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RESEARCH ARTICLE

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The carbon cost of the 2019–20 Australian fires varies with fire severity and forest type

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Abstract

Aim: To estimate loss of above-ground carbon (AGC) and conversion of live carbon to dead carbon following understorey and canopy fire.

Location: South-eastern Australia.

Time period: 2019–2020.

Major taxa studied: Four widespread resprouting eucalypt forests.

Methods: Above-ground carbon was measured in 15 plots in each of four forest types one-year post-fire. We also assessed topkill, that is, trees subject to canopy loss that failed to resprout epicormically.

Results: While canopy fire was associated with greater declines in AGC than understorey fire, this was only statistically significant for only one forest type, where AGC declined from 154 to 85 Mg C ha^{-1} following canopy fire. Significant post-fire increases in dead AGC were observed in one forest type, where dead carbon increased from 22 to 60% after canopy fire. Topkill of trees following canopy fire (48–78% of stems) was higher than topkill after understorey fire (36–53% of stems) and in unburnt forest (12–55%). Topkill occurred primarily in small-diameter stems. Consequently, there was no effect of fire on the proportion of dead AGC in trees, with the exception of the forest with lowest productivity (i.e., lowest biomass) and lowest annual rainfall, where dead tree carbon increased from 8% in unburnt forest to 13 and 53% after understorey and canopy fire, respectively. AGC in understorey vegetation and coarse woody debris was similar or lower in burnt compared with unburnt forest. Litter carbon was significantly lower and pyrogenic carbon significantly higher in burnt forest, with no difference between understorey and canopy fire.

Main conclusions: While increased fire severity was associated with increased changes to carbon stocks, there were differences among forest types. Specifically, the driest forest type had the highest rates of topkill following canopy fire. These results highlight the importance of spatial variability in fire severity and forest type in determining the effects of fire on carbon stocks.

KEYWORDS
Black Summer, carbon stocks, defoliation, fire severity, insects, tree mortality, wildfire

1 | INTRODUCTION

The 2019–20 Australian fire season burned an unprecedented extent of temperate forest (Boer et al., 2020), estimated at 7.2 Mha (Bowman et al., 2021). Of this area, an estimated *c*. 44% was burned at high fire severity, as indicated by complete canopy scorch or consumption during the fires (Collins et al., 2021). The fires produced 38 pyrocumulonimbus clouds, which injected huge quantities of aerosols into the lower stratosphere that subsequently circumnavigated the globe (Kablick III et al., 2020; Peterson et al., 2021). The extent of these fires and the considerable smoke emissions they generated led to concerns about the amount of carbon emitted (Zhang et al., 2020). Estimates of carbon emissions range between 612 and 830 Mt of CO_2 equivalent (Australian Government Department of Industry Science Energy and Resources, 2020; Bowman et al., 2021; Byrne et al., 2021; van der Velde et al., 2021; van der Werf et al., 2017). These estimates exceed Australia's annual carbon emissions, estimated at 499 Mt of CO_2 equivalent for 2020 (Australian Government Department of Industry Science Energy and Resources, 2021). To date, estimates of the carbon implications of the fires have not been validated with field observations, nor do they account for the conversion of live biomass to dead biomass, which is important for longer-term carbon dynamics. Fire-killed biomass decays slowly and produces further carbon emissions over years to decades that might far exceed pyrogenic emissions (Ghimire et al., 2012). Furthermore, dead biomass is more likely to be consumed in subsequent fires than live biomass (Dent et al., 2019). Consequently, total above-ground carbon (AGC) stores are likely to be reduced by repeat short-interval fires (Fairman et al., 2022).

The majority of native vegetation affected by the 2019–20 fire season across southern and eastern Australia was eucalypt forest and woodland, which accounted for an estimated 88% of the native vegetation that burned (Gallagher et al., 2021). Eucalypts are well adapted to fire and will generally recover from fire by either resprouting vegetatively or recruiting from seed, or both (Clarke et al., 2015). The resprouting eucalypt forests and woodlands accounted for the majority of the native vegetation burnt by the fires (Gallagher et al., 2021). Resprouting eucalypts can resprout epicormically along the bole and branches after complete defoliation owing to fire, or they may only resprout basally from underground storage organs.

Fire severity is one of the most important factors governing tree survival and recovery after fire in the resprouting eucalypt forests (Bennett et al., 2016). The majority of resprouting eucalypts will typically survive fires of low severity, because these fires do not impact the canopy. However, fires of high and extreme severity (i.e., those that result in complete canopy scorch or consumption) can lead to much higher rates of tree mortality and topkill. In the case of both topkill and tree mortality, all of the above-ground biomass (AGB) is dead, and the tree has failed to resprout epicormically. For trees with topkill, resprouting may still occur from below-ground storage organs (e.g., lignotubers). In a study on resprouting eucalypt forests, Bennett et al. (2016) observed topkill of 5–12% after low-severity fire, which increased to 24–46% after high-severity fire, in trees >20 cm in diameter at breast height (d.b.h.). Rates of tree mortality and topkill vary with species and plant-level attributes. For fires of high to extreme fire severity, higher rates of mortality and topkill are generally observed in trees with small-diameter stems (Strasser et al., 1996). The effects of fire severity on trees have important implications for ecosystem carbon stocks and fluxes, because trees typically account for the largest portion of AGB in eucalypt forests (Volkova et al., 2015). However, fire severity can also have important effects on other components of forest carbon pools. For example, consumption of coarse woody debris (CWD; fallen dead wood ≥2.5 cm in diameter), although highly variable, does increase with fire intensity (Hollis, Anderson, et al., 2011; Volkova et al., 2019). Thus, fire severity is an important determinant of fire effects on carbon stocks.

In addition to fire severity, climatic gradients can also affect post-fire carbon pools through effects on post-fire resprouting. The proportion of resprouting species within an ecosystem tends to vary with productivity, although the nature of resprouting–productivity relationships is mediated by soil fertility (Hammill et al., 2016; Knox & Clarke, 2005; Pausas et al., 2016; Pausas & Bradstock, 2007). Obligate seeding eucalypts (i.e., those that recover from fire via seed only) dominate areas with a low frequency of high-severity fire, including the high-rainfall montane regions of south-eastern Australia (Bowman et al., 2016) and the low- to moderate-rainfall regions of south-western Australia (Nicolle, 2006). Eucalypts that resprout epicormically dominate much of temperate Australia, transitioning to species that only resprout from below ground in semi-arid regions (Clarke et al., 2015). There are some examples where variation in resprouting has been observed within species across climatic gradients, including *Eucalyptus obliqua*, which loses its resprouting capacity in wetter sites (possibly owing to hybridization with a non-resprouting eucalypt; Ashton & Chappill, 1989; Moore, 2015), and *Eucalyptus delegatensis*, which does not resprout across most of its range apart from a resprouting subspecies found in drier areas (Rodriguez-Cubillo et al., 2020). Thus, there is strong spatial variation in the occurrence of resprouting and non-resprouting eucalypt species, with some evidence that resprouting also varies within species across climatic gradients. However, it is highly uncertain to what extent, if any, rates of post-fire resprouting vary within the resprouting eucalypt forest types. This is reflected in the binary nature of the resprouting classification (Clarke et al., 2015).

Here, we estimate AGC in four resprouting eucalypt forest communities of south-eastern Australia that were impacted by the 2019–20 fires. Included in our study is an assessment of differences in resprouting rates among forest types and fire severity. At 1 year post-fire, resprouting is likely to have been initiated in live eucalypt trees, particularly given that there was above-average rainfall in the year after the fires (Bureau of Meteorology, 2022; Supporting Information Table S1). We hypothesize that: (1) carbon stocks in live biomass will decline with increasing fire severity, owing to higher rates of topkill; (2) there will subsequently be an increase in the proportion of dead biomass with increasing fire severity; and (3) rates of topkill among the four forest types will vary with climate.

2 | METHODS

2.1 | Study area and forest types

Assessments of post-fire tree recovery and AGC stocks were undertaken in four different forest types 1 year after the 2019–20 fires (15 plots per forest type; Figure 1). The four forest types included three dry sclerophyll forest types (western slopes dry sclerophyll, Sydney hinterland dry sclerophyll and south-east dry sclerophyll) and one wet sclerophyll forest type (southern tableland wet sclerophyll). Forest type classifications were based on vegetation classes described by Keith (2004). These four forest types were selected because they met the following criteria: (1) they span a relatively broad climatic gradient (670–1,088 mm mean annual rainfall; Table 1); (2) they exhibit varying site productivity, as evidenced by variation in leaf area index (0.8–1.7) and AGC stocks (84–223 Mg C ha^{-1}; Table 1); (3) they were subject to a range of fire severities during the 2019–20 fires, but some unburnt forest remained in close proximity to burnt forest; and (4) plots could be established in areas where previous fires had not occurred within the minimum tolerable fire intervals established for those forest types (Le Breton et al., 2022). In these forests, minimum tolerable fire intervals range from 10 years for dry sclerophyll forests to 28 years for wet sclerophyll forests (Le Breton et al., 2022). For the dry sclerophyll forests, antecedent fires occurred ≥17 years before the 2019–20 fires, and for the wet sclerophyll forest there was no prior fire history recorded. Soil fertility across all forest types was classified as "low" or "moderately low" (Table 1; Department of Planning Industry and Environment, 2020). In south-eastern Australia, rainfall in the lead up to the fires was either very much below average or the lowest on record (Bureau of Meteorology, 2019), with the region subject to a flash drought in 2019, defined as the rapid intensification of drought conditions over a few weeks (Nguyen et al., 2021). Across the study sites, annual rainfall in 2019 was 41–57% below the long-term average (Supporting Information Table S1). In the year following the fires and immediately preceding field surveys, rainfall was above average across the study sites, ranging from 9 to 66% above average (http://www.bom.gov.au; Supporting Information Table S1).

