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Author/s:

Collins, L;Bennett, AF;Leonard, SWJ;Penman, TD

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DR. LUKE COLLINS (Orcid ID : 0000-0001-8059-0925)

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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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Authors: Collins, L.^{1,2,3}, Bennett, A.F.^{1,2,3}, Leonard, S.W.J.^{1,3,4}, Penman, T.D.⁵

¹ Department of Ecology, Environment & Evolution, La Trobe University, Bundoora, Victoria, Australia 3086

² Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, PO Box 137, Heidelberg, Victoria, Australia 3084

³ Research Centre for Future Landscapes, La Trobe University, Bundoora, Victoria, 3086, Australia

⁴ Natural Values Conservation Branch, Department of Primary Industries, Parks, Water and Environment, GPO Box 44, Hobart Tasmania 7001

⁵ School of Ecosystem and Forest Sciences, University of Melbourne, Creswick, VIC 3363, Australia

Corresponding author: Luke Collins, tel +61 3 9479 3982, email: l.collins3@latrobe.edu.au

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Abstract

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

Introduction

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

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

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

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

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 decreasing fuel mass and continuity (Catchpole, 2002, Fernandes & Botelho, 2003), reducing fire severity and increasing the likelihood of unburnt patches (Bradstock *et al.*, 2010, Collins *et al.*, 2007, Leonard *et al.*, 2014).

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

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

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

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

Materials and Methods

Study area

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

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

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

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

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).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

396

$$SLRV_i = \frac{\sum_j (W_{ij} \times Y_j)}{\sum_j (W_{ij})}$$

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

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

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

Results

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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- 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' ($\text{FFDI} \geq 49$) or ii) 'Moderate' ($\text{FFDI} < 35$) 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) ≥ 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).

Table 2 AIC scores for the models considered in the analysis of the occurrence of refugia during moderate (MOD) fire weather. The ‘Full additive’ model was used as a baseline (presented in italics) and contains the following variables: SPEI+TPI+slope+ASPN+TSF+TSH+VEG+SLRV. Interactions that led to an AIC point reduction of ≥ 4 relative to the ‘Full additive’ model were considered meaningful. The selected model is presented in bold. The NULL model contains only the SLRV. See Table 1 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	<i>Full additive</i>	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

