

Bioclimatic drivers of fire severity across the Australian geographical range of giant *Eucalyptus* forests

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Abstract

1. The relationships between productivity, fire frequency and fire severity shape the distribution of plant communities globally. Dry forests are expected to burn frequently and wet forests to burn infrequently. However, the effect of productivity on intensity and severity of wildfire is less consistent and poorly understood. One productive ecosystem where this is especially true is the Australian tall wet *Eucalyptus*-dominated forest (TWEF), which spans wet areas across the continent. This study aims to characterise how climate shapes the likelihood of low- and high-severity wildfire across Australian TWEF.
2. We performed a continental-scale analysis of fuels in 48 permanent plots in early-mature stage TWEF across four climate regions in Australia. We estimated fuel loads and measured understorey microclimate. We then obtained historical fire-weather observations from nearby meteorological stations and used fuel moisture and fire behaviour equations to predict the historical frequency with which TWEF could burn and what fire severities were expected. We investigated how this varies across the different TWEF climate regions. Lastly, we validated our approach by remeasuring eight plots that burned unexpectedly post-measurement.
3. We found that surface fuels in cooler, moister regions were available to burn 1–16 days per year historically, with only low-severity, surface fire possible most of these days: high-severity fire was only possible under rare, extreme fire-weather conditions. However, in warmer, drier regions, fuels were available to burn 23–35 days annually, and high-severity fire was more likely than low-severity fire. Validation showed that we slightly overestimated flame heights, inflating high-severity risk estimates. If we used elevated fuel loads to predict flame heights, however, high-severity fire was more likely than low-severity fire everywhere. Lastly, the likelihood of high-severity fire increased with increasing temperature and worsening fire weather.
4. *Synthesis.* Fire activity in early-mature TWEF is limited by climatic constraints on fire weather and availability to burn, with high-severity fire more likely in warmer, drier regions than in cooler, wetter ones. This indicates a particularly worrisome vulnerability to climate change, given TWEF's diminished ability to recover from disturbance in a warmer world. The occurrence of both low- and high-severity fire means the fire regimes of TWEF are best described as mixed severity.

KEYWORDS

biogeography, climate change, ecological disturbance, fire ecology, fire severity, macroecology, mixed-severity fires, tall wet *Eucalyptus* forests

1 | INTRODUCTION

A key concept in fire ecology and pyrogeography is the intermediate fire-productivity model, where fire frequency is highest in intermediate-productivity ecosystems (Pausas & Bradstock, 2007; van der Werf et al., 2008). This occurs due to an interaction between climate and resulting productivity: low-productivity ecosystems, such as deserts, are regularly available to burn (i.e. their fuel moisture content is below the point where the fuel becomes combustible) but rarely have enough biomass to do so, whereas productive ecosystems, such as rainforest, have high biomass but are rarely dry enough to ignite (Bradstock, 2010). The middle of the productivity spectrum, however, experiences frequent fire given an intermediate mix of available biomass and relatively frequent fuel dryness (Pausas & Ribeiro, 2013). This relationship between fire frequency and productivity shapes the distribution of rainforest, savanna and desert globally (Bond et al., 2005; Bowman, 2000; Murphy et al., 2013; Pausas & Ribeiro, 2013). Within forest biomes, the driest forests and savannas support the most frequent fire, as these ecosystems occupy the centre of the global productivity spectrum, whereas wetter forests, which are among the most productive ecosystems, experience infrequent fire (Gavin et al., 2003; Knapp & Smith, 2001; Melillo et al., 1993; Pausas & Ribeiro, 2013). In addition to fire frequency, fire severity is a key characteristic of fire regimes within forests (Agee, 1993). Within a vegetation type and growth stage, fire severity (broadly defined as the effect of a fire on vegetation) is generally correlated with intensity (the energy released by a fire; Keeley, 2009). High-severity fire consumes or kills most of an ecosystem's vegetation, whereas low-severity fire typically kills just understorey vegetation, but not the canopy. Often, fire severity and fire frequency are negatively correlated; ecosystems that burn most often, such as savannas, generally do so at low severity (Murphy & Russell-Smith, 2010; Steel et al., 2015), whereas ecosystems that burn infrequently, such as rainforests and high-elevation forests, do so at high severity (Hill, 1982; Schoennagel et al., 2004).

In Australia, *Eucalyptus* forests span the productivity spectrum, with contrasting drivers of fire activity and consequently diverse fire regimes (Keith, 2017; Murphy et al., 2013). Dry *Eucalyptus* forests typically experience fire every 7–15 years (von Platen et al., 2011), and burn with mixed severities (Bradstock et al., 2010), with fire activity being limited by the amount of flammable biomass (Fensham, 1992). However, the drivers of fire frequency and severity are not well understood in the more productive, tall wet *Eucalyptus* forests (TWEF), in which fire is much less frequent, with an expected return interval of 20–100 years or more (Murphy et al., 2013). TWEF occur in wet areas from tropical to temperate regions in Australia (Wardell-Johnson, Neldner, et al., 2017). Commencing from the 'early-mature'

stand-development stage, they have a 'double-canopy' structure, with an extremely tall, 'hyper-emergent' *Eucalyptus* overstorey (up to 100 m) and an understorey composed of broadleaf trees and shrubs, which supports a cool, moist microclimate (Little et al., 2012; Mifsud, 2003; Tng et al., 2013). Overall, tree cover in TWEF can be quite dense, with a total canopy cover of 30%–70% and estimated LAI values of approximately 2–4, though most of this canopy cover is concentrated in the understorey, as the *Eucalyptus* overstorey is relatively open (Hingston et al., 1979; Wardell-Johnson, Neldner, et al., 2017; Woodgate et al., 2015). On the east coast of Australia, these understoreys include many trees and shrubs that are also found in temperate and tropical rainforests, but on the west coast, no rainforest exists (Wardell-Johnson, Neldner, et al., 2017). Mature TWEF are among the most carbon-dense forests on the planet (Keith et al., 2009).

Because of extensive logging over the last 150 years, stands in the 'early-mature' and older stages of TWEF are rare. These mature forests are known to cover 4%–20% of the TWEF range in Victoria and Tasmania; but their extent in the rest of Australia is unknown (Montreal Process Implementation Group for Australia & National Forest Inventory Steering Committee, 2018; Wood et al., 2017). Hence, remaining stands are of high conservation and scientific value (Dean & Wardell-Johnson, 2010; Mifsud, 2003). TWEF have many plant taxa in the understorey that are functionally similar to pyrophobic rainforest species, but the overstorey is composed of *Eucalyptus*, a genus for which fire is an integral part of the life cycle (Burrows, 2013; Crisp et al., 2011). This paradoxical mix of fire-sensitive and fire-adapted species reflects the important, conflicting, roles of high- and low-severity fire in these forests (Ashton, 1981; Bowman, 2000; Tng et al., 2013). Low-severity fire in TWEF kills the understorey but leaves the canopy intact, maintaining structural complexity but creating poor conditions for regeneration of *Eucalyptus* (Ashton, 2000; Benyon & Lane, 2013). On the other hand, high-severity, canopy-defoliating fire plays an important role in TWEF life cycles because *Eucalyptus* trees generally require large canopy openings to regenerate from seed (Ashton, 1981). Critically, without any fire, shade-tolerant rainforest can ultimately replace TWEF through succession (Jackson, 1968). In some TWEF, the dominant eucalypts are post-fire vegetative 'resprouters', that can survive multiple intense fires (Collins, 2020), and hence have a multi-aged structure (Bowman & Kirkpatrick, 1986; Turner et al., 2009). Furthermore, some of these resprouters can regenerate prolifically in the absence of canopy gaps (Wardell-Johnson, 2000). By contrast, other TWEF are dominated by 'obligate seeders', which while technically having the physiological capacity to resprout, generally do not do so after severe fire due to their thin bark and are hence more fire

sensitive (Waters et al., 2010). These obligate seeders produce profuse seedling regeneration post-fire and subsequently are thought to form single-aged stands (Ashton, 1976). However, even in forests dominated by obligate seeders, stands can be multi-aged (Ashton, 2000; Bowman & Kirkpatrick, 1986; Bradshaw & Rayner, 1997; Lindenmayer et al., 2000), which suggests that low-severity fire may not be uncommon. Indeed, the occurrence of low-severity fire is well documented in Queensland, northern New South Wales and Western Australia (Campbell & Clarke, 2006; McCaw et al., 2002; Tng, 2019).

Despite the documented occurrence of low-severity fire in TWEF, such fire has received limited attention, partly due to the fire frequency–severity relationship mentioned above, and partly because of the silvicultural paradigm that intense fire is essential for *Eucalyptus* regeneration (Attwill, 1994). In particular, the relative likelihood of low- and high-severity fire has not been quantified in TWEF. Some studies have quantified area burnt at different fire severities during an individual wildfire (Cruz et al., 2012; Kumar et al., 2008; Ndalila et al., 2018). While these found larger areas had burned at high severity than at low severity in TWEF, they focused on large, high-profile fire events, where low-severity fire was less likely. The focus on high-severity fire also possibly reflects an assumption that because regeneration of this system is usually triggered by high-severity fire, low-severity disturbances are less important (Ashton, 1976). This assumption is operationalised through the near-exclusive use of clearfell-burn-and-sow silviculture (Florence, 2004) in TWEF, where logging is followed by high-intensity burns to stimulate regeneration (Attwill, 1994; Stoneman, 2007). Nonetheless, low-severity fire has been used to reduce fuel loads in some TWEF (McCaw et al., 1996; Tng, 2019) and can create important wildlife habitat (Berry et al., 2016; Lindenmayer et al., 2000). Furthermore, the driving factors behind fire severity in TWEF are not well explored. While fire weather and climate are generally thought to be much more important in determining fire severity than intrinsic factors such as fuel load or arrangement (Bradstock et al., 2010), this has only been investigated in a small subset of TWEF (Bowman et al., 2016), with some authors arguing that disturbance history can still increase the risk of high-severity fire (Taylor et al., 2014). Here, we investigate how climate shapes the likelihood of both high- and low-severity fire in early-mature TWEF. In particular, we ask the following questions: (1) How often are early-mature TWEF fuels dry enough to burn? (2) What is the relative likelihood of low- and high-severity fire? and (3) How does this vary across the continental (and climatic) range of this ecosystem? Answering these questions is important in understanding the range of variability in the fire regime of this ecosystem, thereby informing fire and forest management. Doing so will help illuminate how climate change may alter fire regimes, for example by increasing the likelihood of flames of surface fires reaching the canopy and becoming high-severity fires.