The overstorey of all four forest types was dominated by eucalypts, which are species in the closely related genera of *Eucalyptus*, *Corymbia* and *Angophora* (Table 1). We recorded 13 different eucalypt species across the four forest types, with most plots dominated by two or three species. These eucalypt species all exhibit epicormic resprouting after fire (Clarke et al., 2015). The three dry sclerophyll forest types all supported a shrubby understorey, whereas the wet sclerophyll forest type supported a grassy understorey, with shrub species largely absent (Table 1; Figure 1).

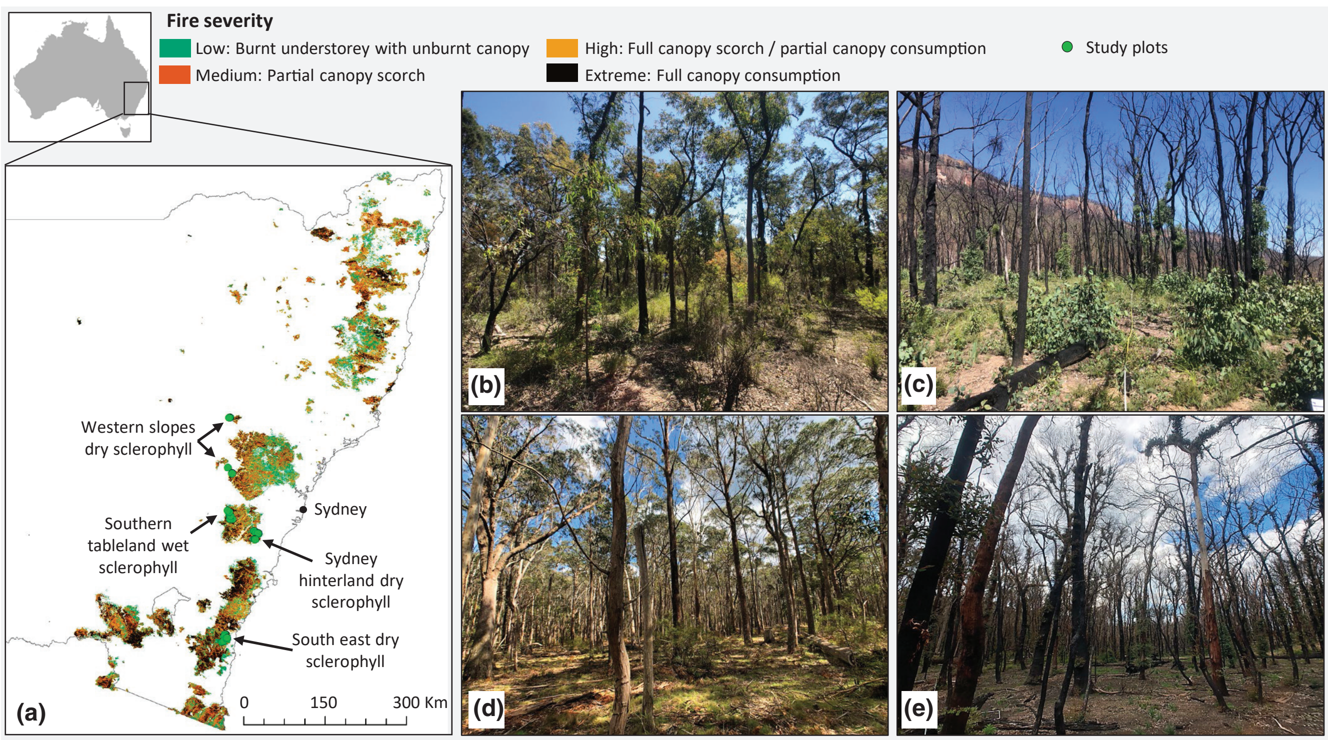

FIGURE 1 (a) Location of study plots, illustrating extent and severity of the 2019–20 fires within the state of New South Wales. Also shown, for western slopes dry sclerophyll forest (top panels) and southern tableland wet sclerophyll forest (bottom panels), are images of: (b,d) unburnt plots; and (c,e) plots burnt at extreme fire severity.

TABLE 1 Description of forest types studied, ordered from lowest to highest above-ground carbon stocks

Characteristic	Forest type: Western slopes dry sclerophyll	South-east dry sclerophyll	Sydney hinterland dry sclerophyll	Southern tableland wet sclerophyll
Number of plots				
Unburnt	3	3	3	3
Low to moderate fire severity (i.e., understorey fire)	4	7	5	7
High to extreme fire severity (i.e., canopy fire)	8	5	7	5
Mean annual rainfall, mm[a]	670	1,062	868	1,088
Mean annual temperature, °C[a]	14.1	14.4	14.3	9.3
Inherent soil fertility class[b,c]	1	2	1	2
Elevation, range, m a.s.l.	402–707	63–161	324–348	1,251–1,320
Maximum tree height, m	16	26	21	22
Leaf area index[d]	0.8 ± 0.1	1.5 ± 0.4	1.7 ± 0.2	1.5 ± 0.3
Dominant tree species	*Eucalyptus sieberi, Eucalyptus fibrosa, Corymbia gummifera*	*Angophora costata, Eucalyptus blaxlandii, Corymbia gummifera*	*Corymbia gummifera, Corymbia eximia, Eucalyptus piperita* subsp. *piperita*	*Eucalyptus dalrympleana, Eucalyptus dives, Eucalyptus radiata*
Epicormic resprouting eucalypts, % of AGC_{Trees}	97.1 ± 1.3	99.1 ± 0.4	99.1 ± 0.5	99.7 ± 1.3
Dominant woody understorey species	*Coprosma quadrifida, Allocasuarina* sp.	*Persoonia* sp., *Banksia spinulosa*	*Banksia spinulosa, Lambertia formosa*	*Eucalyptus* saplings
Tree basal area, m^2/ha	52 ± 21	92 ± 10	100 ± 8	170 ± 28
Tree density, stems/ha				
Trees <20 cm d.b.h.	1,422 ± 539	607 ± 189	1,067 ± 68	533 ± 68
Trees >20 cm d.b.h.	200 ± 75	196 ± 25	175 ± 19	329 ± 25
Shrub density, stems/ha	12,989 ± 7,363	4,472 ± 2,264	10,959 ± 2,847	906 ± 442
AGC, Mg/ha				
Trees	69 ± 19	103 ± 8	123 ± 13	192 ± 36
Understorey	3.9 ± 1.2	1.6 ± 0.6	2.6 ± 0.4	1.5 ± 0.6
Coarse woody debris	5.0 ± 2.2	27.3 ± 3.4	17.8 ± 6.8	20.4 ± 7.0
Litter	6.5 ± 0.3	16.0 ± 2.8	10.5 ± 0.6	10.5 ± 1.9
Total	84 ± 20	148 ± 7	154 ± 10	224 ± 29

Note: Vegetation structural characteristics and AGC are presented for unburnt plots; data shown are the mean ± 1 *SE* ($n = 3$). Post-fire response strategies were characterized from burnt plots ($n = 12$).

Abbreviations: AGC, above-ground carbon; AGC_{Trees}, tree carbon pool; d.b.h., diameter at breast height.

[a]Data obtained from the Australian Bureau of meteorology (http://www.bom.gov.au).

[b]Data obtained from the NSW Government Department of Planning, Industry and Environment (https://www.seed.nsw.gov.au/).

[c]Inherent soil fertility is an indicator of the capacity of the soil to retain and release nutrients and is derived from soil type mapping. Classes are as follows: 1 = very low; 2 = moderately low; 3 = moderate; 4 = moderately high; and 5 = high (Department of Planning Industry and Environment, 2020).

[d]See Supporting Information for methods.

2.2 | Fire severity

Fire severity was classified in the field into one of five categories, following Gibson et al. (2020), based on varying levels of canopy scorch and consumption attributable to fire. Rates of post-fire resprouting in the 12 months after fire do not contribute to fire severity classification (see Table 2 for classifications). We assessed fire severity impacts on different carbon pools by combining the low and moderate categories and the high and extreme categories because they elicit contrasting responses in the dominant tree species (Table 2). When

TABLE 2 Fire severity classifications, following Gibson et al. (2020)

Severity class	Description	Percentage of foliage fire affected	Impacts and responses of trees
Unburnt	Unburnt surface with green canopy	0% canopy and understorey burnt	Canopy foliage retained
Low	Burnt surface with unburnt canopy	>10% burnt understorey, >90% green canopy	Canopy foliage retained
Moderate	Partial canopy scorch	20–90% canopy scorch	Canopy foliage retained, in part
High	Full canopy scorch (±partial canopy consumption)	>90% canopy scorched, <50% canopy biomass consumed	Canopy foliage removed; recovery via resprouting on the canopy branches and bole
Extreme	Full canopy consumption	>50% canopy biomass consumed	Canopy foliage removed; recovery via resprouting on the canopy branches and bole

assessing fire severity impacts on tree resprouting, we also used a remotely sensed metric of fire severity. This enabled us to examine the effects of fire severity on a continuous scale, which allows for a more nuanced assessment of the effects of fire severity on trees. We used the relativized differenced normalized burn ratio (RdNBR), which has been shown to out-perform other indices in characterizing fire severity (Miller et al., 2009). Increasing RdNBR values indicate increasing fire severity. However, given that RdNBR is a relativized ratio, the scale varies between different vegetation types (i.e., a particular value will not indicate the same level of severity across different vegetation types) (Miller et al., 2009). The RdNBR was produced following Gibson et al. (2020). Briefly, we used Sentinel-2 satellite imagery with low cloud cover, with images selected as close as possible to the start and end dates for each of the fires. Sentinel-2 tiles were downloaded from the Copernicus Hub (http://nci.org.au). The RdNBR is calculated from the difference between the pre-fire and post-fire normalized burn ratio (dNBR), which is an index that uses near infrared and short-wave infrared bands and is sensitive to chlorophyll, water content and ash (Miller et al., 2009). The dNBR is then relativized with the pre-fire normalized burn ratio to calculate the RdNBR (Miller et al., 2009).