Figure captions

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

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

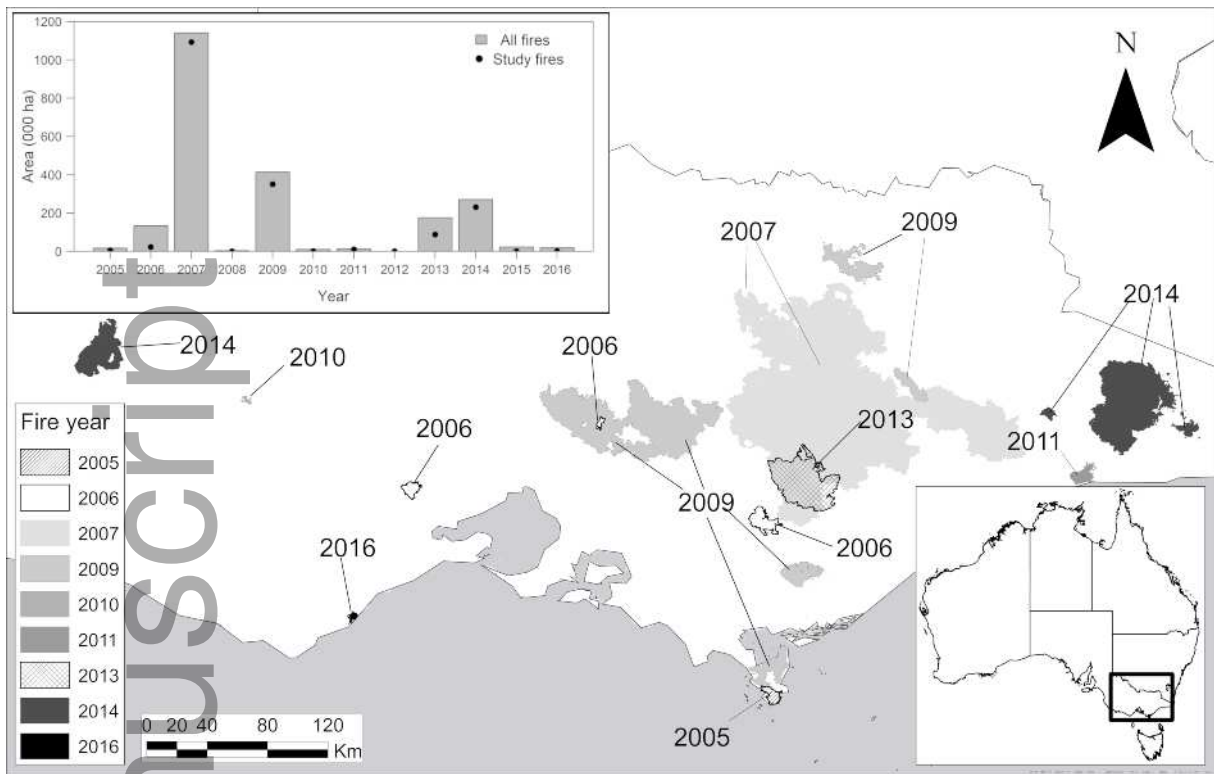
Figure 3 (a) Mean ($\pm$ S.E.) percent of unburnt forest within the burn perimeter for dry and mesic forest types under ‘severe’ (SEV) and ‘moderate’ (MOD) fire weather; and (b) an example of observed pattern of unburnt patches for the Goongerah (south) fire in 2014 under SEV and MOD weather.

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

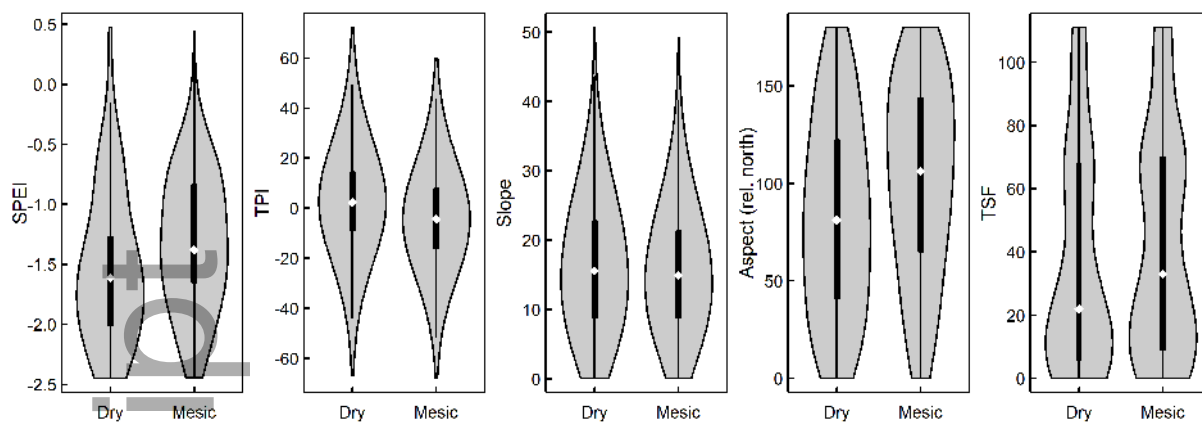
Figure 5 The probability of the occurrence of fire refugia in mesic forest (Mist forest) in response to (a) standardised precipitation evapotranspiration index (SPEI) and topographic