Fire regime studies are particularly problematic in TWEF, as the long fire return interval makes fire-severity data sparse, and the lack of clear annual growth rings precludes dendrochronological studies

of tree ages (Brookhouse, 2006; Pearson & Searson, 2002). Indeed, current fire return intervals are based on expert elicitation rather than empirical data (Murphy et al., 2013). Therefore, to answer our research questions, we undertook a continental-scale modelling analysis of fuels, microclimate and historical climate data using a network of permanent plots: the Terrestrial Ecosystem Research Network (TERN) Ausplots-Forests network (Wood, Prior, et al., 2015). This plot network (hereafter Ausplots) consists of 48 permanent plots across 7 macroecological and 4 climatic regions (defined below). The Ausplots are located in TWEF stands in the 'early-mature' stage of forest stand development. At each of the Ausplots, we measured fuel load and structure. We recorded the understorey microclimate using dataloggers and analysed historical fire-weather observations from nearby meteorological stations to assess how often TWEF has been dry enough to burn over the past 50 years, as explained below. We then combined fuels and climate data to predict the likelihood of low- and high-severity fires on days in which these forests were available to burn. To do this, we used the McArthur fire behaviour equations, which underlie a model routinely used by fire managers in these ecosystems to predict flame height and rate of spread (Cruz et al., 2014; Neale & May, 2018; Noble et al., 1980). We operationally defined low-severity fires as fires that leave the canopy intact, and high-severity fires as those that consume or fully scorch the canopy. Finally, unplanned low-intensity fires occurred after fuel measurement in eight plots spread across the macroecological range of TWEF, and we utilised this opportunity to partially validate our prediction of flame height.

2 | MATERIALS AND METHODS

2.1 | Study system

This study focuses on tall wet *Eucalyptus*-dominated forests (TWEF), defined here as forests that are dominated by eucalypts (*Eucalyptus* spp., *Angophora* spp. and *Corymbia* spp.) that are >30 m in height and have a canopy cover of 30%–70% (Tng et al., 2012; Wardell-Johnson, Neldner, et al., 2017). TWEF occur on moderately fertile soils in high-rainfall areas with mean annual precipitation (MAP) ranging from 900 to 3,500 mm (Tng et al., 2012). They are generally distributed in a discontinuous arc around southern and eastern Australia and represent roughly 4% of the continent's forested landscape. Their climate ranges from tropical in the north east, to temperate-marine in the southeast, to Mediterranean in the southwest (Figure 1; Wood, Prior, et al., 2015).

2.2 | Ausplots Forests Monitoring Network

The TERN Ausplots Forests Monitoring Network consists of 48 1-hectare permanent plots across Australia. These plots are 100 m × 100 m, subdivided into 20 m × 20 m subplots. The network was set up as a nationwide permanent plot network to investigate the

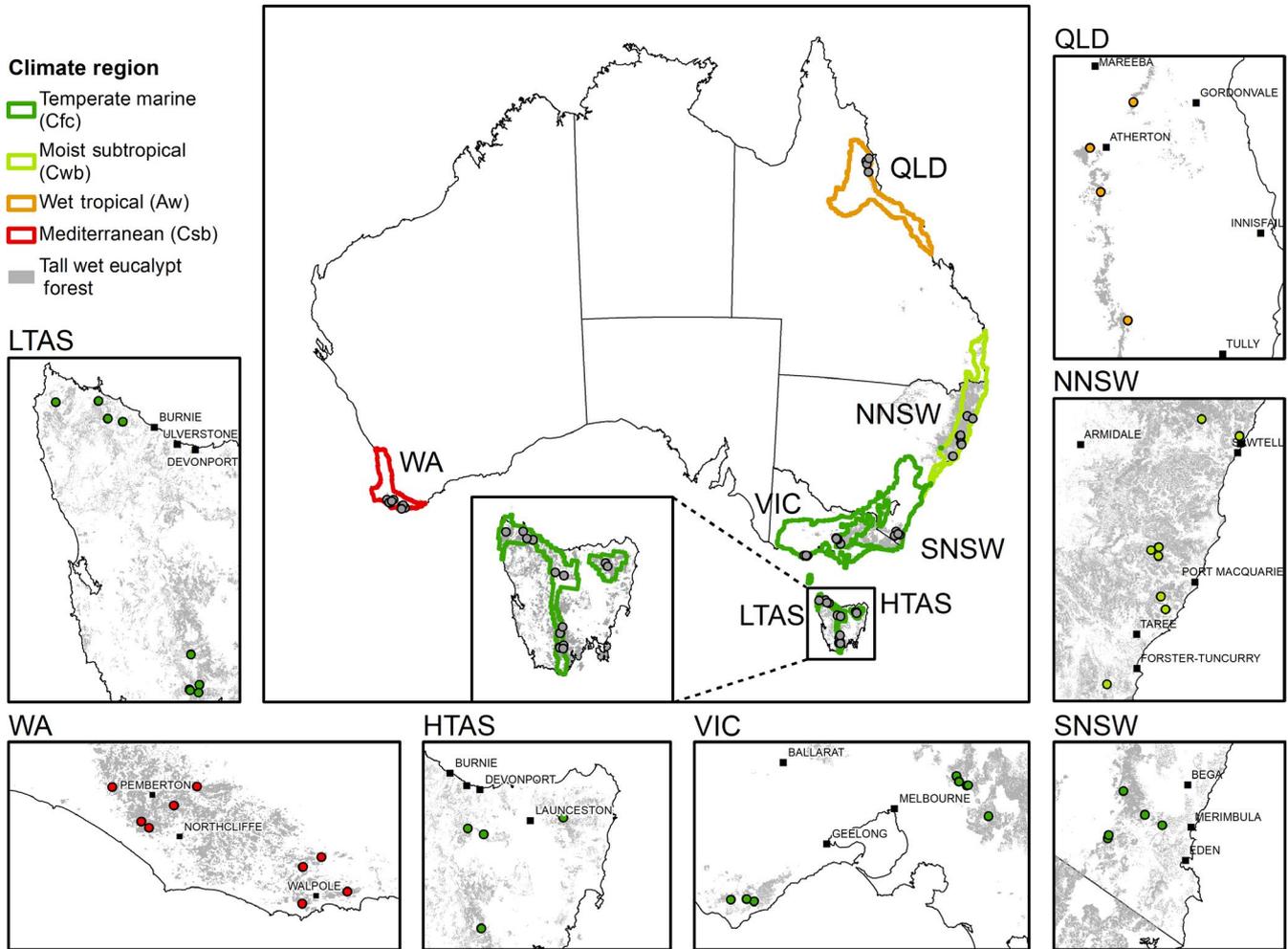


FIGURE 1 Study sites. Map of the locations of the 48 permanent plots in the Terrestrial Ecosystem Research Network Ausplots Forests Monitoring Network. Fire-weather climate regions [as described by Williamson et al. (2016)] are given, and shaded based on their Köppen climate zone as defined by Kottek et al. (2006). Macroecological regions are shown in the insets with corresponding labels in the centre map

macroecological variation in growth dynamics and carbon storage in early-mature TWEF. The plots were originally selected to minimise the variation in stand age, forest type and site-level productivity and hence isolate the effect of climate on these forests. Therefore, forest stands were chosen on productive sites with a single, tall (>45 m) cohort of old, but not senescent, trees in the *Eucalyptus* overstorey. Stands with such characteristics have been defined by Mifsud (2003) as being in the ‘early-mature’ stage of stand development. Where possible, sites were located in forest that established after a known high-severity fire between 1852 and 1939, but in regions which had poorly documented recent fire histories, structurally analogous sites were chosen (Wood, Prior, et al., 2015). Site selection was uninformed by any consideration of fuel loads, which were measured after the plots had been established (Wood et al., 2015). The forests containing the plots can be grouped into seven general macro-ecological regions: North Queensland (QLD), Northern New South Wales (NNSW), Southern New South Wales (SNSW), Victoria (VIC), Southwest Western Australia (WA), High-elevation Tasmania (HTAS) and Low-elevation Tasmania (LTAS; Table 1; Figure 1; Wood,

Prior, et al., 2015). These macro-ecological regions occupy a range of climates, which we describe as temperate-marine (LTAS, HTAS, VIC and SNSW), Mediterranean (WA), moist subtropical (NNSW) and wet tropical (QLD; Hutchinson et al., 2005; Kottek et al., 2006; Wood, Prior, et al., 2015). For more details on the Ausplots Forests Monitoring Network, including detailed site descriptions, see Wood, Stephens, et al. (2015) and Wood, Prior, et al. (2015).

2.3 | Fuels and vegetation sampling protocol

At each plot, to characterise the structure and fuel load of the canopy, we measured the diameter at a breast height of 1.3 m (d_{bh}) of every live stem with $d_{bh} > 10$ cm across the 1-hectare plot and measured the height and height to crown base (HCB) of a representative subsample of all major tree species across their diameter range (see Section 2). To measure smaller trees, shrubs, ferns and tree ferns, we set up a 28.3 m transect between diagonally opposite corners of four 20 m × 20 m subplots. We measured 20 plants along each transect

TABLE 1 Characteristics of plots across the seven macro-ecological regions. Summary of the seven macroecological regions. The number of plots, target species and Köppen climate zone (with its associated code in parentheses), as defined by Kottek et al. (2006), are given. We also list the mean and the range of plot-level means (in parentheses) for selected environmental and structural variables. The maximum height of both eucalypts and non-eucalypts in each region (along with the plot-level range) are also given. Table is adapted from Wood, Prior, et al. (2015)

Region	No. plots	Target species	Köppen climate zone (code)	Elevation (m)	MAT (°C)	MAP (mm)	Canopy cover (%)	Mean height dominants (m)		Maximum height (m)	
								Eucalypt	Non-Euc	Eucalypt	Non-Euc
Northern NSW (NSW)	8	<i>E. pilularis</i> , <i>E. grandis</i>	Moist Subtropical (Cwb)	418 (75–683)	16.3 (15.3–18)	1,533 (1,323–1,895)	70 (48–80)	53 (45–59)	70 (57–77)	31 (19–44)	
Southern NSW (SNSW)	5	<i>E. fastigata</i> , <i>E. obliqua</i>	Temperate-Marine (Cfc)	739 (420–955)	11.3 (10–13.1)	927 (853–1,000)	63 (56–71)	45 (40–50)	56 (49–64)	12 (8–21)	
Victoria (VIC)	8	<i>E. regnans</i>	Temperate-Marine (Cfc)	578 (337–863)	11.1 (10.3–11.7)	1,624 (1,445–1,869)	77 (68–84)	66 (60–74)	82 (72–89)	36 (22–52)	
Far North Queensland (QLD)	4	<i>E. grandis</i>	Wet Tropical (Aw)	1,012 (795–1,148)	19.6 (18.9–20.5)	1,609 (1,376–1,732)	66 (55–78)	36 (28–41)	48 (40–56)	28 (17–46)	
Western Australia (WA)	9	<i>E. diversicolor</i> , <i>E. jacksonii</i>	Mediterranean (Csb)	153 (93–239)	14.8 (14.8–15.3)	1,114 (1,006–1,204)	69 (62–82)	65 (40–65)	64 (53–77)	20 (15–28)	
Low Elevation Tasmania (LTAS)	9	<i>E. obliqua</i> , <i>E. regnans</i>	Temperate-Marine (Cfc)	201 (49–560)	11.1 (9.7–12.4)	1,337 (1,139–1,477)	78 (71–84)	48 (39–54)	61 (57–66)	36 (24–49)	
High-Elevation Tasmania (HTAS)	5	<i>E. delegatensis</i> ^a	Temperate-Marine (Cfc)	797 (691–910)	7.8 (6.6–8.7)	1,424 (1,309–1,723)	73 (72–74)	40 (33–43)	48 (40–52)	29 (23–37)	
Ausplots Network	48	—	—	476 (49–1,148)	13 (6.6–20.5)	1,364 (853–1,895)	71 (48–84)	50 (28–74)	63 (40–89)	28 (8–52)	

^aTasmanian *E. delegatensis* (subsp. *tasmaniensis*) resprouts in response to fire, unlike its Victorian counterpart subsp. *delegatensis*.

using a variable-area rectangular subplot selection procedure (see Supporting information). At two fixed points on each transect, we used a 1 m × 1 m quadrat to destructively sample dead fuels in the surface layer (forest floor) and live fuels in the near-surface layer (all non-woody forbs, graminoids, vines and bryophytes, not including ferns). We did this according to the TERN Ausplots Survey Protocol Manual (Wood et al., 2015) and used these measurements to estimate total biomass as described below. We also placed two Thermochron and one Hygrochron iButton® (Maxim/Dallas Semiconductor Corp.) dataloggers about 0.75 m above the ground in each plot to measure understorey temperature and humidity. The dataloggers took measurements every 4 hr for 1 year between October 2014 and January 2016, with start dates varying based on the original measurement date. We provide a detailed description of the fuel measurement methodology in the Supporting Information.

