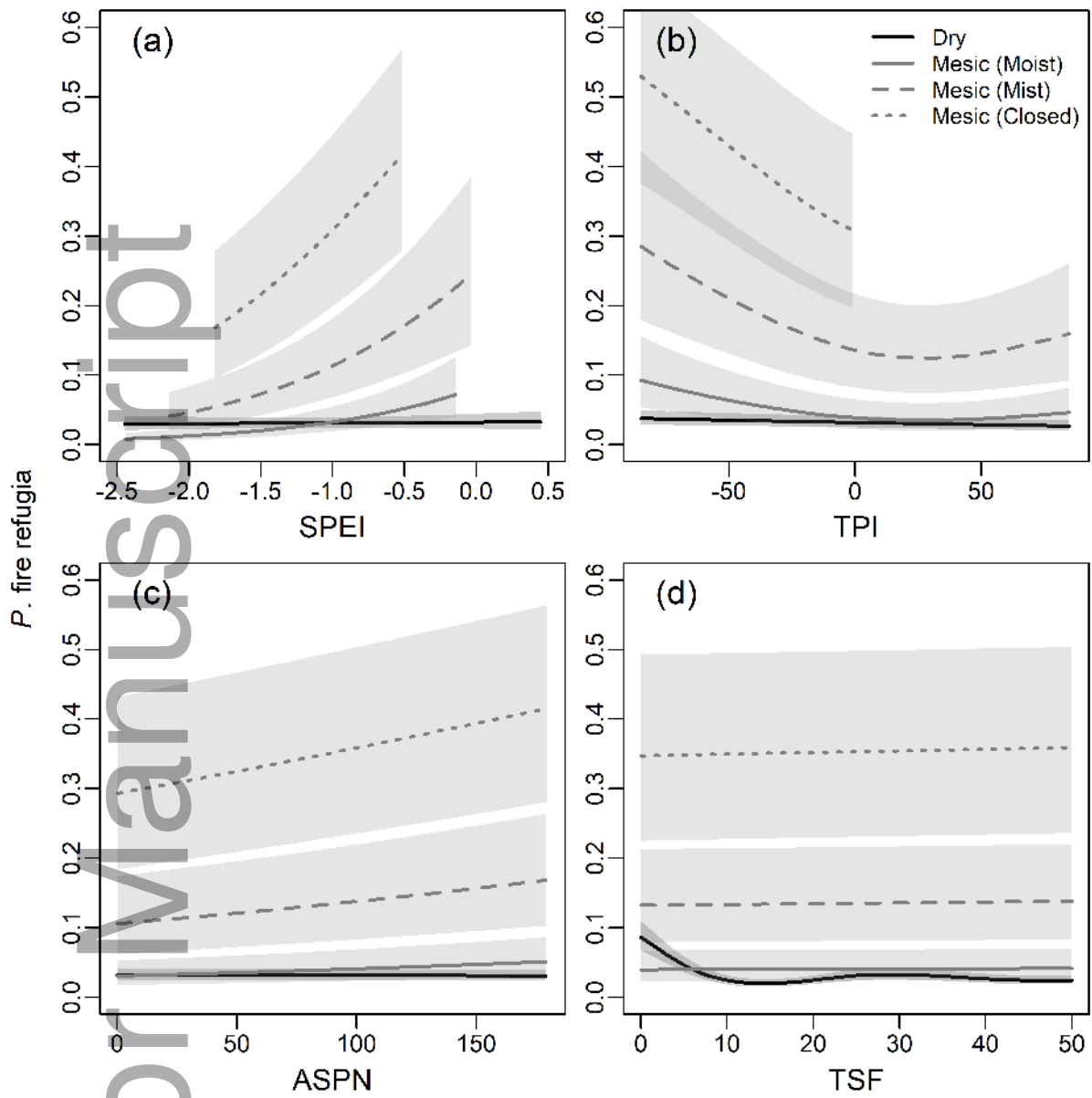
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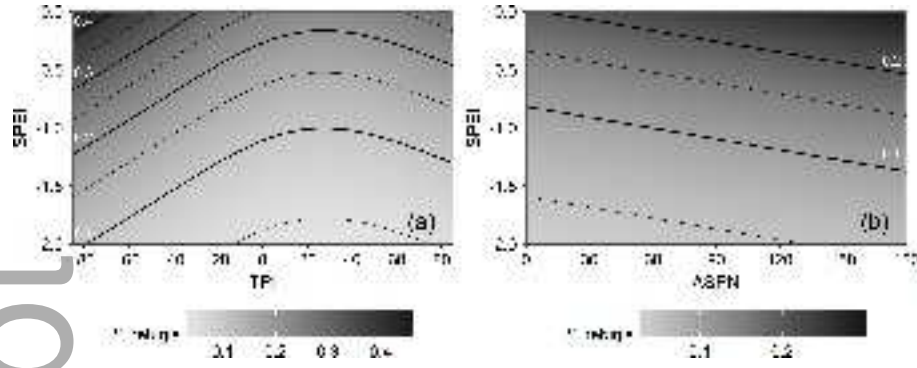


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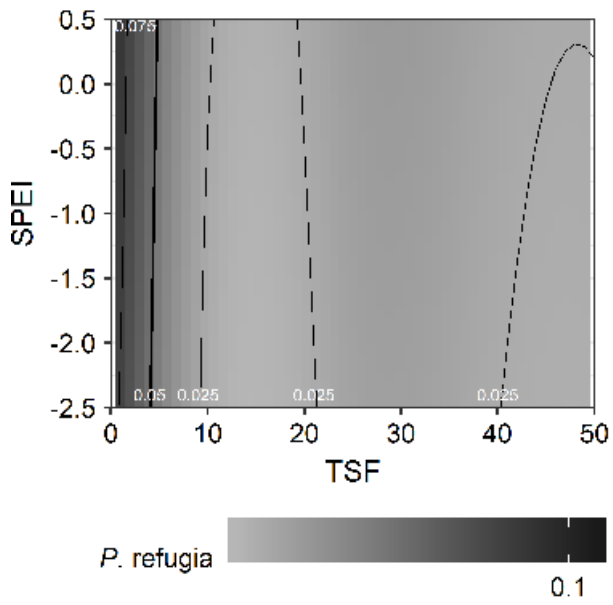
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