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

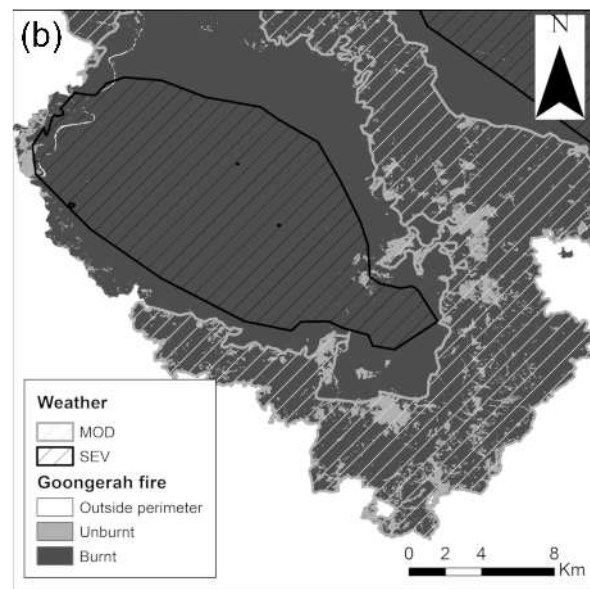
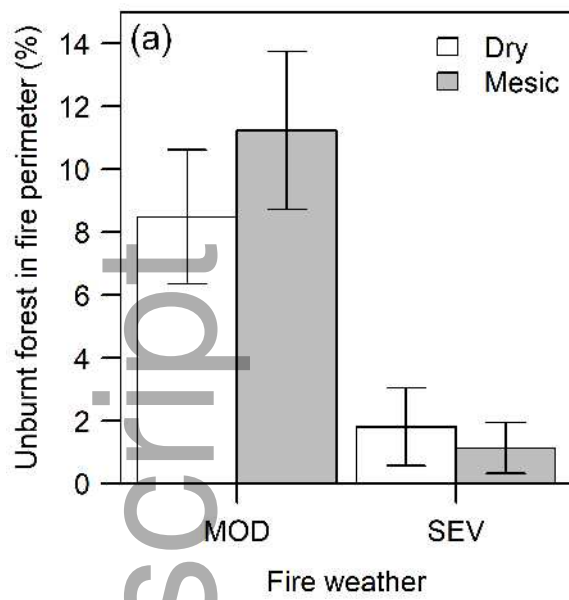
Figure 6 Interactive effects of time since fire and standardised precipitation evapotranspiration index (SPEI) on the probability of the occurrence of fire refugia in dry forest. Topographic variables were held constant at their mean values, TSH was held constant at the >30 years category and vegetation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