2.4 | Measurement of burnt plots

Between 2014 and 2019, unexpected low-severity fires burned eight of the 48 plots: two in the wet tropical zone in the late dry season (QLD-LR and QLD-HER), as well as five in the temperate-marine zone (HTAS-McK, LTAS-ARV, LTAS-BT, LTAS-WS and LTAS-WEL) and one in the Mediterranean zone (WA-SUT) in January, peak fire season in southern Australia (Furlaud & Bowman, 2020). Summaries of these fires are presented in Table 2. We returned to these plots approximately 10 months after the fires (or 12 and 24 months for QLD-LR and QLD-HER, respectively) and measured the char height on the stems of trees with non-fibrous bark, a good surrogate for flame height (Alexander & Cruz, 2012). In all cases except WA-SUT, this involved measuring charring on only the non-eucalypts in the mid-storey (i.e. >10 cm d_{bh}). In WA-SUT, all mid-storey trees were of the genera *Eucalyptus* or *Corymbia*, both eucalypts, so we measured charring on the tessellated bark of *C. calophylla* in the mid-storey. In all plots, we measured charring on all relevant trees within 15 m or 17 m of each transect, or within the subplot containing each transect, depending on the density of stems.

2.5 | Data analysis

2.5.1 | Fuel loads

We estimated the mass (i.e. fuel load in t/ha) of dead fine fuels (namely, leaves, branches and stems <0.6 cm in diameter) in the surface layer, and of living fuels in the near-surface layer, directly from their corresponding masses in the quadrats. We estimated the biomass of live fine fuels (leaves and twigs <1.5 cm diameter) in the 20 smaller plants we had measured for our fire-severity analysis, along with that of the large (>10 cm d_{bh}) trees and shrubs for descriptive purposes only, using allometric equations. In all, 12 equations, one for each of the 12 growth form classes recorded in the plots, were used to predict an individual's biomass from its d_{bh} , basal diameter (d_{10}), and/or height (ht ; Table S1). We utilised published equations where available, and developed our own equations for tree ferns and understorey trees from published data (see Table S1; Beets et al., 2012; Falster et al., 2015; Fedrigo et al., 2014; Kieth et al., 2000; Paul & Roxburgh, 2017; Paul et al., 2016).

For subsequent analyses, we divided the fuels into four categories: surface fuels, elevated layer, sub-canopy and canopy, as follows. We combined fuel load estimates from the surface and near-surface layers, along with from ground ferns measured along the transect, into a single mass, referred to as the 'surface fuels', as these fuel components usually burn together (Hines et al., 2010). We considered all other small plants measured along the fuel transects to compose an 'elevated layer'. We lastly divided the large overstorey plants (i.e. ≥10 cm d_{bh}) into a 'canopy' (trees from the genera *Eucalyptus* and *Corymbia*) and a 'sub-canopy' (all other species), to reflect the double-canopy structure of these forests (Tng et al., 2012). The elevated layer and sub-canopy together form what is commonly referred to as either the live understorey or ladder fuels, but we considered these two layers separately to account for their different roles in driving fire behaviour (Cruz et al., 2003; Hines et al., 2010). We calculated fine fuel loads for each of these layers. To represent vertical connectivity, we calculated the combined gap height between

TABLE 2 Summaries of eight low- to moderate-severity fires in measured plots. Summary of the fires that burned eight plots after initial measurement. We give the potential date range during which the plots could have burned and the corresponding range in McArthur Forest Fire Danger Index (FFDI) values on those dates. The enclosing climate zone of each plot is also listed, along with whether it was burned by a wildfire or prescribed burn

Plot name	Climate zone	Fire type	Potential burn date range (local time)	Potential FFDI range
HTAS-McK	Temperate-Marine (Cf)	Wildfire	23/01/2016 13:57–24/01/2016 15:20	1–6
LTAS-ARV	Temperate-Marine (Cf)	Wildfire	21/01/2019 15:34–22/01/2019 15:05	1–16
LTAS-BT	Temperate-Marine (Cf)	Wildfire	24/01/2019 17:00–28/01/2019 17:30	1–15
LTAS-WEL	Temperate-Marine (Cf)	Wildfire	26/01/2019 15:31–27/01/2019 15:12	1–12
LTAS-WS	Temperate-Marine (Cf)	Wildfire	28/01/2019 9:00–28/01/2019 17:30	4–7
QLD-LR	Wet Tropical (Aw)	Prescribed Burn	28/10/2014 9:00–28/10/2014 18:00	3–20
QLD-HER	Wet Tropical (Aw)	Prescribed Burn	11/08/2015 0:00–13/08/2015 20:00	1–15
WA-SUT	Mediterranean (Csb)	Prescribed Burn	20/01/2017 9:00–20/01/2017 18:00	1–6

layers, namely the sum of the distance between the mean elevated plant height and mean sub-canopy HCB, and the distance between the mean sub-canopy top height and the mean canopy HCB. For a more detailed description of measurement methods, see the TERN Ausplots Survey Protocol Manual (Wood et al., 2015).

2.5.2 | Prediction of historical fuel moisture and fire weather

To determine the conditions under which fires could have burned historically, we imputed the number of days per year surface fuels were available to burn between 1960 and 2011 and described the fire weather when this was the case. We estimated fuel dryness (and hence availability to burn) using fuel moisture index (FMI; a simplified model to represent fuel moisture based on temperature and humidity; Sharples et al., 2009), of the understorey microclimate, using observations from our dataloggers. *Eucalyptus* litter is generally dry enough to sustain a fire front when $FMI < 25$ (Nyman et al., 2015; Sullivan et al., 2012). To estimate the number of days in which surface fuels were dry enough to burn between 2014 and 2016 (when the dataloggers were in the forest), we calculated three daily statistics of FMI: daily mean (FMI_{avg}), afternoon FMI (FMI_{af} ; from observations between 12:00 hr and 20:00 hr local time), and daily minimum FMI (FMI_{min}) for each Ausplot from the dataloggers in the understorey. We use the variation inherent in these data to account for the uncertainty associated with estimating fuel dryness from understorey FMI (Nyman et al., 2015).

While these estimates quantified fuel dryness for roughly 1 year, they could not characterise historical availability to burn of fuels over a long time period. To do this, we needed to relate meteorological conditions (for which there are long-term records) to these fuel moisture estimates. For this, we used a dataset of modelled historical weather in a 12×12 km grid (BARRA; Su et al., 2019, see Supporting Information), as it provided weather observations during the time period in which we took understorey FMI measurements. However, this modelled dataset was only available from 1990 onwards, so to estimate historical availability to burn we used a reliable high-resolution historical dataset of meteorological observations (SILO; Jeffrey et al., 2001, see Supporting Information), which extends from 1960 to 2011. We used the modelled BARRA data from 2014 to 2016 to estimate the regional meteorological conditions (i.e. outside the forest) at which TWEF understorey FMI dropped below 25 (i.e. surface fuels were dry enough to burn; Figure 2a), then used the observed SILO data to impute the number of times these conditions occurred between 1960 and 2011 (Figure 2b). To ensure this substitution was valid, we compared the two datasets for the period of 1990–2011 and found a minor correction for bias was required, as detailed in the Supporting Information.

We then characterised the fire weather on the days in which each plot would have been available to burn using daily maximum McArthur's Forest Fire Danger Index (FFDI; Noble et al., 1980). The period between 1960 and 2011 included four of Australia's most catastrophic fire disasters: the 1961 West Australian bushfires (WA), the 1967 Hobart fires (LTAS), the 2009 Black Saturday fires (VIC) and the 1983 Ash Wednesday fires (VIC; Bianchi et al., 2014;

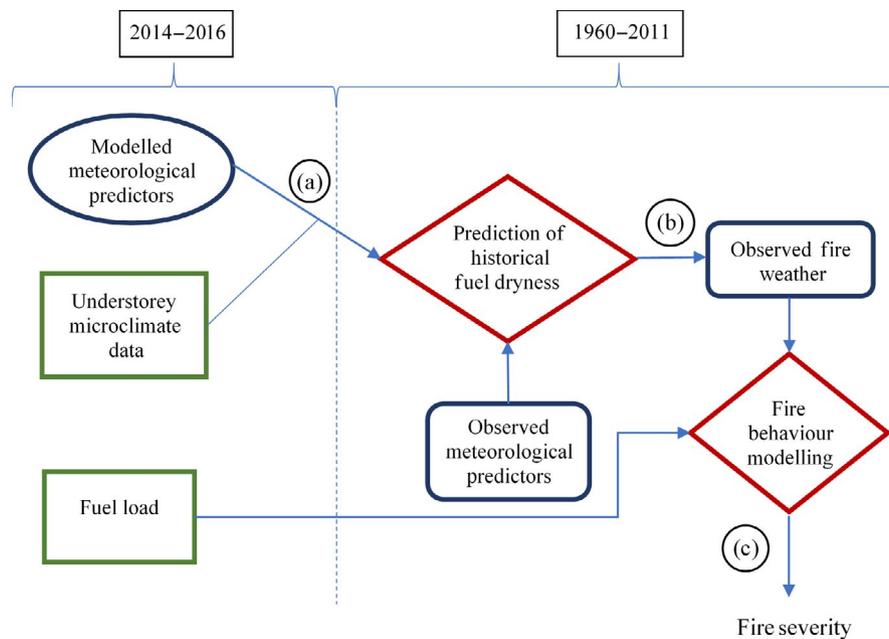


FIGURE 2 Flow diagram of modelling approach. Flow diagram overviewing our approach to predict the historical frequency with which low- and high-severity fire was possible in tall wet *Eucalyptus* forests. We used a combination of field collected data (green boxes), observed (blue rounded boxes) and modelled (blue oval) meteorological data, and fire behaviour and fuel moisture models (red diamonds). We estimated sequentially: (a) meteorological predictors of surface fuel availability to burn, (b) frequency of historical days in which surface fuels were available to burn, and (c) flame height on such days. The date range on top indicates the time period represented by the data and modelling approaches shown below it

Rodger, 1961; Solomon & Dell, 1967). We highlighted the weather records from these days for contextualisation. For a more detailed account of our estimation of historical availability to burn and fire weather, see the Supporting Information.