2.3 | Plot design

We established 15 plots in each of the four forest types (60 plots total), which included three unburnt plots. We aimed for three plots in each of the other fire severity classes. However, there were not many locations across south-eastern Australia where low and extreme fire severity were located within the same forest type. Furthermore, given the extensive burn area of the 2019–20 fire season, locating unburnt forest was a key limitation in selecting study locations. As a result, for some fire severity classes only one or two plots were established, and for others three or four plots were established (Table 1). Plot design followed Jenkins et al. (2016). At each site, two 45 m transects were laid out, one along a north–south axis and one along an east–west axis.

2.4 | Assessments of trees

All trees with a d.b.h. of ≥2.5 cm were measured within 5 m of one side of one of the two transects (i.e., in a 225 m^2 area). All trees ≥20 cm d.b.h. were measured within 5 m of both sides of both transects. Accounting for the intersection of the two transects, the total area wherein large trees were measured was 800 m^2. In addition to measuring all standing trees, we also measured trees that had fallen after the fires. These trees were identifiable by examination of charring patterns and retention of fine branches. For each tree, we recorded species or genus, where possible, and d.b.h. Trees were classified as topkilled if there was no foliage present on the bole or branches.

We estimated the AGB of trees following allometric equations presented by Paul et al. (2016), based on stem d.b.h. We used one equation derived for eucalypts (Equation 1) and another, derived for other single-stemmed trees of relatively high wood density, for non-eucalypt species (Equation 2).

$$\mathrm{AGB} = \exp[2.375\ln(\mathrm{d.b.h.}) - 2.016] \times 1.0668 \quad (1)$$

$$\mathrm{AGB} = \exp[2.220\ln(\mathrm{d.b.h.}) - 1.693] \times 1.0436 \quad (2)$$

These equations were developed from >15,000 measurements of plant biomass across Australia. Paul et al. (2016) showed that these equations explained 90–95% of variation in biomass. Importantly, when validating these equations, Paul et al. (2016) found that the mean absolute percentage error when using species-specific models was on average 12%, and only increased to 17% when using the generalized models.

For tree stumps, which accounted for <2% of tree stems measured, we measured the diameter and height and calculated the volume assuming the stump approximated a cylinder. We then converted from volume to biomass by multiplying by wood density values used for CWD, described below.

2.5 | Understorey vegetation

Understorey vegetation incorporated ground-cover vegetation, such as grasses, and elevated vegetation, such as shrubs and tree saplings. Ground-cover vegetation was classified as biomass <50 cm in height, not including litter, and was harvested in three 1 m^2 quadrats per plot. Each quadrat was placed 17.5 m from the centre of the plot, along the transects. Sampled vegetation was oven dried

(105°C for a minimum of 48 h) and weighed. Elevated vegetation was classified as any live biomass >50 cm in height, but not classified as a tree. Elevated vegetation was measured at the same three locations as ground-cover vegetation, but in circular sub-plots of either 5 m or 3 m diameter, depending on plant density. The majority of vegetation was shrubs or tree saplings, but also included all non-woody plants. For the shrubs and saplings, we measured stem diameter at 10 cm above the ground (D_{10}). We estimated AGB similarly to that for trees, but using allometric equations described in (Nolan et al. 2022; Equation 3).

$$AGB = 0.07 \times {D_{10}}^{2.11} \tag{3}$$

This equation was developed on seven species in New South Wales and had a root-mean square error of 0.04 kg. This generalized model was found to perform similarly well to species-specific models.

For non-woody plants, we either harvested the entire plant or a sub-section of the plant. For example, for large sedges, we counted the number of leaves on a plant, then harvested a sub-section of leaves and measured oven-dry biomass.

2.6 | Coarse woody debris, litter and pyrogenic carbon

The mass of CWD (fallen dead wood ≥2.5 cm diameter) was estimated along each transect (i.e., 90 m per plot) using the line intercept method (Van Wagner, 1968). Briefly, the diameter of CWD intercepting the transect was measured, and converted to biomass using wood density values following (Roxburgh et al. 2006; Supporting Information Table S2). For burnt plots, we also assessed whether CWD had fallen post-fire as evidenced by the absence of bark decomposition and/or charring. Litter (dead biomass <2.5 cm diameter) and pyrogenic carbon (charred biomass produced from incomplete combustion) was collected in the same three 1 m^2 quadrats as ground-cover vegetation and oven dried (≥48 h at 105°C) and weighed.

2.7 | Estimation of net effects of fire severity on forest carbon

We converted AGB into AGC stocks by multiplying trees, shrubs and CWD by 0.5, herbaceous understorey vegetation by 0.53 and litter by 0.54, following the national carbon accounting system (Gifford, 2000). For pyrogenic carbon, we used a multiplier of 0.59 based on research in temperate eucalypt forest (Volkova et al., 2014).

For each forest type, we estimated the net effects of fire severity on forest carbon by comparing burnt and unburnt plots. For burnt plots, we used the same fire categories as previously described (i.e., low to moderate fire severity and high to extreme fire severity). For each plot, we calculated total AGC, total AGC in dead carbon pools and the percentage of dead AGC.

2.8 | Statistical analyses

All analyses were undertaken in R v.4.1.0 (R Core Team, 2020). For the tree carbon pool (AGC_{Trees}), we assessed fire severity impacts using categorical fire severity. For fire severity classes, we assessed differences in: (1) total AGC_{Trees} (i.e., including dead and live carbon); (2) the percentage of stems with topkill; and (3) the percentage of AGC_{Trees} with topkill (i.e., the percentage of dead carbon in trees). For each forest type, we undertook an ANOVA, and when this was significant, we undertook Tukey's adjusted multiple comparisons. We confirmed that the data met ANOVA assumptions of homogeneity of variance, assessed with Levene's test, and normality.

For the eucalypts, which accounted for >97% of AGC_{Trees} (Table 1), we also analysed the drivers of topkill for individual trees within burnt plots. We fitted a generalized linear mixed-effects model (GLMM) to model the probability of topkill. Fixed effects were d.b.h., remotely sensed fire severity (RdNBR) and forest type, with plot included as a random effect. The model also tested for interactions between factors, including a three-way interaction. The lme4 package (Bates et al., 2015) was used to fit the GLMM, with a binomial distribution with a logit link function. To achieve model convergence, we rescaled RdNBR. We also applied a natural logarithmic transformation to d.b.h.

For understorey carbon pools (i.e., understorey vegetation), CWD, litter and pyrogenic carbon, we assessed fire severity impacts in the same way as we assessed impacts on AGC_{Trees} (i.e., using the fire severity classes). For understorey vegetation, we examined differences in total AGC and the percentage of AGC that was dead. For CWD, we examined differences in total observed CWD, in addition to CWD excluding post-fire inputs. For each forest type, we undertook an ANOVA, and when this was significant, we undertook Tukey's adjusted multiple comparisons. For pyrogenic carbon, the data violated the assumptions of normality and homogeneity of variance, owing to a large number of zero observations in unburnt plots. For these data, the Kruskal–Wallis test was fitted, followed by Dunn's post-hoc test.

To assess the net effects of fire on carbon pools, we examined differences in total AGC, in addition to the percentage of AGC that was dead. Similar to previous analyses, for each forest type we undertook an ANOVA, and when this was significant, we undertook Tukey's adjusted multiple comparisons.

3 | RESULTS

3.1 | Effects of fire severity on tree carbon

Trees accounted for the largest component of AGC in the unburnt plots (70–86%; Table 1). At the plot scale, the effect of fire severity on trees depended on whether we examined differences in total above-ground carbon (AGC_{Trees}), the percentage of stems with topkill or the percentage of AGC_{Trees} with topkill. In summary, increasing fire severity generally resulted in an increasing percentage of stems with topkill, but this did not necessarily translate into significantly more tree carbon with topkill. For total AGC_{Trees} (i.e., including live and dead biomass) there was no effect of fire severity, with the exception of the Sydney hinterland dry sclerophyll forest. For this forest type there was significantly lower AGC_{Trees} in forest burnt at high to extreme severity, compared with either unburnt forest or forest burnt at low to moderate fire severity (Figure 2a–d; Supporting Information Table S3). The percentage of stems with topkill did not differ between unburnt forest (12–55%) and forest burnt at low to moderate fire severity (36–53%, $p > .05$; Supporting Information Table S3). However, as expected, there was a significantly higher percentage of stems with topkill in forest burnt at high to extreme severity (47–78%) compared with unburnt forest ($p < .05$; Figure 2e–h), except for wet sclerophyll forest. Despite differences in stem topkill with fire severity, we found no effect of fire severity on the percentage of AGC_{Trees} with topkill, with the exception of the western slopes dry sclerophyll forest. For this forest type, the percentage of AGC_{Trees} with topkill was significantly higher in forest burnt at high to extreme severity (53%) compared with forest burnt at low to moderate severity (13%) and unburnt forest (8%).

When examining individual eucalypt trees within burnt plots, we found that the probability of post-fire topkill was a function of d.b.h. and fire severity (using the remotely sensed fire severity metric RdNBR), with a significant interaction between fire severity and forest type (Supporting Information Table S4). The probability of topkill declined with increasing d.b.h. for all forest types (Figure 3). With the exception of the wet sclerophyll forest, increasing fire severity increased the probability of topkill (Figure 3d), with the western slopes dry sclerophyll forest being most vulnerable to topkill. For example, when RdNBR was at a maximum (i.e., fire severity most extreme), the d.b.h. associated with a .5 probability of topkill was 37 cm for the western slopes dry sclerophyll forest, but 15–20 cm for the other forest types.