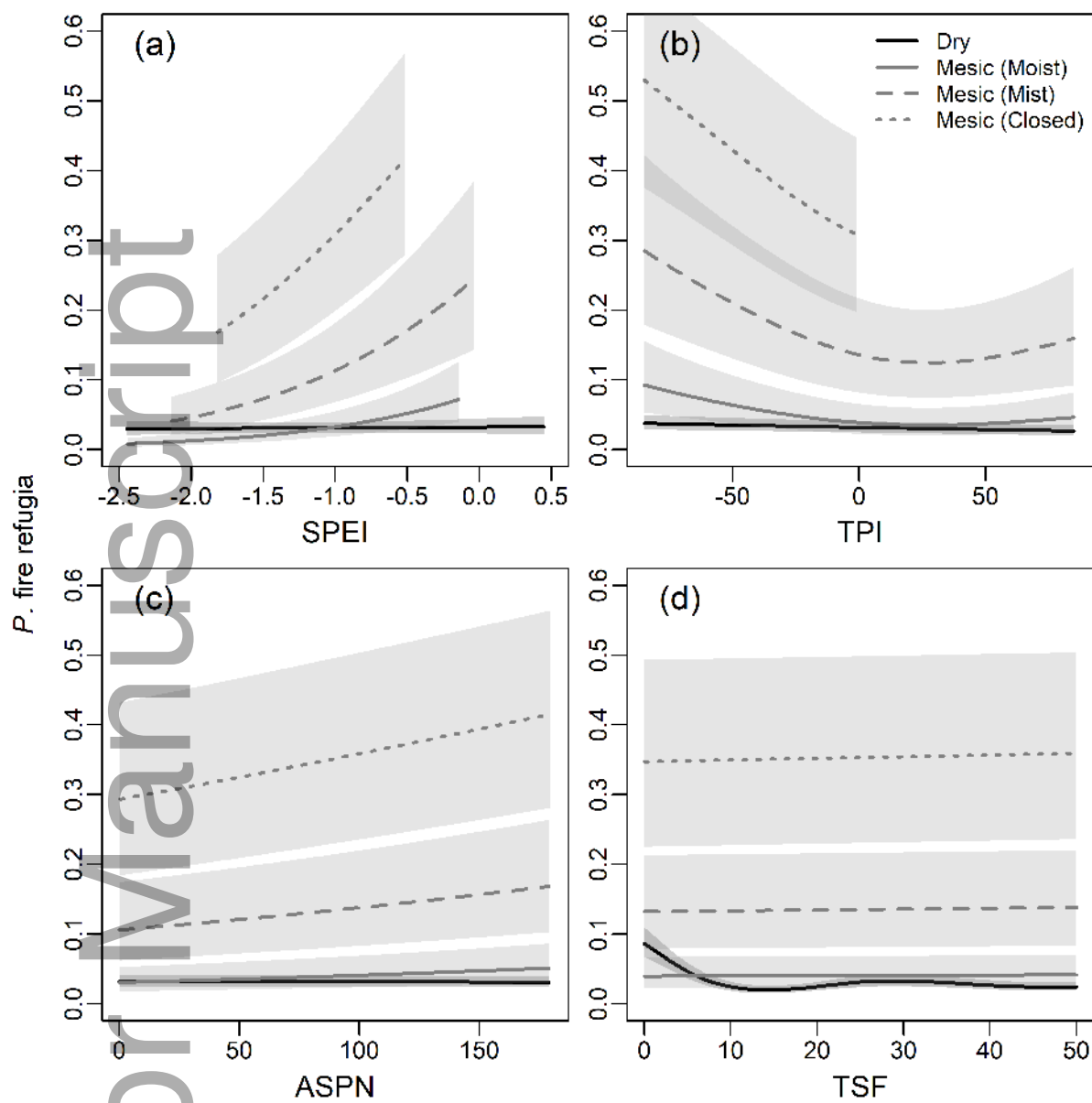
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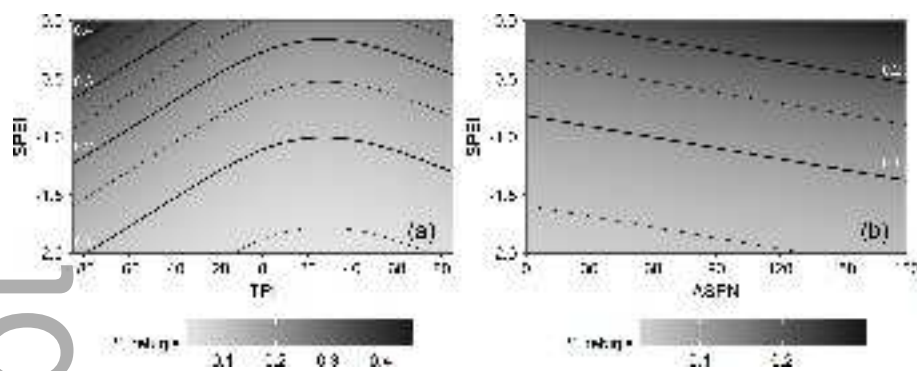
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gcb_14735_f3.tif



gcb_14735_f4.tiff



gcb_14735_f5.tiff