2.5.3 | Fire behaviour modelling

We used the estimates derived above, along with empirically derived McArthur's Mk5 fire behaviour equations, to estimate the average number of days per month during the 52-year period in which (1) these forests were dry enough to burn (namely could support fires of any severity)—as described above, (2) only low-severity fires (which did not damage the canopy) were possible and (3) high-severity crown-defoliating (either through scorch or combustion) fires were possible. The McArthur equations predict rate of spread and flame height (not length) of fires as a function of fuel load, fire weather and slope (Noble et al., 1980), and underpin Phoenix Rapidfire, the standard operational fire behaviour model for southeast Australian fire agencies (Neale & May, 2018; Tolhurst et al., 2008). We estimated flame height from the McArthur equations, along with scorch height using equations developed by Gould et al. (1997). Estimating flame and scorch heights, and comparing these to canopy heights, allowed us to obtain an estimate of fire severity; estimates of fire intensity would not have been suitable as its relationship with severity varies by vegetation type, species and canopy height (Keeley, 2009). On each day between 1960 and 2011 that fuels were dry enough to burn, we used surface fuel load and slope estimates from each plot, and daily maximum FFDI, to predict the maximum flame and scorch height for each day (Figure 2c). If flame height exceeded the measured mean canopy height to crown base for that plot, or if scorch height exceeded mean canopy tree height, we operationally defined this as a day in which high-severity fire was possible. If neither of these conditions were met, we defined the day as one in which only low-severity fire was possible. We then calculated the *relative* probability of low- and high-severity fire, defined as the probability of a low- or high-severity fire, respectively, occurring on days in which fuels were dry enough to burn. We did this to independently analyse trends in both fire severity and availability to burn. For more details on this approach, see the Supporting Information.

Surface fires can ignite fuels in the elevated layer to cause a 'coupled fire', where surface fuels and elevated fuels burn together, causing higher flames (Zylstra et al., 2016). Conditions in which the elevated layer ignites in TWEF, however, are virtually unknown, due to the low flammability of the species in the elevated fuel layer (Dickinson & Kirkpatrick, 1985; Zylstra et al., 2016). We therefore repeated the same flame-height estimation procedure assuming combustion of the elevated layer, using an approach similar to that used in the Phoenix model. This approach involved adding fuel-load estimates from the elevated layer to estimates of surface fuel load to obtain a combined surface-elevated fine fuel load estimate to use for flame-height and scorch-height predictions (Cruz et al., 2014). This

allowed for prediction of flame heights and scorch heights under the two alternative assumptions that (1) elevated fuels do not ignite and (2) that elevated fuels do ignite.

To investigate potential bioclimatic drivers of fire severity, we quantified the relationships between climate, fuels and fire regime among the seven macroecological and four climate regions using regression analysis, treating each Ausplot as a data point. To determine the significant drivers of fire regime in TWEF, we regressed (1) the relative probability of high-severity fire and (2) the number of days when high-severity fires were possible, against the following explanatory variables, calculated from the entire dataset between 1960 and 2011: seasonality of precipitation [see Murphy et al. (2013)], mean annual FMI, precipitation:evapotranspiration ratio, MAT, MAP, annual cumulative FFDI (Σ FFDI; Fox-Hughes et al., 2014), the fuel load and structure variables described above, and the percent of obligate seeders in the overstorey. For the regression, we used Gaussian or binomial generalised linear models (GLMs), depending on the response variable.

2.5.4 | Validation of flame-height predictions

To validate our predictions of flame height, we measured char heights at eight plots that had experienced low- to moderate-severity prescribed burns and wildfires (Table 2). Given uncertainties surrounding the daily activity of large wildfires and remote prescribed burns, we were unable to ascertain the exact date and time when these plots burned. We were, however, able to estimate daily fire progression using information from land managers (L. McCaw, K. Goetze, S. Ferguson 2017, J. Richley 2020, pers. comm.), and hotspot data from the Visible Infrared Imaging Radiometer Suite (VIIRS) 375 m thermal anomalies/active fire product (NASA; earthdata.nasa.gov), which allowed us to estimate a range of times in which each fire could have passed through each plot (Table 2). To approximate weather conditions at the time of these fires, we extracted weather data from these range of dates using the same modelled 12 km \times 12 km national grid that we used for the microclimate analysis (Su et al., 2019) and calculated the minimum and maximum FFDI experienced during that period. We then employed the McArthur equations using our pre-fire fuel load measurements from these plots to calculate the minimum and maximum flame heights expected during this period. This enabled comparison of predicted flame heights with the measured heights of charring on non-fibrous barked trees, which can be used as an approximation for observed flame height (Alexander & Cruz, 2012).

2.5.5 | Software

All statistical and graphical analyses were performed in R (R Core Team, R Foundation for Statistical Computing, <http://www.R-project.org/>). All geographical analyses were performed in ArcGIS geospatial software (ESRI Inc., www.esri.com).

3 | RESULTS

3.1 | Vegetation structure and fuel load

Across the early-mature tall wet *Eucalyptus* forest (TWEF) domain, we found some consistent patterns in fuel structure and regeneration strategies (Table 3). With the exceptions of monodominant obligate seeder *E. regnans* forests in Victoria, and resprouter *E. delegatensis* forests in Tasmania and *E. diversicolor/E. jackonii* forests in WA, sampled stands contained a mix of resprouting and obligate-seeding *Eucalyptus* species (Table 3). Surface fuels (combined fuel load of the surface and near-surface layers) were similar across the macroecological range of TWEF, ranging between 16 and 20 t/ha of fuel. The exception to this was forests in the Mediterranean climate of WA, where fuel loads were markedly higher (34.8 t/ha; Table 3). By contrast, elevated fuel loads showed more variability, with maximum fuel loads of 64.3 t/ha in tropical QLD and minimum fuel loads of 6.2 t/ha in temperate-marine SNSW (Table 3). There was also substantial variation in the vertical connectivity of live fuels, with the sum of gaps between fuel strata ranging between 4.6 m in tropical QLD and 21.5 m in temperate-marine VIC (Table 3).

3.2 | Fuel moisture and fire weather

Measurements from our understorey microclimate dataloggers between October 2014 and January 2016 suggest fuels were below the moisture threshold for combustion (16% water content by weight) for a substantial period (Figure 3g), though our estimates of the length of this period varied depending on which daily measure of fuel dryness (average, afternoon average or minimum) was used. We found the best meteorological predictor for understorey FMI was screen FMI, namely FMI calculated from modelled screen temperature and humidity outside the forest (Figure 3). For each region, we then imputed a threshold screen FMI (FMI_b), namely the modelled screen FMI at which understorey FMI < 25 (conditions when surface fuels are dry enough to burn); this varied between 8.7 and 13.1, depending on region (Figure 3). We found understorey FMI to be consistently higher than screen FMI outside the forest, though the relationship between the two was nonlinear. This indicated that understoreys are effective at maintaining high moisture levels, but that this effectiveness is reduced in dry conditions, especially in warmer climates (Figure 3e–g).

We used this imputed regional FMI_b threshold (after making a small bias correction to account for different data sources; see Supporting Information) to estimate the historical availability to burn of TWEF fuels between 1960 and 2011. We found that the average number of days per year when the surface fuels were dry enough to burn was much less than estimates from our dataloggers from the period of late 2014 to early 2016 (Figure 3g), indicating the year in which our dataloggers took measurements was unusually dry. Historical fuel dryness varied markedly, both within and among climate regions. In the plots in cool, wet temperate-marine

TABLE 3 Fuel loads and vegetation structure. Mean fuel loads and canopy profile heights for the seven macroecological regions. HCB refers to height to crown base. The relative proportion of eucalypt trees that are obligate seeders is also given. The range of plot-level averages is given in parentheses

Region	Surface fuel load (t/ha)	Elevated fuel load (t/ha)	Sub-canopy fuel load (t/ha)	Canopy fuel load (t/ha)	% Eucalypt obligate seeders	Canopy HCB (m)	Canopy height (m)	Combined fuel strata gap height (m)
LTAS	18.7 (11.2–28.3)	17.6 (5.4–35)	16.5 (9–27.6)	12 (5.9–18.5)	23 (0–7)	23.3 (20.5–24.8)	40.6 (33.2–44.5)	12.8 (9–17)
HTAS	25.5 (13.1–58)	19.7 (4.7–26.1)	15 (2.1–32.9)	13.9 (10.3–17.5)	0 (0–0)	17.6 (16.7–18.4)	32.2 (31.5–33.0)	10.7 (9.6–11.9)
VIC	20.8 (14.5–25.7)	26.8 (14.5–47.1)	10.9 (0.1–25.3)	20.2 (12.8–26.2)	100 (99–100)	35.4 (30.8–40.7)	62.6 (56.6–70.8)	21.5 (17.4–26.7)
SNSW	18.6 (13.1–22.2)	6.2 (0.4–17.4)	4 (0–14.9)	14.3 (11.5–16.7)	37 (4–73)	16.8 (16.2–17.8)	34.4 (28.6–38.3)	9.9 (7–14.7)
WA	34.8 (23.9–46.5)	21.6 (4.1–62.5)	5.7 (0.3–18.2)	10.4 (5.4–18.6)	0 (0–0)	20.4 (10.3–32.3)	38.7 (24.5–52.3)	8.9 (0.1–17.7)
NNSW	25.6 (15.9–31.2)	14.9 (6.6–22.7)	18.3 (6.9–38.1)	8 (4.6–11.5)	76 (26–100)	22.3 (16.3–27.8)	44.4 (33.2–57.6)	8.1 (4.7–11.1)
QLD	16.2 (10.8–28.3)	64.3 (10.7–114.8)	25.6 (15.3–39.1)	4.8 (4.4–5.1)	69 (37–89)	15.3 (9.3–17.6)	30.1 (21.7–33.0)	4.6 (1.7–6)