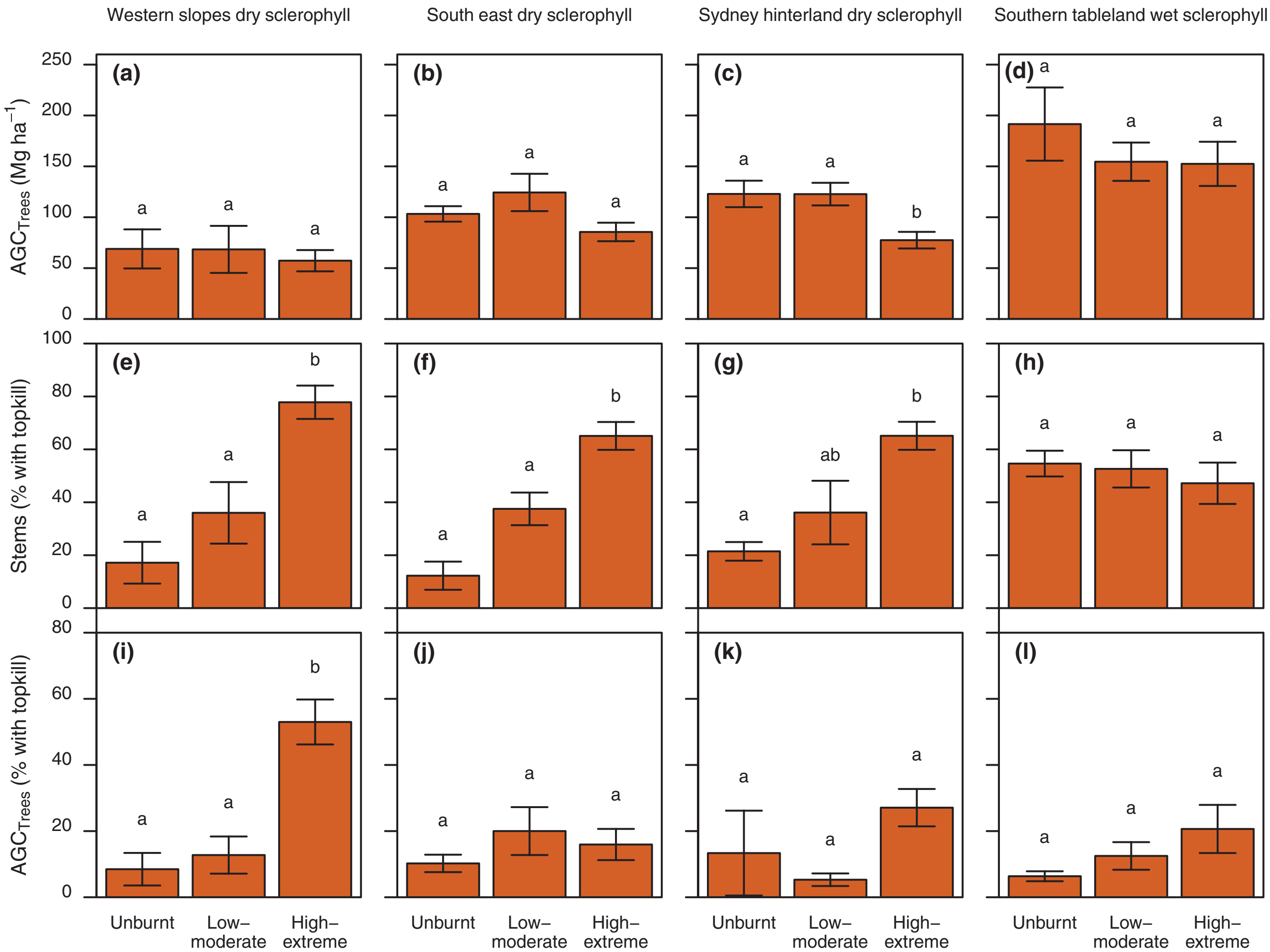

FIGURE 2 Variation in: (a–d) above-ground carbon stocks in trees, including live and dead trees (AGC_{Trees}); (e–h) the percentage of stems with topkill; and (i–l) the percentage of AGC_{Trees} with topkill. Data illustrated are means ±1 *SE*. Within each panel, differing letters indicate significant differences among severity classes.

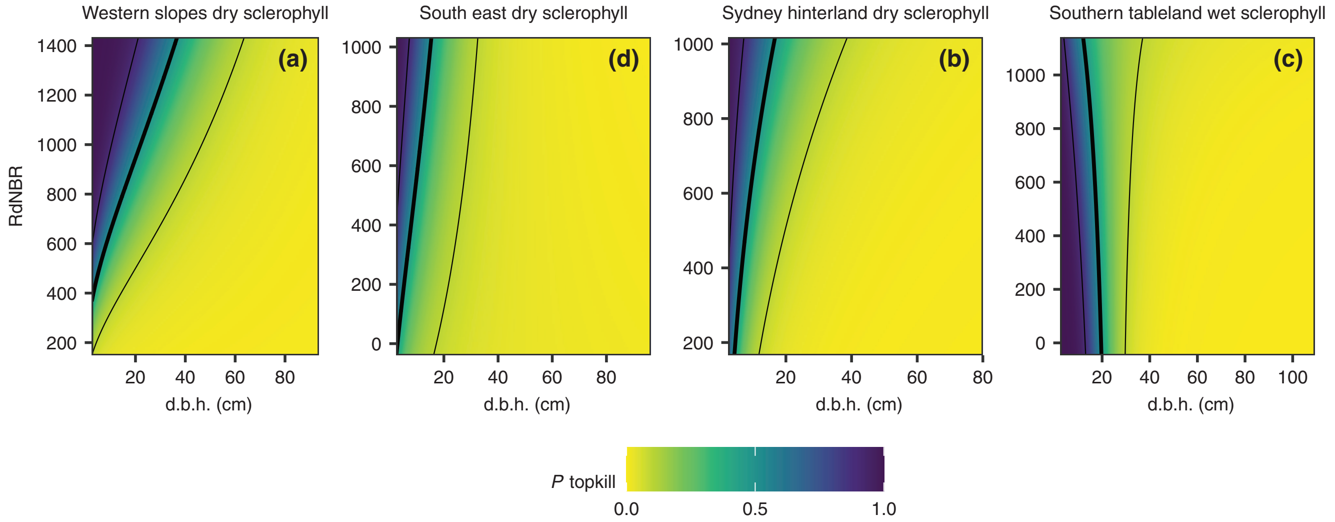

FIGURE 3 (a–d) Heat maps showing the effect of diameter at breast height (d.b.h.) and fire severity (RdNBR) on the probability of topkill for eucalypts within each of the four forest types, as predicted by the generalized linear mixed-effects model. Unburnt plots are not included here. The thick continuous line represents a probability of topkill of .5, and the thin continuous lines represent a probability of .1 and .9. Given that RdNBR is a relativized ratio, the scale varies between different vegetation types (i.e., a particular value will not indicate the same level of severity across different vegetation types) (Miller et al., 2009).

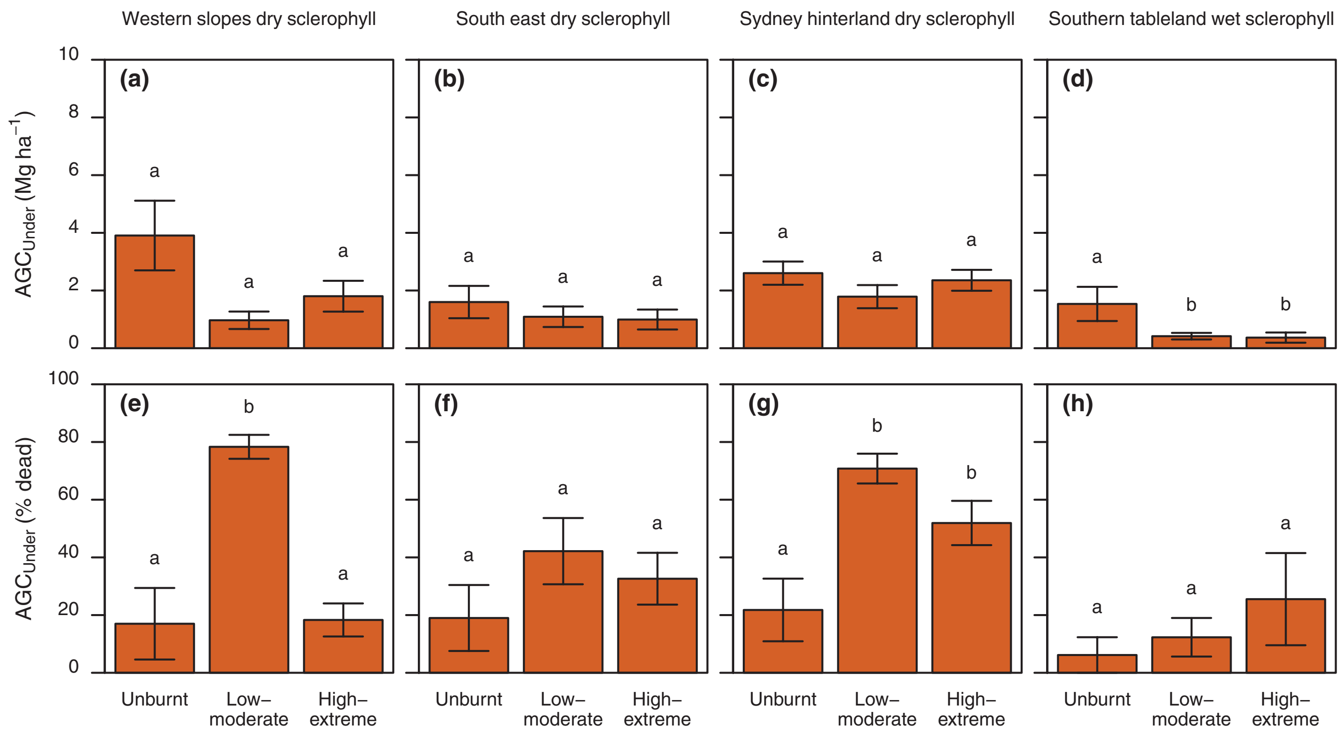

FIGURE 4 Variation as a function of fire severity classes, for each forest type, in: (a–d) total above-ground carbon within understorey vegetation (AGC_{Under}); and (e–h) the percentage of dead AGC_{Under}. Data illustrated are means ± 1 *SE*. Within each panel, differing letters indicate significant differences among fire severity classes.