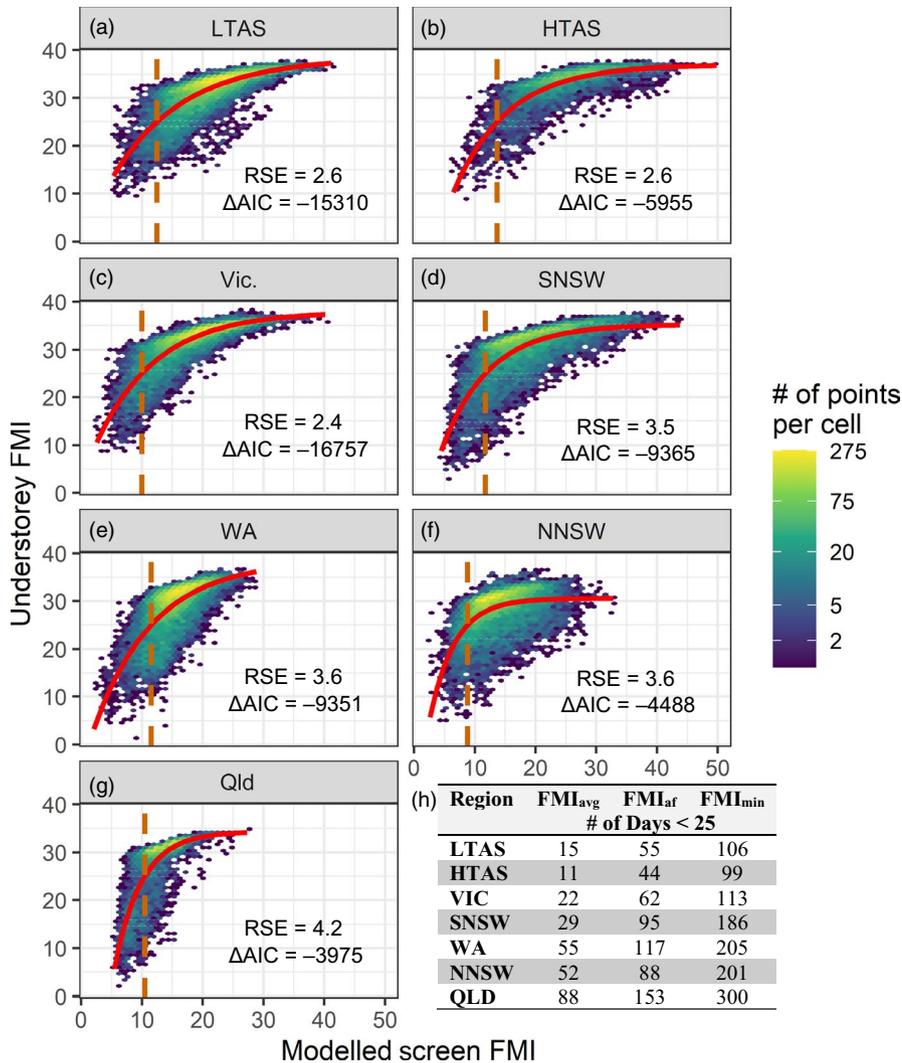


FIGURE 3 Availability to burn. Density plots of modelled screen Fuel Moisture Index (FMI), and understorey FMI, as measured by data loggers between 2014 and 2016, separated by region. The colour gradient represents the number of observations per plot grid cell on a log scale as indicated. The solid red line represents the expected understorey FMI for a given screen FMI according to the nonlinear least squares regression model. The dashed orange line represents FMI_b , the screen FMI at which the understorey FMI = 25, roughly equivalent to the fuel moisture content at which *Eucalyptus* litter can sustain a fire. Model residual standard error (RSE) and the change in AIC from the null model (ΔAIC) are also given. The table in (h) represents the number of days per year during the sampling period (2014–2016) in which daily mean (FMI_{avg}), mean afternoon FMI (FMI_{af}), and daily minimum FMI (FMI_{min}) were <25

Tasmania (HTAS, LTAS), and moist subtropical NNSW, surface fuels were available to burn, on average, 1–3 days a year between 1960 and 2011. In the slightly warmer, drier plots in the temperate-marine regions of mainland Australia (VIC, SNSW), surface fuels were dry enough to burn 13–16 days per year. In the warmest (tropical) and driest (Mediterranean) climate regions, fuels were dry enough to burn 23 and 35 days per year, respectively (Figure 4). The average monthly number of days available to burn did not exceed 12 in any month for any region (Figure 5a). Analysis of seasonal timing and length of availability to burn revealed substantial regional differences in the sampled TWEF (Figure 5a). TWEF in temperate-marine and Mediterranean climates on mainland Australia were primarily available to burn during the austral summer (December–March), and for smaller portions of the shoulder seasons (October–November and April) in WA and SNSW. TWEF in the wet tropics were available to burn between the months of August and December, with a higher proportion of days occurring in the early fire season months than in temperate-marine climates (Figure 5a). Subtropical and Tasmanian TWEF were only rarely available to burn, averaging less than thrice per year. In Tasmania, this occurred from December–February, and in the subtropics between September and December.

When TWEF surface fuels were dry enough to burn, the fire weather they experienced was typically consistent and mild across all regions, with the exception of a few notable outliers (Figure 4). The large majority of days fell within the range of a ‘high’ fire weather danger day or lower, according to the fire danger rating scale (NSW Rural Fire Service, 2017). Across all regions, FFDI exceeded 40 only on 99.9th percentile FFDI days, and in tropical QLD and temperate-marine HTAS, FFDI never exceeded 40. Australia’s four largest fire disasters in that time period all occurred on outlier days with FFDI > 40, indicating the importance of rare but extreme fire weather causing extreme fires in the TWEF (red dots in Figure 3).

3.3 | Flame height and fire severity

When we modelled flame heights based on surface fuel loads, there were distinct regional trends in the likelihood of low- and high-severity fire (Figure 5b), indicating that high-severity fire was more likely in warmer, drier climates. In the most southerly, temperate-marine regions (HTAS, LTAS, VIC and SNSW),

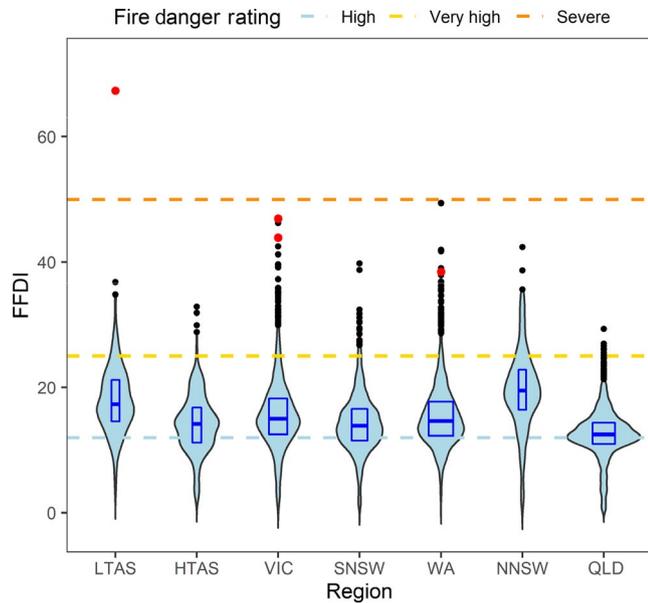


FIGURE 4 Fire weather in tall wet *Eucalyptus* forests. Box and violin plot representing the distribution of fire weather for each region recorded on days between 1960 and 2011 in which surface fuels were available to burn. Dark blue boxes represent values between the 25th and 75th percentiles of selected forest fire danger index (FFDI) values, and the centre line represents the regional median. The actual percentage of days during which these fuels were available to burn is listed on the bottom of the plot for each region, and box widths are varied proportionally to this value. Black dots represent outliers, defined as 2 times the interquartile range (IQR; 25th–75th percentile) above the 75th percentile value. Red dots highlight the regional average maximum FFDI observation near our sites on days of Australia's four most extreme fire events. Dashed lines represent thresholds above which fire danger ratings are classified as 'High', 'Very High' and 'Severe' (NSW Rural Fire Service, 2017). For this plot daily maximum FFDI values were averaged across all stations within a region

low-severity surface fire is much more likely than high-severity fire. In Tasmania (HTAS and LTAS), in the austral summer months, high-severity, crown-defoliating fire was possible <1 day per month in January and February, and virtually impossible in other months. Meanwhile, low-severity fire was possible 0.5–1.5 days a month, on average, through the entire austral summer (Figure 5b). Temperate-marine climates on mainland Australia (VIC, SNSW) experienced conditions for low-severity fire more often, 1–5 days per month in November–March. Conditions for high-severity fire here were rarer, occurring <3 days a month, mostly in December–March (Figure 5b). High-severity fire was more likely in hot tropical climates and dry Mediterranean climates. Low-severity fire and high-severity fire were equally likely in the hottest climate (tropical QLD), with both possible 0–4 days per month between August and December. In Mediterranean TWEF, high-severity fire was possible 3–12 days a month during the austral summer, with low-severity fire possible less than one day a month (Figure 5b). While NNSW averaged 2 days total per year in which fuels were dry enough to burn, on those days

during which the fuels were flammable, high-severity fire was twice as likely as low-severity fire during September–December. We found regional fire weather to be the strongest driver of fire severity, with annual cumulative FFDI explaining 45% of the variation in the number of days in which high-severity fire was possible (Figure 6a). We also found the observation that warmer climates supported more high-severity fire had statistical significance: the average daily maximum temperature was a significant predictor of the relative probability of a high-severity fire (Figure 6b), with a pseudo- R^2 of 0.15. However, we found no other strong correlates between fuel or climate metrics and fire severity.

Although high-severity fire was unlikely in some regions if only surface fuels burned, our analysis indicated that if surface fire ignited the elevated fuels (live small trees and shrubs in the understorey) and coupled fire developed, high-severity fire became more likely than low-severity fire in all regions (Figure 5c). Under this assumption, the relative probability of a high-severity fire became substantially higher in the cool, southeast temperate regions (LTAS, HTAS, VIC and SNSW), with values ranging from 0.6 to 0.92 in the summer months. However, probabilities of low-severity fire remained substantial in the spring months (0.16–0.55 in September–November). In Mediterranean, subtropical and wet tropical climates, the relative probability of high-severity fire was close to 1 during the fire season. Regardless of whether a coupled fire developed, the percent of days in which high-severity fire is possible was highest in WA, due to its consistently hot, dry summers. Importantly, there was also substantial variation in the probability of low- and high-severity fire among plots within a given region (Figure 5).

3.4 | Validation of flame-height estimation approach

Our analysis of fire weather surrounding the eight burnt Ausplots found that each of the plots burned under relatively mild fire-weather conditions, with possible FFDI values ranging from 1 to 20 (corresponding to a fire danger rating of low–high; Table 2; Figure 4). When we compared observed char heights in the burnt plots with flame heights predicted under the estimated prevailing weather conditions during the time of fire, we found predictions overestimated flame height (Figure 7). The degree of overprediction was extremely sensitive to fire-weather inputs, as indicated by the vertical error bars in Figure 7. If each plot burned under the mildest fire weather during the potential burn period, our flame-height estimates would be roughly accurate. However, if the plots burned under the most extreme fire weather during this burn period, predictions were roughly 2–5 times higher than actual char heights. On average, potential predicted flame heights were roughly 1.5 times higher than the actual char heights, though this varied regionally, with overestimates being much higher in tropical QLD than in other regions.