3.2 | Effects of fire severity on other carbon pools

3.2.1 | Understorey vegetation

Above-ground carbon stocks in understorey vegetation (AGC_{Under}) accounted for the smallest component of AGC in the unburnt plots (1–5%; Table 1). Within forest types, there was no significant effect of fire severity on the amount of post-fire AGC_{Under}, except for the wet sclerophyll forest type, where burnt forest had significantly lower AGC than unburnt forest (Figure 4a–d; Supporting Information Table S3). The effect of fire severity on the percentage of AGC_{Under} that was dead was variable within forest types. For two of the four forest types, the percentage of dead biomass in the AGC_{Under} pool was significantly higher in burnt plots compared with unburnt plots, whereas for the other two forest types there was no effect of fire severity (Figure 4e–h). These results indicate that fire consumed the understorey biomass only in part, with dead biomass retained following fire. Additionally, in the year after the fire, regrowth in the understorey will have contributed to restoration of the understorey carbon pool.

3.2.2 | Coarse woody debris, litter and pyrogenic carbon

After trees, the carbon mass of coarse woody debris (CWD-C) accounted for the largest component of AGC in the unburnt plots (6–18%; Table 1). Litter (Litter-C) accounted for 5–11% of AGC in unburnt plots (Table 1), and only negligible amounts of pyrogenic carbon were present within some unburnt plots. For only two of the forest types was CWD-C significantly lower in burnt plots compared with unburnt plots, indicating either that CWD-C consumption by fire was spatially variable and/or that pre-fire CWD-C was spatially variable. Across all forest types, there was no effect of increasing fire severity on CWD-C, indicating that fire severity did not affect consumption of this carbon pool (Figure 5a–d; Supporting Information Table S3). For all forest types, there was also no evidence that increasing fire severity affected Litter-C consumption (Figure 5e–h; Supporting Information Table S3) or production of pyrogenic carbon (Figure 5i–l; Supporting Information Table S3). These carbon pools were affected simply by the presence or absence of fire. On average, burnt plots exhibited 66–88% lower Litter-C than unburnt plots.

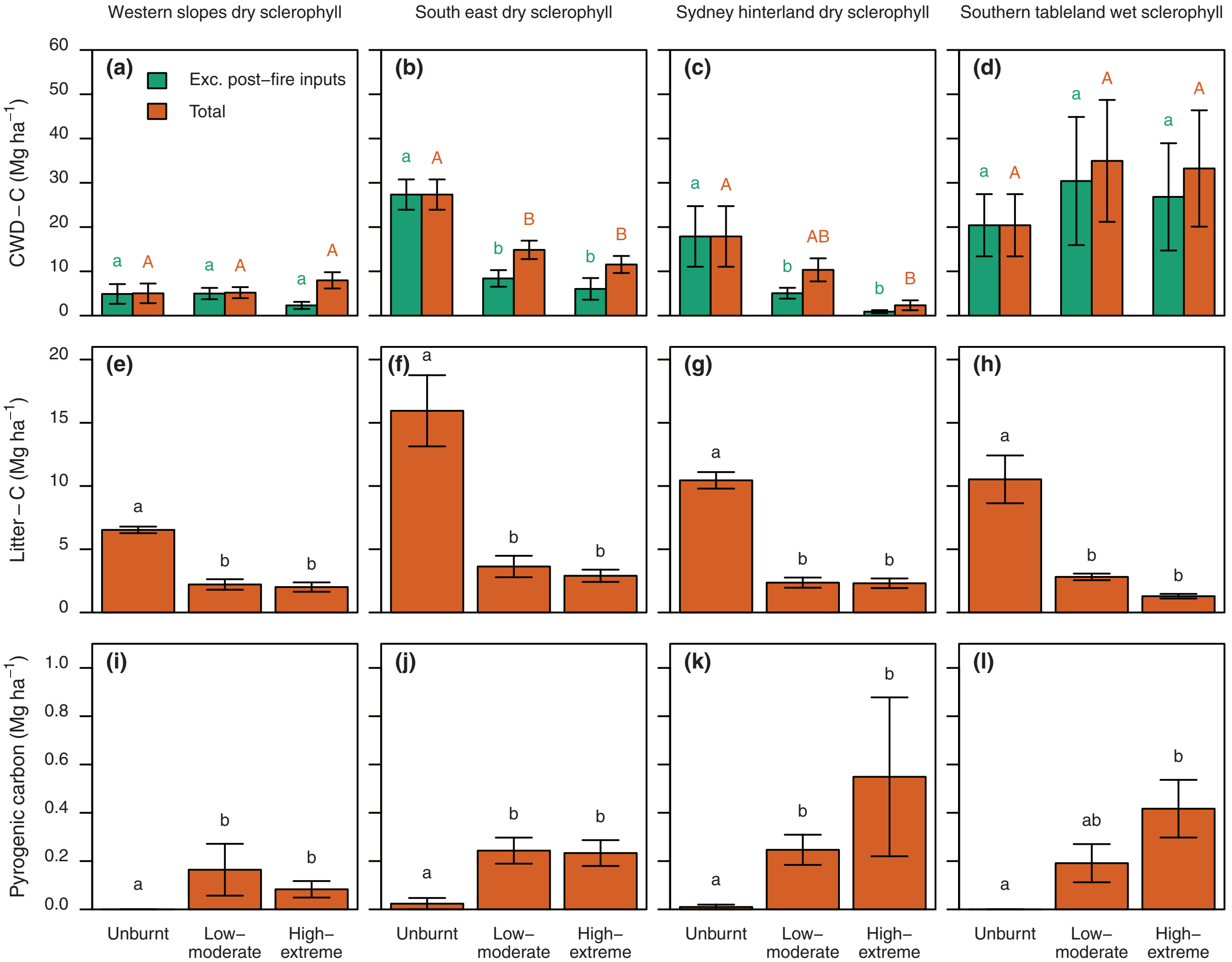

FIGURE 5 Variation as a function of fire severity classes, for each forest type, in: (a–d) carbon stocks of coarse woody debris (CWD-C); (e–h) litter (Litter-C); and (i–l) pyrogenic carbon. For CWD-C, data presented include the total CWD-C observed, in addition to the total observed subtracting post-fire inputs (i.e., CWD that had decreased since the fire). Data illustrated are means ± 1 *SE*. Within each panel, differing letters indicate significant differences among severity classes.

3.3 | Net effects of fire severity on forest carbon

Increasing fire severity was generally associated with greater declines in total AGC (Figures 6 and 7). However, these declines were statistically significant for only one of the forest types (Sydney hinterland dry sclerophyll forest, Figure 6c; Supporting Information Table S3). For this forest type, total AGC declined from 154 Mg C ha^{-1} in unburnt forest to 85 Mg C ha^{-1} in forest burnt at high to extreme fire severity, a decline in carbon stocks of 49%. The percentage of dead carbon did not vary between burnt and unburnt forest, with the exception of the western slopes dry sclerophyll forest (Figure 6; Supporting Information Table S3). For this forest type, the percentage of dead carbon increased from 22% in unburnt forest to 60% in forest burnt at high to extreme fire severity (Figure 6e). In this forest type, the dead AGC pool doubled in forest burnt at high to extreme fire severity (40 Mg C ha^{-1}) compared with unburnt forest (20 Mg C ha^{-1}).

4 | DISCUSSION

4.1 | Effects of fire severity on tree carbon

Our results indicate that only small amounts of tree carbon were consumed during fire (Figure 2c). The biggest impact of fire on tree carbon came from fire triggering topkill and converting live biomass to dead biomass. This dead biomass can then decompose slowly over time and is likely to be more available to burn during future fires (Dent et al., 2019; Ghimire et al., 2012).

As expected, fire severity and tree size influenced rates of topkill in eucalypt trees significantly. The percentage of topkilled trees increased with fire severity for all forest types, except for the wet sclerophyll forest (Figures 2 and 3). However, these effects were not uniform, with the western slopes dry sclerophyll forest exhibiting the greatest vulnerability to topkill (68%) compared with the other forest types (33–50%). Rates of topkill for these three forest types (i.e., excluding the western slopes dry sclerophyll forest) were similar to values previously reported in the literature for resprouting eucalypt forests, which are generally close to 50% (Etchells et al., 2020; Strasser et al., 1996; Trouvé et al., 2021), although lower (21%; Collins, 2020) and higher (58%; Nolan et al., 2020) values have also been reported. Why did the western slopes dry sclerophyll forest (hereafter referred to as the "western forest") exhibit such high rates of topkill in comparison to the other forest types in this study and to previously reported values? We examine plausible explanations, including site productivity, pre-fire drought stress and biotic factors.

The western forest had the lowest mean annual rainfall and site productivity of all the forest types studied (Table 1). As hypothesized, site productivity might have influenced resprouting success, hence rates of topkill, because several studies have shown that resprouting species decline at lower-productivity sites (Knox & Clarke, 2005; Pausas et al., 2016; Pausas & Bradstock, 2007). However, we found no evidence that the variation in productivity