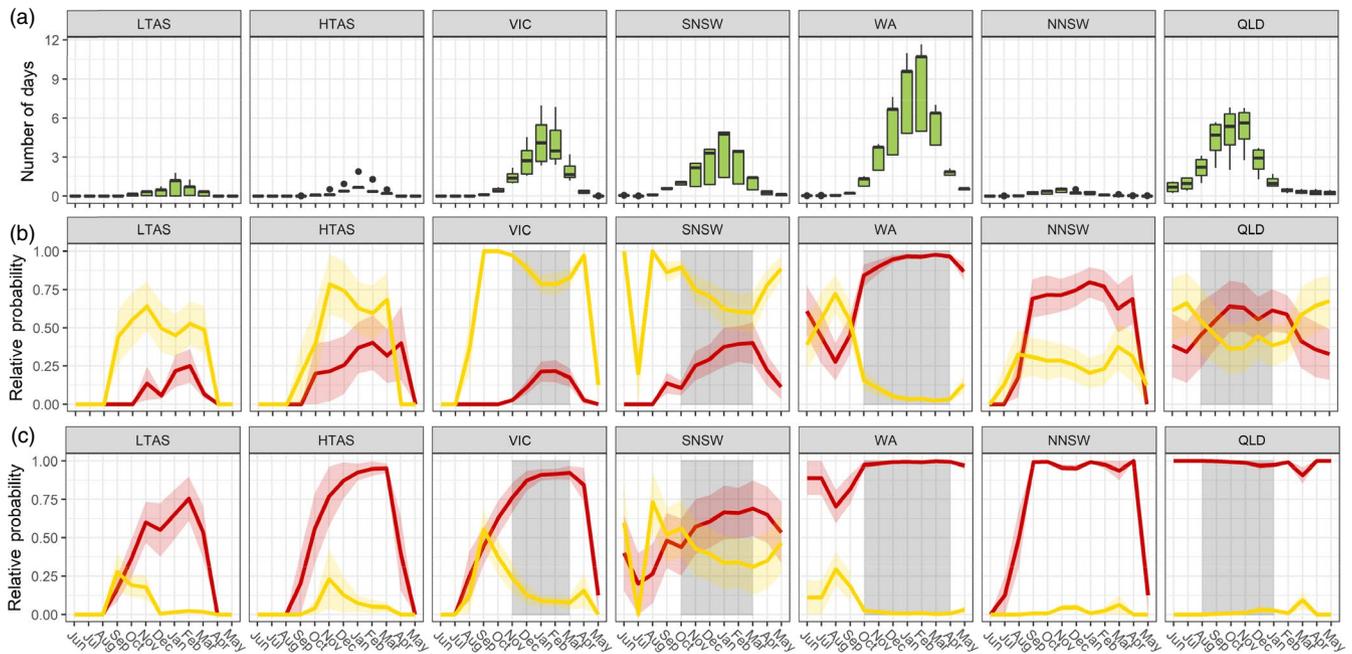


FIGURE 5 The seasonality of flammability in tall wet *Eucalyptus* forests. (a) Box and whisker plots displaying availability to burn in each region as represented by the average number of days per month at each plot in which surface fuels were dry enough to burn. Boxes represent interquartile range (IQR), and outliers represent values more than 1.5 times the IQR away from the boxes. (b) Monthly relative probability of a low-severity (yellow line) and high-severity (red line) fire on days where fuels were available to burn, as averaged across all plots for the region, assuming only surface fuels burned. (c) Monthly relative probability of a low- and high-severity fire [as in (b)], assuming elevated fuels burned as well. Coloured shaded ribbons represent the mean plus or minus one standard error, and grey bars in the background of (b) and (c) represent the months of the year during which fuel were, on average, dry enough to burn on more than one day

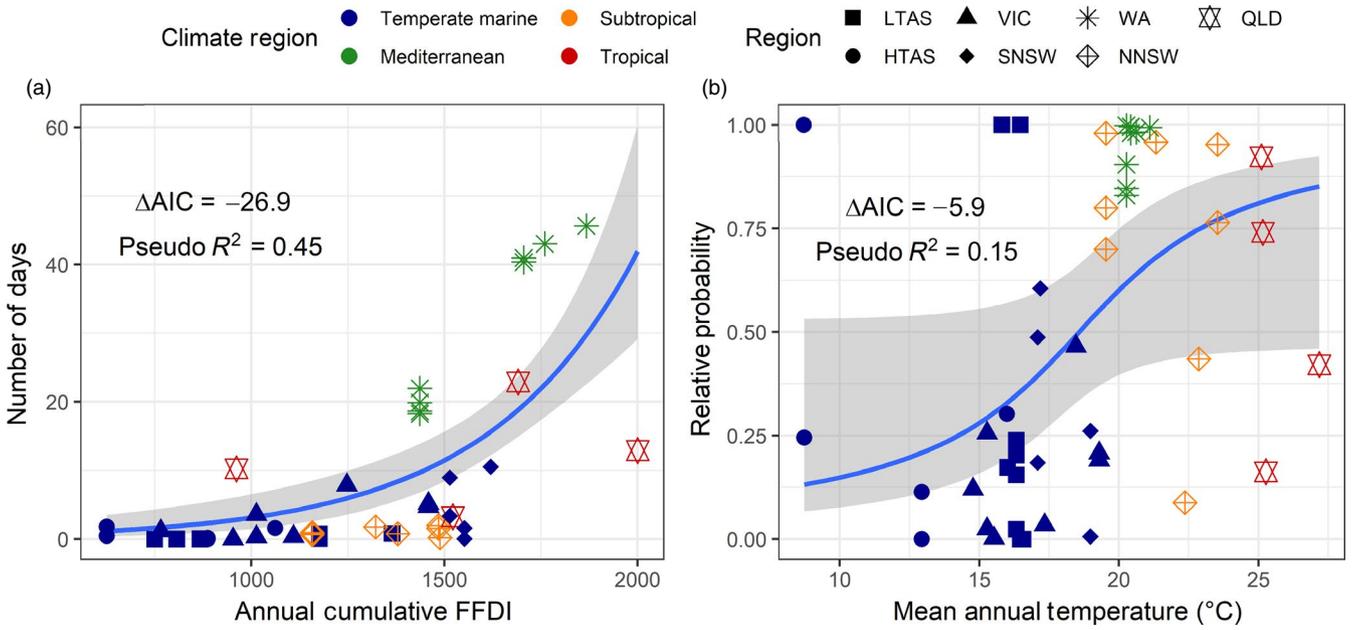


FIGURE 6 Climate and fire severity. Scatterplots of (a) the annual number of days in which high-severity fires are possible versus the annual cumulative maximum daily forest fire danger index (FFDI) and (b) mean annual daily maximum temperature versus the relative probability of a high-severity fire. The region and climate region of each plot is represented by different symbols and colours as indicated. Blue lines represent predictions from (a) a gaussian GLM (b) a binomial GLM, with grey ribbons representing one standard error. The ΔAIC (from comparison of the full model to the null model) and pseudo R^2 from these models are also given

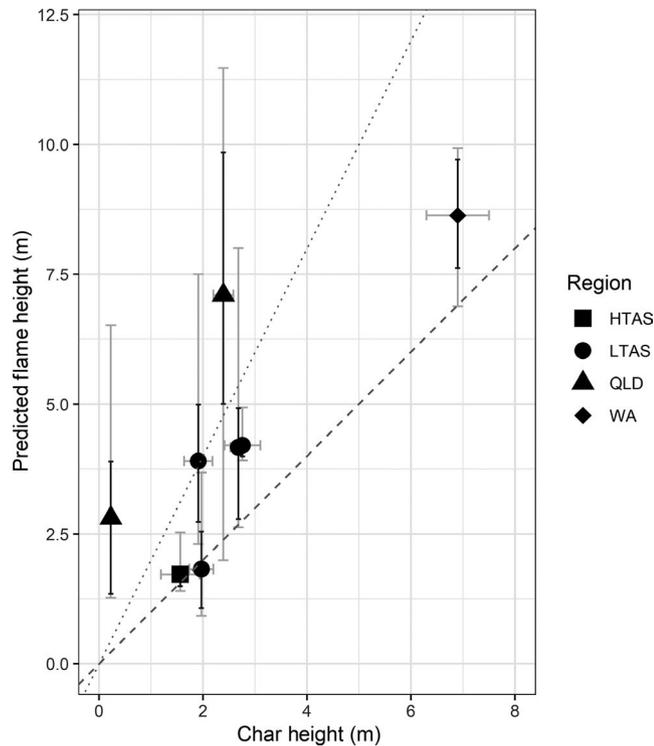


FIGURE 7 Flame height estimation validation. Scatterplot of mean predicted flame height and mean observed char height for each of eight burnt permanent plots in the indicated regions. Flame height predictions were made for every hourly observation during which each plot could have burned. Grey vertical error bars represent flame height predictions based on minimum and maximum forest fire danger index (FFDI) values, and black bars represent predictions based on 25th and 75th percentile FFDI values. Horizontal error bars represent the standard error of measured char heights. The dashed line represents a 1:1 perfect agreement, and the dotted line represents the point at which flame height prediction is twice that of char heights

4 | DISCUSSION

In this macroecological study, we combined fuels data, meteorological observations and a fire behaviour model to estimate the likelihood of low- and high-severity fire across the Australian range of early-mature tall wet *Eucalyptus* forests (TWEF). We found surface and elevated fuel loads were universally high, but these forests' moist understorey microclimate caused them to be rarely available to burn. Thus, fire occurrence in TWEF was limited by fuel moisture, not mass. There were clear seasonal patterns in both the availability of fuels to burn and expected fire severity across the TWEF range. Our fire behaviour modelling, based on surface fuel loads, showed that TWEF in the early-mature stage were most likely to support low-severity surface fire in the coolest, wettest regions and most likely to support high-severity crown-defoliating fire in the warmest driest regions. However, if we included elevated fuel biomass in the modelling, then high-severity fire became substantially more likely in every region. Overall, our modelling suggests a mix of low- and

high-severity fire is an integral feature of all TWEF. Below, we explore the causes of geographical variation in mixed-severity fire across the TWEF range, and discuss how this affects forest dynamics and should influence forest management. Finally, we consider the implications of climate change for the flammability of these forests.

4.1 | Understorey microclimate and macroclimate in TWEF

The TWEF climate envelope we sampled can be characterised by relatively mild 90th–99th percentile fire weather when compared to large swaths of temperate Australia (Figure 4; Williamson et al., 2016). The FFDI values recorded near TWEF on the days of Australia's worst fire disasters were substantially lower than the maximum values reported from elsewhere during these fires (Figure 4; Bianchi et al., 2014). Furthermore, FMI was several times higher in the understorey of TWEF than in modelled conditions outside the forest (Figure 3). These two effects likely contributed to the high likelihood of fire being of low severity in many of our sites. This effect of understorey microclimate on temperature and humidity is supported by previous research in temperate-marine (Cawson et al., 2017) and tropical (Little et al., 2012) TWEF. We found forests in temperate-marine regions, which have more prevalent broadleaf mesic understoreys, including rainforest species, were more effective at maintaining fuel moisture in dry conditions than those in tropical regions, where grassy understoreys are more common, and those in Mediterranean regions, where rainforest understoreys are non-existent (Figure 3; Wardell-Johnson, Neldner, et al., 2017). The rainforest understoreys that form in late successional stages in eastern TWEF are thought to result in reduced flammability when compared to other *Eucalyptus* forest (Ashton, 1981; Jackson, 1968), due to moister microclimates and the lower flammability of rainforest tree species (Baker, Jordan, Dalton, & Baker, 2014; Dickinson & Kirkpatrick, 1985; Little et al., 2012). Dense understoreys also reduce wind speed (Moon et al., 2019) that, in concert with the moist microclimates, substantially moderate ambient fire weather (Little et al., 2012) and reduce flame heights. Importantly, our analysis was based on early-mature TWEF (Mifsud, 2003; Wood et al., 2017), thereby controlling for stand age effects, but as a result we cannot extrapolate our results to dense young, regrowth TWEF, or more structurally complex, multi-cohort, late-mature TWEF; the microclimates of these growth stages are thought to differ markedly from those of single-aged, early-mature forest (Cawson et al., 2017; Jackson, 1968). Studies in the northern hemisphere have shown that the structural complexity of older forest understoreys makes them more efficient at retaining moisture and buffering temperatures than young, regrowth forests (Kovács et al., 2017; Norris et al., 2012). While our results show that early-mature TWEF understoreys are structurally complex (Table 3), the direction of the effect of stand age on microclimate in TWEF is still disputed (Burton et al., 2019; Cawson et al., 2017).

4.2 | Fuel availability

At a global scale, fire activity in wetter, productive forests is primarily limited by fuel moisture (Krawchuk & Moritz, 2011; Meyn et al., 2007). While this has been shown for TWEF using remotely sensed data (Nolan et al., 2016), we offer the first empirical estimates of fuel moisture across the forests' range. We estimated fuels to be rarely dry enough to burn between 1960 and 2011, which aligns with the fact that fires have been rare in TWEF (Wardell-Johnson, Neldner, et al., 2017). Our empirical measurements also indicate that these forests were dry enough to burn much more between 2014 and 2016 than between 1960 and 2011 (Figure 3h). We are confident this difference is not an artefact of the different sources of climate data, as evidenced by our supplementary analysis and bias correction (see Figure S1), rather it most likely reflects a prolonged, severe drought across Australia, which preceded extensive fires in Tasmania and Victoria in 2016 (Bowman et al., 2019; Inspector-General for Emergency Management, 2016; Rodriguez-Cubillo et al., 2020), and possibly a changing climate (Nolan et al., 2016). We acknowledge that FMI calculations based on temperature and humidity measured in the understorey microclimate are less precise than measurements in the litter pack (Nyman et al., 2015), but we offset the loss of precision by taking a greater number of within and between site measurements than other fuel moisture studies in TWEF (Figure 3; Burton et al., 2019; Cawson et al., 2017; Nyman et al., 2015). Furthermore, despite the reduced precision, surface fuels are still, on average, dry enough to burn when microclimate FMI < 25, indicating that this estimate is unbiased for our purposes (Nyman et al., 2015; Sharples et al., 2009).

4.3 | Fire severity and ecological implications

We estimated flame height and fire severity using the McArthur equations (Noble et al., 1980), due to their simplicity, ease of implementation and suitability for our data. While the McArthur model is not the most accurate fire behaviour model available for *Eucalyptus* forests (Cruz et al., 2014; McCaw et al., 2008), it is the basis for the most widely used operational model in Australia (Neale & May, 2018), and more accurate models (Gould et al., 2007; Zylstra et al., 2016) were incompatible with our fuels data. Furthermore, we validated our methodology, finding small, but consistent overestimations of flame height, in most cases by 1–2 metres (Figure 7). This overestimation was likely due to the crudeness of the McArthur model in predicting soil moisture (Kumar & Dharssi, 2017; Yeo et al., 2015), and the reduced flammability of TWEF litter when compared to that of dry *Eucalyptus* forest (Clarke, Prior, et al., 2014; Dickinson & Kirkpatrick, 1985), and means that our methods may have overestimated the likelihood of a high-severity fire. However, the consistency of this overestimation suggests that comparisons between regions are still valid. It is also important to note that these validations are based on fire behaviour under fire-weather conditions that were less

extreme than what is possible in TWEF (Figure 4; Table 2), and the McArthur model is thought to be especially ill-suited for extreme fire weather (Cruz et al., 2014). Therefore, further observations of fire behaviour in TWEF from high-intensity fires should be a research priority. We also operationally defined high-severity fire using a simple comparison of flame and scorch heights to canopy height, an approach designed to enable comparative analyses of the relative likelihood of low- and high-severity fire across different forest regions. We acknowledge that this represents an oversimplification of the complex processes surrounding the development of crown fire (especially the role of bark; Ashton, 1981; Van Wagner, 1977), and its impacts on tree mortality (Benyon & Lane, 2013; Collins, 2020). While the relationship between surface fire intensity and crown fire initiation is well studied in conifer forests (Alexander & Cruz, 2011), it remains poorly understood in *Eucalyptus* forests. However, unlike in conifer forest, crown combustion in *Eucalyptus* forest is thought to generally occur only after flame contact from a surface fire (Alexander & Cruz, 2012; Zylstra, 2011). Furthermore, specific fire intensity values at which mortality occurs is unknown for most *Eucalyptus* species. This is why we compared flame height to crown height as a measure of severity, and we are not the first study to do so (McCull-Gausden & Penman, 2019). These issues, however, are both complex and poorly understood processes and hence demand further inquiry.

Furthermore, as mentioned above, our analyses only considered early-mature TWEF, and our method of stand selection favoured even-aged stands (Wood et al., 2017), which were substantially younger than the reported 500+ year-old ages that even-aged stands can achieve prior to succession to rainforests (Wood et al., 2010). Therefore, we cannot extrapolate our results to regrowth or late-mature TWEF. The large-scale conversion of primary forests to regrowth forests in Victoria is posited to have permanently altered the landscape-scale flammability of these forests by changing the microclimate, structure and species composition (Lindenmayer et al., 2009), increasing the landscape-scale probability of high-severity fire and thereby creating a 'landscape trap' (Lindenmayer et al., 2011). Landscape analyses suggest that the probability of a high-severity fire in TWEF decreases with age (Bowman et al., 2016; Taylor et al., 2014; Zylstra, 2018) because of the increasing canopy height and development of a less-flammable understorey, the latter due to succession to rainforest species (Jackson, 1968; Lindenmayer et al., 2000) and the microclimate dynamics mentioned above. Nonetheless, field-based chronosequence research has indicated that structural changes in some older obligate seeder forests actually increase fire hazard (Cawson et al., 2018), suggesting that old-growth forests might actually have a higher fire risk than early-mature forest. Thus, how the risk of high-severity fire is affected by forest age and resulting understorey microclimate requires further study.

Our results highlight the importance of live understorey combustion in driving fire behaviour. Elevated fuels in the live understorey comprised the highest proportion of the forests' fuel load in most regions (Table 3), and the development of a coupled fire made

canopy scorch or combustion substantially more likely than low-severity fire activity in all regions (Figure 5c). This suggests that in individual fire events on days with a high fire weather danger rating, the spatial pattern of low- and high-severity fire is likely partially controlled by the distribution of flammable and non-flammable understorey species. Despite this, the flammability, and specifically the ignitability, of these live understorey fuels is poorly understood. Some rainforest species are known to be less flammable than other understorey species in TWEF, which are, in turn, less flammable than the *Eucalyptus* overstorey (Dickinson & Kirkpatrick, 1985). The absence of rainforest understoreys is thought to increase fire hazard in TWEF in the Mediterranean climate of Western Australia, whereas widespread rainforest understoreys in south-eastern Australia have been assumed to reduce it (Clarke, Knox, et al., 2014; Jackson, 1968; Little et al., 2012; Wardell-Johnson, Neldner, et al., 2017). While the landscape-scale flammability of live TWEF fuels increases dramatically below a wet:dry weight threshold of 100% (Nolan et al., 2016), the conditions under which each of the live rainforest and wet sclerophyll species ignite are poorly understood. Due to uncertainty about the ignitability of live understorey fuels, and the inadequacy of the McArthur model's representation of live fuels (Zylstra et al., 2016), modelling results for coupled fires, using combined surface and elevated fuel loads, are likely to be much less accurate than those using only surface fuel loads. While the results from the coupled fire modelling underscore the importance of the live understorey, the accuracy of their flame-height predictions is unknown. However, the modelling of combustion of surface fuels more closely aligns with the assumptions of the McArthur model (McArthur, 1967), and is sufficiently accurate to infer likely differences in fire severity between regions (Figure 7). Below, we consider only the surface fire model results (Figure 5b), which reveal clear regional trends.

The highest intensity fire in Australian ecosystems can occur in TWEF (Gill & Moore, 1990; Murphy et al., 2013), although our modelling suggests that there is considerable variation in flame height and fire severity (both correlated with intensity; Keeley, 2009), within the TWEF domain. TWEF in the driest climate we sampled (the Mediterranean climate of WA) were most likely to support high-severity (and hence high intensity) fire driven by surface fuel combustion 3–12 days a month during the austral summer, and would rarely experience exclusively low-severity fire during the summer fire season (Figures 5b and 8), reflecting a combination of a dry, hot climate (Figure 4) and exceptionally high surface fuel loads (Table 3). Combined with the fact this region is more prone to lightning-ignited fire than other regions in our study (Kuleshov et al., 2006; McCaw & Hanstrum, 2003), this indicates WA is the most fire-prone region in our study. However, we may have slightly overestimated the probability of high-severity fire in the region, given our overestimates of flame height (Figure 7). Low-severity fire is possible in Mediterranean TWEF, as demonstrated by the regular, low-severity fires (prescribed burns) that are intentionally lit in cool weather in the summer and early autumn months (Burrows & McCaw, 2013).

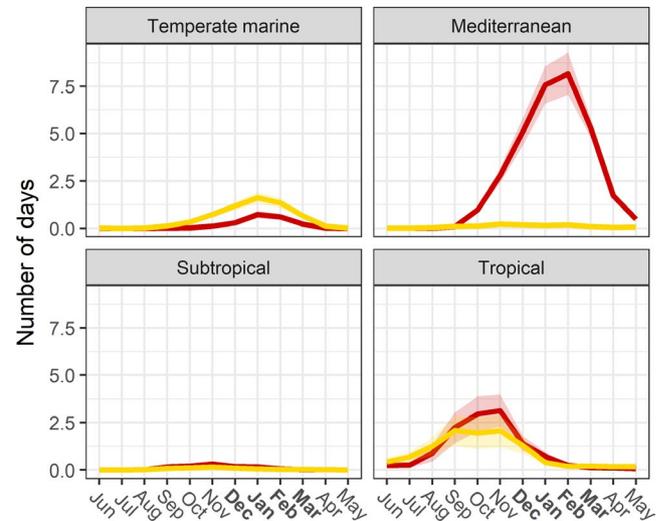


FIGURE 8 Summary of regional fire severity in tall wet *Eucalyptus* forests. Average number of days per month in which high-severity fire (red lines) and low-severity fire (yellow lines) was possible between 1960 and 2011 for each climate region. Shaded ribbons capture variation between Ausplots, representing one standard error. Austral summer months are in bold

In contrast, TWEF in temperate-marine climates (the coolest, wettest climate we sampled) were rarely available to burn and had the highest relative probability of low-severity fire. This was due to a combination of taller canopies, more mild fire weather and/or lower surface fuel loads than their counterparts in warmer, drier climates (Table 3; Figure 4). In these TWEF, high-severity fire was possible, on average, less than one day per month in the summer (Figures 5b and 8). Such rare hot, dry conditions can lead to very intense fires which can cause stand replacement, especially in forests dominated by obligate seeders (Ashton, 1976; Bowman, Murphy, et al., 2014; Gilbert, 1959). It is important to note that complete stand mortality is exceptional, because most temperate-marine TWEF are multi-aged (Bowman & Kirkpatrick, 1986; Turner et al., 2009), due to the prevalence of epicormic resprouters capable of surviving multiple crown fires (Table 1; Burrows, 2013; Collins, 2020). However, even obligate seeder stands can be multi-aged (Ashton, 2000; Lindenmayer et al., 2000), and we found no relationship between the prevalence of obligate seeders and the estimated likelihood of a high-severity fire. In fact, days supporting only low-severity fire were most common in VIC (1–5 days a month in the summer; Figure 5b), where the canopy was composed entirely of the obligate seeder *E. regnans* (Table 3).

Our analyses suggest TWEF in tropical climates were available to burn 3–6 days a month in the spring, and importantly were available to burn more days, especially in the initial months of the fire season, than the forests in temperate-marine climates (Figure 5a). Conditions suitable for prescribed burning in tropical forests are generally more frequent than in temperate forests, in part resulting in a greater extent of grassy understoreys (Henderson & Keith, 2002; Tng et al., 2014; Unwin, 1989; Williams, Parsons, et al., 2012). Our analysis suggested these forests experienced a roughly even mix of

days supporting high- and low-severity fire (Figures 5b and 8). We suspect, however, that this model prediction is an artefact of our analysis, as crown fire is thought to be unlikely in tropical TWEF, due to milder extremes in fire weather (Figure 3; Tng et al., 2014). Indeed, our overprediction of flame height appeared worse for tropical QLD than for temperate-marine and Mediterranean regions (Figure 7).