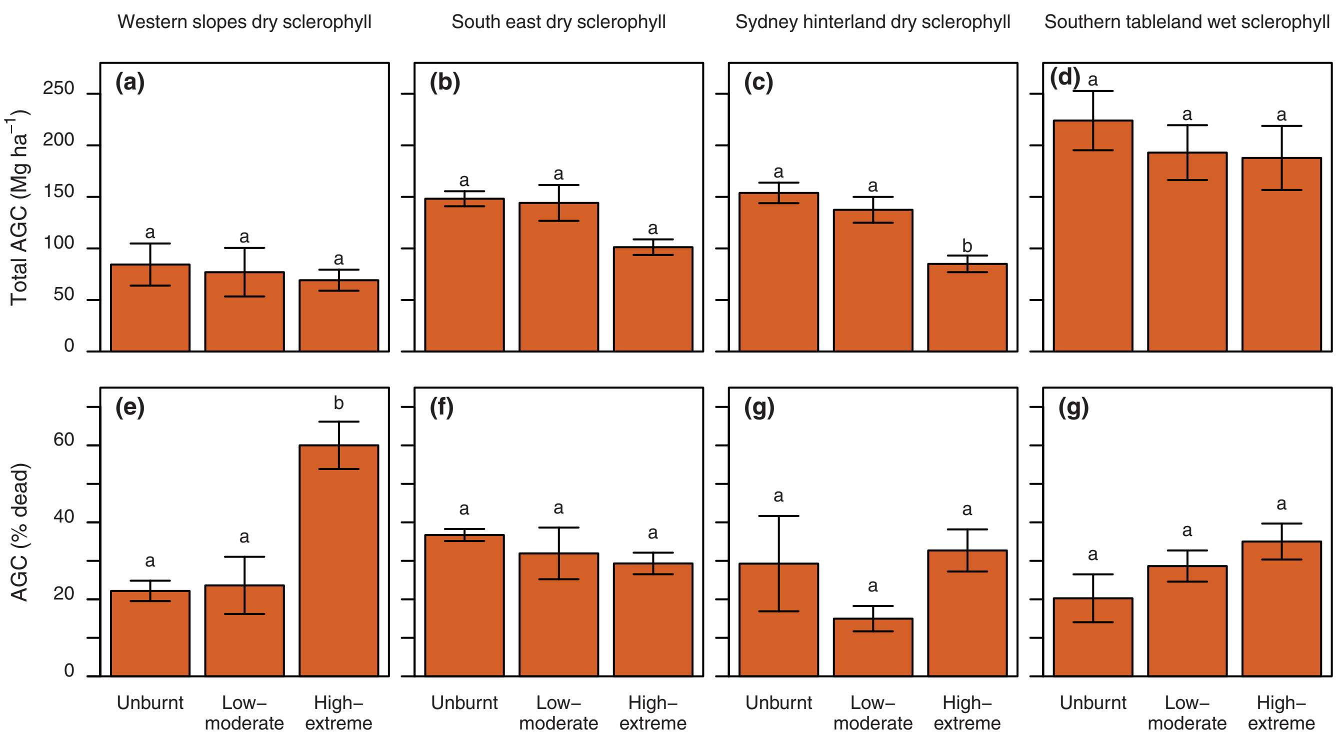

FIGURE 6 Variation in: (a–d) total above-ground carbon (AGC); and (e–h) the percentage of the AGC pool that is in the dead carbon pool. Data illustrated are means ± 1 *SE*. Within each panel, differing letters indicate significant differences among severity classes.

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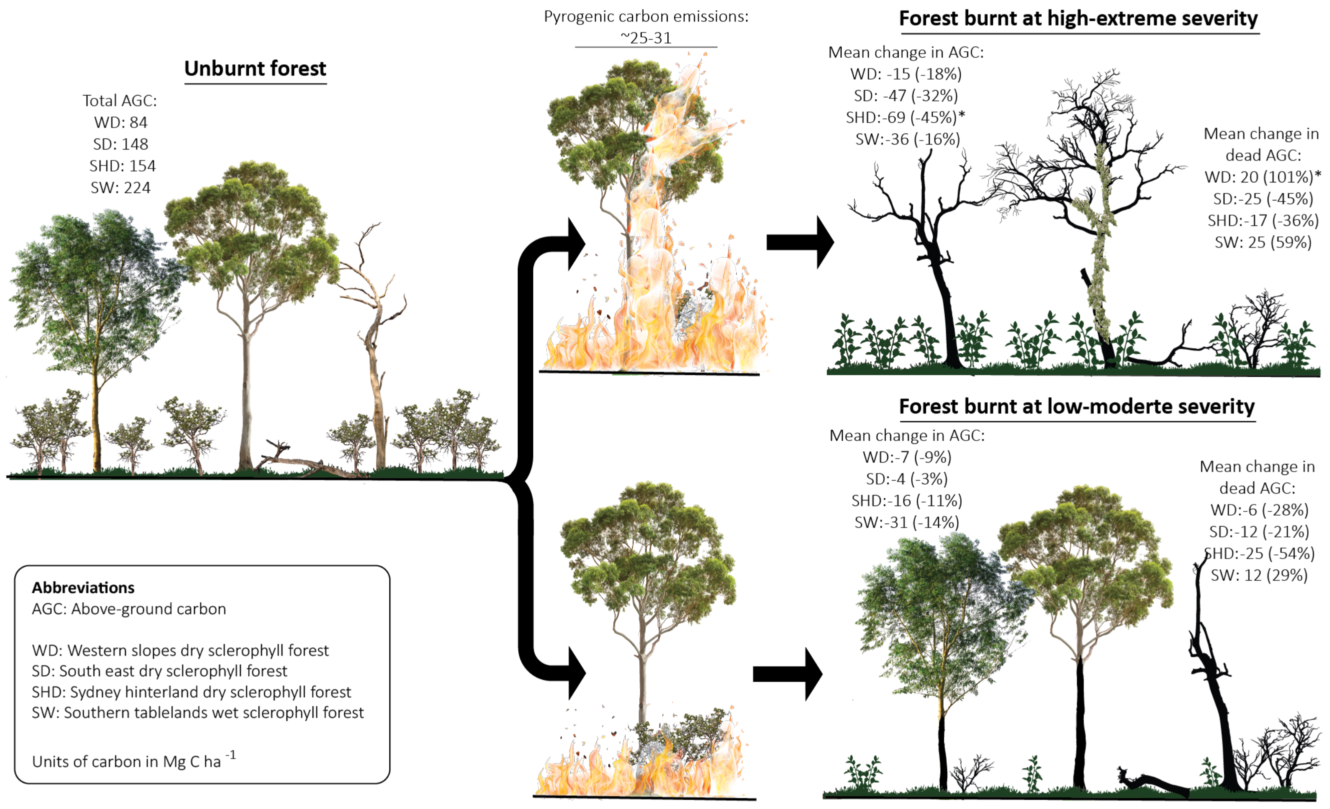

FIGURE 7 Summary of plot-level estimates of total above-ground carbon in unburnt forest (left side) and mean loss of carbon and change in dead carbon stocks in burnt forest (right side). *Statistically significant changes in carbon stocks (see Figure 6). Also shown are pyrogenic carbon emissions (in the centre) estimated from the papers by Bowman et al. (2021), van der Velde et al. (2021) and the Australian Government Department of Industry Science Energy and Resources (2020), and converted from CO_2-equivalent emissions to carbon (in megagrams of carbon per hectare).

among the other forest types manifested in differing resprouting success (Figure 2). Furthermore, the trees in the western forest were more vulnerable to topkill than trees in a similar study in resprouting eucalypt forest located in a similar rainfall zone (*c*. 600 mm annual rainfall). In that study, Fairman et al. (2019) found that the d.b.h. associated with a .5 probability of topkill was 15 cm, which contrasts with the 37 cm observed for the western forest (Figure 3a). Productivity might have affected resprouting success indirectly by influencing tree sizes or other plant attributes, such as bark thickness. Indeed, the western forest did have a higher density of small trees than the other forest types studied (Table 1), and small trees are more vulnerable to topkill (Figure 3; Strasser et al., 1996). However, this does not fully explain the variation in topkill among our forest types, because the western forest had a higher probability of topkill for trees of the same size, subject to extreme fire severity, compared with the other forest types (Figure 3).

Variation in pre-fire drought and heat stress could potentially contribute to variation in rates of post-fire topkill. Pre-fire drought and heat stress might trigger topkill irrespective of fire or might weaken the capacity of trees to resprout after fire by depleting non-structural carbohydrate reserves and triggering hydraulic failure (Karavani et al., 2018; Nolan, Collins, et al., 2021). The drought preceding the 2019–20 fires was the most severe on record, combined with the highest temperatures on record (Bureau of Meteorology, 2019), and resulted in extensive canopy dieback across resprouting eucalypt forests in the region (De Kauwe et al., 2020; Nolan, Gauthey, et al., 2021). However, the degree of pre-fire drought stress, relative to mean site water availability, was similar across sites. We used the difference between precipitation (P) and potential evapotranspiration (PET) as a measure of site water availability. We calculated 2-year P-PET percentiles for the study area region over 1950–2020 and found that average values for each forest type studied were all ≤0.3 percentile (Supporting Information Figure S1), indicating similar extreme drought stress. Estimated root-zone soil moisture also indicated that all study sites were subject to similar extreme drought stress (Supporting Information Figure S2). However, similar levels of drought and heat stress can affect vegetation differently. Studies have shown that plants on the dry edge of their climatic distribution are more vulnerable to drought stress (Anderegg et al., 2019). Conversely, trees located in more arid climates often have wider hydraulic safety margins than trees from wetter climates (Peters et al., 2021). Thus, although there is no clear evidence that the pre-fire drought and heat stress impacted the western forest type differentially, we cannot rule out the possibility that this forest type was more drought stressed owing to either species-specific factors, such as vulnerability to cavitation, or site-specific factors, such as soil properties.

A final potential explanation is that biotic factors contributed to post-fire topkill. Immediately after the fires there were anecdotal observations that the western forest resprouted epicormically, but this new foliage was consumed by sawfly larvae, and the trees did not resprout again (NSW National Parks and Wildlife Service, pers. comm.). Furthermore, during field surveys 1 year post-fire, we observed historical defoliation of epicormic regrowth (Supporting Information Figure S3). Sawflies are hymenopterans in the suborder Symphyta and are known to cause significant defoliation in eucalypt plantations (Jordan et al., 2002). Drought stress followed by severe insect defoliation is known to drive increased mortality rates of resprouting eucalypts (Crombie & Milburn, 1988). To date, we are not aware of any studies that have observed this phenomenon following fire and a single defoliation event.

We are unable to conclude what factor or factors drove the higher rates of topkill in the western forests. However, our results highlight that spatial variation in post-fire topkill does occur across resprouting eucalypt forests, and this is not only attributable to fire severity and might include complex interactions with site productivity, drought stress and biotic factors. Furthermore, characteristics of the fire itself might have influenced rates of tree mortality. Although fire severity provides a valuable metric for the impacts of fire on vegetation (Keeley, 2009), it does not capture other aspects of the fire that might have been important. For example, the duration of heating of tree stems and roots might influence heat penetration through bark and the extent of root damage (Hood et al., 2018).

4.2 | Effects of fire severity on other carbon pools

In contrast to trees, there was no clear effect of increasing fire severity on any of the other carbon pools examined (i.e., understorey, litter, CWD and pyrogenic carbon). This reflects the location of these other carbon pools in the understorey or on the forest floor, where canopy fire did not increase rates of biomass consumption.

Understorey AGC was not significantly reduced by fire in the dry sclerophyll forest types, but there was a significant reduction in the wet sclerophyll forest type (Figure 4). However, fire did increase the percentage of dead biomass for two of the dry sclerophyll forest types. These results might reflect a combination of smaller impacts of fire on the understorey in forest burnt at low to moderate fire severity, and rapid recovery of understorey biomass in forest burnt at high to extreme severity in the year after the fire. In forest burnt at high to extreme severity, the high-light and high-nutrient environment facilitates prolific post-fire recruitment in eucalypt forests (Bennett et al., 2016; Etchells et al., 2020; Gordon et al., 2017).

Amounts of CWD-C were either similar or lower in burnt compared with unburnt forest (Figure 5a–d). Although we observed influxes of CWD-C after fire, these were not enough to change the observed patterns of CWD-C with fire severity. These findings are in contrast to those of Hollis, Anderson, et al. (2011) and Volkova et al. (2019), who found that CWD consumption generally increased with fire intensity (which typically scales with fire severity) in eucalypt forests. Our results might reflect low fuel moisture conditions during the fires. Although the moisture content of CWD has not been shown to influence consumption directly in eucalypt forests (Hollis, Matthews, et al., 2011), studies in North American forests have shown that low moisture content increases woody fuel consumption (Knapp et al., 2005; Prichard et al., 2017). Given the severe drought conditions, the moisture content of CWD was likely to be uniformly low. For the wet sclerophyll forest type, we observed no difference in CWD-C between burnt and unburnt plots (Figure 5c). These results are unexpected, but are likely to reflect a large spatial variation in CWD-C in this forest, with the standard error within burnt plots being more than twice that of other forest types. For the western forest type, likewise, we observed no difference in CWD-C between burnt and unburnt forest, which reflects the low CWD-C present within this forest (5 Mg C ha^{-1}) compared with the other forest types (18–27 Mg C ha^{-1}). Low amounts of CWD-C in the western forest are consistent with the low productivity of this forest, with CWD typically reflecting standing biomass (Burton et al., 2021).

For Litter-C, burnt plots uniformly had less mass than unburnt plots, with the opposite trend for pyrogenic carbon. These results are consistent with a previous study on litter, which showed no difference in litter loads after a low-intensity prescribed burn or a high-intensity wildfire (Volkova et al., 2019). We are not aware of any studies explicitly examining the effects of fire severity on production of pyrogenic carbon. However, our observations of pyrogenic carbon (<0.6 Mg C ha^{-1}) are similar to those of Jenkins et al. (2016), who observed pyrogenic carbon of ≤8.4 Mg C ha^{-1} immediately post-fire, which diminished rapidly and was undetectable by 1 year post-fire. Pyrogenic carbon is a recalcitrant form of carbon and is therefore important as a long-term carbon sink where it remains on site (i.e., is incorporated into the soil and not transported via erosion) (Santín et al., 2016). Our estimates of pyrogenic carbon are likely to be under-estimates, because we did not attempt to quantify charred material on CWD or on standing biomass, nor fine particles within soil. Nevertheless, our results indicate that fire severity might not affect this carbon pool significantly.

4.3 | Net effects of fire severity on forest carbon

We observed a significant decrease in AGC stocks following fire in only one of the four forest types, 1 year after fire (Figures 6 and 7). Our observations incorporate post-fire plant growth in the understorey over 1 year post-fire and are thus an under-estimate of carbon emitted during the fires, although probably not by much, given that this carbon pool accounts for <5% of AGC in unburnt forest (Table 1). We also observed a significant increase in the percentage of dead AGC stocks following fire in only one of the four forest types (Figures 6 and 7), namely, the western forest type, which exhibited the largest rates of topkill. Our results do not account for the conversion of live to dead carbon and the loss of foliage within individual trees that exhibit post-fire epicormic resprouting. Although trees might have resprouted successfully following fire, they might have lower overall leaf area and a higher proportion of dead branches compared with unburnt trees. We suggest that assessing these within-tree changes might lead to further improvements in the estimates of the impacts of fire on carbon stocks.

Our estimates of net AGC losses of 4–31 Mg C ha^{-1} for understorey fire and 15–69 Mg C ha^{-1} for canopy fire compare with modelled estimates of mean carbon emissions of 25–31 Mg C ha^{-1} (Figure 7; Australian Government Department of Industry Science Energy and Resources, 2020; Bowman et al., 2021; van der Velde et al., 2021). The main source of uncertainty in our estimates, and in other estimates, relates to the consumption of trees. Standing trees are generally not consumed during fire, unless they are already dead (Volkova et al., 2014; Volkova & Weston, 2015) or are hollow (Keith et al., 2014). We observed that in unburnt forest, trees with topkill accounted for 7.7–16.9 Mg C ha^{-1} of AGC, whereas in forest burnt at high to extreme fire severity, trees with topkill accounted for 14.6–32.2 Mg C ha^{-1} of AGC. If there is a repeat short-interval fire of high to extreme severity, this could substantially increase net carbon emissions from that fire. Thus, accounting for trees with topkill and potential consumption of those trees during fire has the potential to increase estimated CO_2 emissions from fires substantially, but it remains highly uncertain. There are additional uncertainties in our estimates owing to the allometric equations used, particularly for trees, which accounted for the largest biomass pool. The equation used to estimate tree biomass has a root mean square error of 0.36 (Paul et al., 2016), whereas the equation used for shrubs has a root mean square error of 0.04 (Nolan et al., 2022). The use of species-specific allometric equations would have improved our estimates (Paul et al., 2016), although such equations are not readily available for many species across Australia.

Our results demonstrate that spatial variability in AGC, fire severity and rates of topkill are important determinants of the net carbon effects of wildfires. In a recent remote sensing-based regional assessment of the post-fire recovery dynamics following the 2019–20 fires in south-eastern Australia (Gibson & Hislop, 2022), high spatial variation in spectral recovery was also observed. Although there was generally strong spectral recovery, with >50% of the total burned area having >80% of the pre-fire spectral index value after 1 year, several locations had recovery responses divergent from trends in surrounding areas, including the region incorporating our plots in the western forest. There was also strong biogeographical variation in the effect of fire severity on post-fire spectral recovery. This highlights several regions of concern that might have compromised ecosystem resilience owing to compounding threatening processes, which urgently require research prioritization to determine the mechanisms driving post-fire recovery dynamics.

Quantification of the effects of fire on forest carbon dynamics requires long-term monitoring of post-fire recovery. Over the long term, net carbon emissions from fires are thought to be balanced by carbon uptake from regenerating vegetation (Bowman et al., 2009; Williams et al., 2012). However, the capacity for forests to return to their pre-fire state might be threatened by shorter fire-return intervals and more frequent drought under climate change (Enright et al., 2015). As a result of the 2019–20 fires, up to one-third of vegetation might have burnt too frequently, placing it at risk of vegetation transitions (Le Breton et al., 2022). The fire severity of repeat fires is important, with short-interval prescribed burns or repeat understorey wildfires likely to have much lower impact on carbon stocks than repeated high-severity fires (Bennett et al., 2014; Collins et al., 2019; Gordon et al., 2018). Monitoring post-fire recovery in carbon fluxes is also important for assessing the long-term effects of fire on forest carbon dynamics. There are few studies that investigate post-fire carbon fluxes in resprouting forests. However, a study by Sun et al. (2020) in a semi-arid eucalypt woodland observed recovery of net ecosystem production within 3 years after a canopy-defoliating fire. Furthermore, in a study in temperate eucalypt forest, Nolan et al. (2014) observed that post-fire regrowth exhibited photosynthetic rates that were ≤21% higher than unburnt forest, which is likely to facilitate rapid post-fire recovery.

4.4 | Conclusions

Our study highlights the importance of fire severity in governing post-fire carbon dynamics. Recent advancements in mapping fire severity (e.g., Collins et al., 2020; Gibson et al., 2020; Yin et al., 2020) will improve assessments of fire impacts. Importantly, our results demonstrate that fires that do not impact the tree canopy are likely to have limited impacts on carbon stocks. In the 2019–20 fires, an estimated 37% of the mapped burn area was either unburnt or did not impact the canopy (Collins et al., 2021). Our results also highlight the importance of other abiotic and biotic factors in governing post-fire tree recovery, and subsequently, post-fire carbon dynamics. We conclude that improved models of tree mortality or topkill are key to improving assessments of fire impacts on forest carbon dynamics.

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DATA AVAILABILITY STATEMENT

The data used in this manuscript are available at: https://data.mendeley.com/datasets/4xdgbbf2tx (Nolan, 2022).

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REFERENCES

Anderegg, W. R. L., Anderegg, L. D. L., Kerr, K. L., & Trugman, A. T. (2019). Widespread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. *Global Change Biology*, *25*(11), 3793–3802.

Ashton, D., & Chappill, J. (1989). Secondary succession in post-fire scrub dominated by *Acacia verticillata* (L'Hérit.) Willd. At Wilsons promontory, Victoria. *Australian Journal of Botany*, *37*(1), 1–18.

Australian Government Department of Industry Science Energy and Resources. (2020). *Estimating greenhouse gas emissions from bushfires in Australia's temperate forests: focus on 2019–20*. Commonwealth of Australia.

Australian Government Department of Industry Science Energy and Resources. (2021). *Quarterly update of Australia's National Greenhouse Gas Inventory: December 2020*. Commonwealth of Australia.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bennett, L. T., Aponte, C., Baker, T. G., & Tolhurst, K. G. (2014). Evaluating long-term effects of prescribed fire regimes on carbon stocks in a temperate eucalypt forest. *Forest Ecology and Management*, *328*, 219–228.

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

Boer, M. M., Resco de Dios, V., & Bradstock, R. (2020). Unprecedented burn area of Australian mega forest fires. *Nature Climate Change*, *10*(3), 171–172.