Our modelling suggests subtropical forests likely experience both high- and low-severity fire but were only dry enough to burn less than one day a month in the spring, reflecting the region's lack of distinct seasonal trends in rainfall (Thackway & Cresswell, 1995). However, intense fires in late 2019, along with our empirical estimates of low fuel moisture in 2015 (Figure 3h), highlight that these forests may become increasingly at risk to lower fuel moisture and more severe fire seasons (Nolan et al., 2016, 2020).

Disturbance by fire is a crucial process in TWEF to prevent succession to rainforest, as it is necessary for the establishment of the next cohort of *Eucalyptus* seedlings (Gill, 1997; Jackson, 1968). The archetypal succession model generally depicts this disturbance as a high-severity fire (Forestry Tasmania, 2009), likely due to the importance of the large pulse of *Eucalyptus* regeneration following a high-severity fire (Ashton, 1976). However, disturbance by low-severity fire could still prevent succession to rainforest, as seedling establishment can still occur under small canopy gaps (formed by the death of understorey trees), or even in the absence of canopy gaps (Wardell-Johnson, 2000). Furthermore, low-severity fire can kill all the understorey rainforest trees while leaving the overstorey intact (Furlaud & Bowman, 2020). Low-severity fire can also create and maintain structural properties of early-mature TWEF that have high ecological value, such as large cavity-bearing live trees which can provide habitat for wildlife (Lindenmayer & Franklin, 1997), an understorey microclimate more favourable for liverwort and understorey vascular plant diversity (Baker, Jordan, Dalton, & Baker, 2014; Baker, Jordan, Steel, et al., 2014; Turner & Kirkpatrick, 2009), and better conditions for the regeneration of mesic understorey species that provide food and habitat for wildlife (Bassett et al., 2017; Lindenmayer & Franklin, 1997).

4.4 | Mixed-severity fire regimes

An important concept in fire ecology is that of the fire regime, which refers to spatiotemporal variation in fire behaviour, along with its effects in a given ecosystem (Gill, 1975; Pausas & Keeley, 2009). Evolutionary and life-history traits of *Eucalyptus* species indicate that recurrent fire is an integral part of every system in which the genus dominates (Burrows, 2013; Crisp et al., 2011; Waters et al., 2010). Given this understood importance of fire in TWEF, and that we have shown both low- and high-severity fire to be likely, we suggest these forests support what is known as a mixed-severity fire regime. This term is generally used in connection with North American forests, and is defined by a substantial amount of low- and high-severity fire activity (Agee, 1993). TWEF share characteristics with other forests with mixed-severity fire regimes (Poulos et al., 2018; Schoennagel

et al., 2004). TWEF contain a mix of *Eucalyptus* overstorey species with traits likely to be selected for by both low-severity fire (thick bark; Lawes et al., 2013; Ondei et al., 2016; Waters et al., 2010), and high-severity fire (epicormic resprouting and obligate seeding; Burrows, 2013; Crisp et al., 2011; Nicolle, 2006; Waters et al., 2010), which are characteristics shared by a number of North American conifer species that experience mixed-severity fire regimes (Poulos et al., 2018; Roy, 1966; Stuart & Scott, 2006). Individual fires in TWEF contain a patchy mosaic of low- and high-severity fire activity, even after extreme events (Cruz et al., 2012; Ndalila et al., 2018; Rodriguez-Cubillo et al., 2020), which matches fire mosaic patterns in mixed conifer forests of the northwest USA (Perry et al., 2011). Furthermore, TWEF are characterised by multi-aged forest structures across their range (Ashton, 2000; Bowman & Kirkpatrick, 1986; Bradshaw & Rayner, 1997; Lindenmayer et al., 2000; Turner et al., 2009), as dominant *Eucalyptus* species can survive high-intensity fire (Collins, 2020) or regenerate after high- or low-severity fire (Ashton, 1976; Wardell-Johnson, 2000).

More specifically, the fire ecology of TWEF has parallels with similarly gigantic forests around the world, such as *Sequoia sempervirens*, *Sequoia giganteum* and *Fitzroya cupressoides*-dominated forests of western North America and the southern Andes (Tng et al., 2012). These three species experience mixed-severity fire as well: regenerating prolifically after high-severity fire (Harvey et al., 1980; Lara et al., 1999; Person & Hallin, 1942), and surviving repeated low-intensity fires, such as those frequent fires lit by Native Americans (Swetnam, 1993; Orville, 2008; Veblen et al., 1999). Likewise, although *E. regnans* forests are promoted as exemplars of infrequent, stand-replacing fires, there is an evidence that infrequent low-severity fires, possibly set by Indigenous Australians, may have maintained grassy understories in some of these forests prior to European invasion (Ashton, 1958, 1981), though aboriginal management of TWEF was likely much less intensive than that of drier forests (Wardell-Johnson et al., 2019).

4.5 | Climate change and management implications

Our results indicate that the likelihood of a high-severity fire is much higher in TWEF in hotter, drier climates than in cooler, wetter climates. These biogeographic differences suggest that the interaction between climate, vegetation structure and weather may substantially increase the probability of high-severity fire in TWEF as the climate warms (Figure 6). The effects of climate change on the temperate-marine regions in our study are likely to be relatively mild. Climate change is expected to increase temperature in southern Tasmania by 1.1–2.1°C and decrease precipitation by 3%–6% by 2070 (Williams et al., 2009), but the change in summer FFDI is projected to be lower in regions surrounding TWEF than in other regions of Tasmania, with an expected increase in cumulative annual FFDI of 200–300 (Fox-Hughes et al., 2014). Similar changes are expected to take place in southeastern New South Wales (Clarke & Evans, 2019). However, our results indicate that the number of days in which high-severity fire is possible is highly sensitive to even small

changes in FFDI across the geographical range of TWEF (Figure 6a). Meanwhile, in other regions containing TWEF, the effects of climate change are predicted to be more severe, with Mediterranean climates in southwest Western Australia projected to experience a 1–3°C temperature increase and a 10%–20% decrease in rainfall (Williams et al., 2009), which will lead to reductions in water tables and soil moisture content, and lengthen the fire season (Wardell-Johnson et al., 2015). Tropical and subtropical climates in our study, meanwhile, are projected to experience the highest percent increase in cumulative FFDI (30%–60%) of all the forested regions in Australia (Williams et al., 2001).

More generally, our results indicate that these increases in temperature and dryness will reduce the ability of the understorey microclimate to retain moisture (Figure 3), and increase the probability of high-severity fires (Figure 6). Indeed, the marked increase in fuel dryness we estimated due to the 2015 drought (Figure 3), combined with the potential for increased drought to disproportionately impact large trees (Bennett et al., 2015; Prior & Bowman, 2014), and decrease inter-fire intervals and hence increase the likelihood of demographic collapse (Enright et al., 2015), could indicate these forests are especially vulnerable to the increased drought resulting from climate change. This would be very consequential, as TWEF are among the world's most carbon-dense forests (Keith et al., 2009; Wood, Prior, et al., 2015), supporting Australia's native forestry industry (Florence, 2004), and supplying water to some of the region's most densely populated areas (Benyon & Lane, 2013). Furthermore, increasing frequency of high-severity fire has been shown to convert obligate-seeder-dominated TWEF to non-*Eucalyptus* forest (Bowman, Murphy, et al., 2014; Bowman et al., 2016), and a similar effect could occur in resprouter-dominated forests (Fairman et al., 2016). Climate change will likely also negatively impact the ability of TWEF to recover from high-severity fires, as reduced growth rates of up to 17% (Bowman, Williamson, et al., 2014; Wardell-Johnson, Neldner, et al., 2017) can increase the amount of time necessary for resprouting forests to fully recover from a high-severity fire (Wardell-Johnson, Crellin, et al., 2017), which will lead to decreased carbon stocks in both soil and above-ground biomass (Dean & Wardell-Johnson, 2010; Williams, Bradstock, et al., 2012).

The recognition of mixed-severity fire regimes in TWEF underscores the ecological imperative for management to mimic both low- and high-severity fire. Such approaches could reduce fire risk and support the forest industry while maintaining natural processes. These approaches include broadening silvicultural practices beyond the widely applied 'clearfell, burn and sow' (CBS) model (predicated on the predominance of high-severity fire) to include practices such as variable-density thinning (Carey, 2003) and dispersed-retention harvesting (Neyland et al., 2009). These approaches would create more of the structural heterogeneity that is characteristic of older TWEF (Lindenmayer et al., 2000), and reduce the smoke pollution caused by burning large quantities of logging debris (Bowman, Daniels, et al., 2018). Novel fuel reduction techniques, such as mechanical thinning and removal of the understorey (Hurteau & Brooks, 2011), 'shaded' fire breaks (Agee et al., 2000), and candling

(i.e. controlled winter burning of hazardous bark; Planned Burning Project, 2017), could also be implemented to remove pathways for crown fire development through the bark and live understorey. Such treatments could allow for more frequent prescribed burning in the understorey in temperate-marine TWEF, where it is rarely practiced (except SNSW), especially given the potential for widening prescribed burning weather windows in the region (Clarke et al., 2019).

5 | CONCLUSIONS

Overall, our results indicate that climatic constraints on fire weather and fuel availability, not fuel load, are the key drivers of fire severity in these forests, which has been the general consensus on TWEF (Cawson et al., 2020). Fuel loads do not vary substantially between regions (except in Mediterranean climates, where they are higher), and the likelihood of high-severity fire is correlated with the temperature and fire-weather conditions associated with the local climate (Figure 6), and not strongly correlated with any intrinsic fuel-related factor, including fuel load or the relative abundance of obligate seeders. While combustion of the live understorey is a key predictor of fire severity, the flammability of these live plants is primarily governed by fuel moisture and hence climate (Nolan et al., 2016). Extrinsic factors (such as climate and fire weather) have been well documented to play a dominant role in determining fire severity when compared to intrinsic factors (such as fuel load and arrangement), both in TWEF (Bowman et al., 2016) and in *Eucalyptus* forests more broadly (Penman et al., 2013; Price & Bradstock, 2011). This suggests these systems are particularly vulnerable to climate change, and given an increased likelihood of high-severity fire in a warming climate, need to be managed to reduce this likelihood and make these forests more resilient. This can be achieved by greater recognition of the ecological role of low-severity fires in these ecosystems.

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AUTHORS' CONTRIBUTIONS

D.M.J.S.B., L.D.P. and G.J.W. conceived the ideas and designed the methodology for data collection; J.M.F., G.J.W. and D.M.J.S.B.

conceived of and designed the analysis approach; J.M.F. analysed the data; J.M.F., L.D.P. and D.M.J.S.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All fuel and microclimate measurements, along with numerous other measurements from the Ausplots, are available from the Ausplots Forest Monitoring Network—Forest Fuel Survey, 2014–2016 dataset (Bowman, Furlaud, et al., 2018) on the TERN Aekos Data Portal: <http://doi.org/10.4227/05/5899149e044d9>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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