Bowman, D., Williamson, G. J., Price, O. F., Ndalila, M. N., & Bradstock, R. A. (2021). Australian forests, megafires and the risk of dwindling carbon stocks. *Plant, Cell & Environment*, *44*(2), 347–355.

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., … Pyne, S. J. (2009). Fire in the earth system. *Science*, *324*(5926), 481–484.

Bowman, D. M. J. S., Williamson, G. J., Prior, L. D., & Murphy, B. P. (2016). The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Global Ecology and Biogeography*, *25*(10), 1166–1172.

Bureau of Meteorology. (2019). *Special Climate Statement 70—drought conditions in Australia and impact on water resources in the Murray–Darling Basin*. Commonwealth of Australia.

Bureau of Meteorology, (2022). *Australian Government*. Commonwealth of Australia. http://www.bom.gov.au/

Burton, J. E., Bennett, L. T., Kasel, S., Nitschke, C. R., Tanase, M. A., Fairman, T. A., Parker, L., Fedrigo, M., & Aponte, C. (2021). Fire, drought and productivity as drivers of dead wood biomass in eucalypt forests of South-Eastern Australia. *Forest Ecology and Management*, *482*, 118859.

Byrne, B., Liu, J., Lee, M., Yin, Y., Bowman, K. W., Miyazaki, K., Norton, A. J., Joiner, J., Pollard, D. F., Griffith, D. W., & Velazco, V. A. (2021). The carbon cycle of Southeast Australia during 2019–2020: Drought, fires, and subsequent recovery. *AGU Advances*, *2*(4), e2021AV000469.

Clarke, P. J., Lawes, M. J., Murphy, B. P., Russell-Smith, J., Nano, C. E. M., Bradstock, R., Enright, N. J., Fontaine, J. B., Gosper, C. R., Radford, I., Midgley, J. J., & Gunton, R. M. (2015). A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Science of the Total Environment*, *534*, 31–42.

Collins, L. (2020). Eucalypt forests dominated by epicormic resprouters are resilient to repeated canopy fires. *Journal of Ecology*, *108*, 310–324.

Collins, L., Bradstock, R., Ximenes, F., Horsey, B., Sawyer, R., & Penman, T. (2019). Aboveground forest carbon shows different responses to fire frequency in harvested and unharvested forests. *Ecological Applications*, *29*(1), 14.

Collins, L., Bradstock, R. A., Clarke, H., Clarke, M. F., Nolan, R. H., & Penman, T. D. (2021). The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters*, *16*, 044029.

Collins, L., McCarthy, G., Mellor, A., Newell, G., & Smith, L. (2020). Training data requirements for fire severity mapping using Landsat imagery and random forest. *Remote Sensing of Environment*, *245*, 111839.

Core Team, R. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Crombie, D. S., & Milburn, J. A. (1988). Water relations of rural eucalypt dieback. *Australian Journal of Botany*, *36*, 233–237.

De Kauwe, M. G., Medlyn, B. E., Ukkola, A. M., Mu, M., Sabot, M. E., Pitman, A. J., Meir, P., Cernusak, L. A., Rifai, S. W., Choat, B., Tissue, D. T., Blackman, C. J., Li, X., Roderick, M., & Briggs, P. R. (2020). Identifying areas at risk of drought-induced tree mortality across south-eastern Australia. *Global Change Biology*, *26*, 5716–5733.

Dent, J. M., Buckley, H. L., Lustig, A., & Curran, T. J. (2019). Flame temperatures saturate with increasing dead material in *Ulex europaeus*, but flame duration, fuel consumption and overall flammability continue to increase. *Fire*, *2*(1), 6.

Department of Planning Industry and Environment. (2020). *Estimated Inherent Soil Fertility of NSW, Version 4*. I.a.E. NSW Department of Planning.

Enright, N. J., Fontaine, J. B., Bowman, D., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment*, *13*(5), 265–272.

Etchells, H., O'Donnell, A. J., McCaw, W. L., & Grierson, P. F. (2020). Fire severity impacts on tree mortality and post-fire recruitment in tall eucalypt forests of Southwest Australia. *Forest Ecology and Management*, *459*, 117850.

Fairman, T. A., Bennett, L. T., & Nitschke, C. R. (2019). Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *Journal of Environmental Management*, *231*, 59–65.

Fairman, T. A., Nitschke, C. R., & Bennett, L. T. (2022). Carbon stocks and stability are diminished by short-interval wildfires in fire-tolerant eucalypt forests. *Forest Ecology and Management*, *505*, 119919.

Gallagher, R. V., Allen, S., Mackenzie, B. D. E., Yates, C. J., Gosper, C. R., Keith, D. A., Merow, C., White, M. D., Wenk, E., Maitner, B. S., He, K., Adams, V. M., & Auld, T. D. (2021). High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity. *Diversity and Distributions*, *27*(7), 1166–1179.

Ghimire, B., Williams, C. A., Collatz, G. J., & Vanderhoof, M. (2012). Fire-induced carbon emissions and regrowth uptake in western U.S. forests: Documenting variation across forest types, fire severity, and climate regions. *Journal of Geophysical Research-Biogeosciences*, *117*, 29.

Gibson, R., Danaher, T., Hehir, W., & Collins, L. (2020). A remote sensing approach to mapping fire severity in South-Eastern Australia using sentinel 2 and random forest. *Remote Sensing of Environment*, *240*, 111702.

Gibson, R. K., & Hislop, A. (2022). Signs of resilience in resprouting Eucalyptus forests, but areas of concern: One year of post-fire recovery from Australia's Black Summer of 2019–20. *International Journal of Wildland Fire*.

Gifford, R. M. (2000). *National carbon accounting system technical report no. 22: Carbon contents of above-ground tissues of Forest and woodland trees*. Australian Greenhouse Office.

Gordon, C. E., Bendall, E. R., Stares, M. G., Collins, L., & Bradstock, R. A. (2018). Aboveground carbon sequestration in dry temperate forests varies with climate not fire regime. *Global Change Biology*, *24*(9), 4280–4292.

Gordon, C. E., Price, O. F., Tasker, E. M., & Denham, A. J. (2017). *Acacia* shrubs respond positively to high severity wildfire: Implications for conservation and fuel hazard management. *Science of the Total Environment*, *575*, 858–868.

Hammill, K., Penman, T., & Bradstock, R. (2016). Responses of resilience traits to gradients of temperature, rainfall and fire frequency in fire-prone, Australian forests: Potential consequences of climate change. *Plant Ecology*, *217*(6), 725–741.

Hollis, J. J., Anderson, W. R., McCaw, W. L., Cruz, M. G., Burrows, N. D., Ward, B., Tolhurst, K. G., & Gould, J. S. (2011). The effect of fireline intensity on woody fuel consumption in southern Australian eucalypt forest fires. *Australian Forestry*, *74*(2), 81–96.

Hollis, J. J., Matthews, S., Anderson, W. R., Cruz, M. G., & Burrows, N. D. (2011). Behind the flaming zone: Predicting woody fuel consumption in eucalypt forest fires in southern Australia. *Forest Ecology and Management*, *261*(11), 2049–2067.

Hood, S. M., Varner, J. M., van Mantgem, P., & Cansler, C. A. (2018). Fire and tree death: Understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters*, *13*(11), 113004.

Jenkins, M. E., Bell, T. L., Poon, L. F., Aponte, C., & Adams, M. A. (2016). Production of pyrogenic carbon during planned fires in forests of East Gippsland, Victoria. *Forest Ecology and Management*, *373*, 9–16.

Jordan, G. J., Potts, B. M., & Clarke, A. R. (2002). Susceptibility of *Eucalyptus globulus* ssp. *globulus* to sawfly (*Perga affinis* ssp. *insularis*) attack and its potential impact on plantation productivity. *Forest Ecology and Management*, *160*(1), 189–199.

Kablick, G. P., III, Allen, D. R., Fromm, M. D., & Nedoluha, G. E. (2020). Australian pyroCb smoke generates synoptic-scale stratospheric anticyclones. *Geophysical Research Letters*, *47*(13), e2020GL088101.

Karavani, A., Boer, M. M., Baudena, M., Colinas, C., Díaz-Sierra, R., Pemán, J., de Luis, M., Enríquez-de-Salamanca, Á., & Resco de Dios, V. (2018). Fire-induced deforestation in drought-prone Mediterranean forests: Drivers and unknowns from leaves to communities. *Ecological Monographs*, *88*(2), 141–169.

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire*, *18*(1), 116–126.

Keith, D. A. (2004). *Ocean shores to desert dunes: Native vegetation of New South Wales and the ACT*. NSW Department of Environment & Conservation.

Keith, H., Lindenmayer, D. B., Mackey, B. G., Blair, D., Carter, L., McBurney, L., Okada, S., & Konishi-Nagano, T. (2014). Accounting for biomass carbon stock change due to wildfire in temperate forest landscapes in Australia. *PLoS One*, *9*(9), e107126.

Knapp, E. E., Keeley, J. E., Ballenger, E. A., & Brennan, T. J. (2005). Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management*, *208*(1–3), 383–397.

Knox, K. J. E., & Clarke, P. J. (2005). Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Functional Ecology*, *19*(4), 690–698.

Le Breton, T. D., Lyons, M. B., Nolan, R. H., Penman, T., Williamson, G. J., & Ooi, M. K. (2022). Megafire-induced interval squeeze threatens vegetation at landscape scales. *Frontiers in Ecology and the Environment*.

Miller, J. D., Knapp, E. E., Key, C. H., Skinner, C. N., Isbell, C. J., Creasy, R. M., & Sherlock, J. W. (2009). Calibration and validation of the relative differenced normalized burn ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sensing of Environment*, *113*(3), 645–656.

Moore, G. M. (2015). The role of lignotubers (basal burls) in the stress recovery of messmate stringybark, *Eucalyptus obliqua* L'Herit. seedlings and its arboricultural implications. *Arboricultural Journal*, *37*(2), 113–125.

Nguyen, H., Wheeler, M. C., Hendon, H. H., Lim, E. P., & Otkin, J. A. (2021). The 2019 flash droughts in subtropical eastern Australia and their association with large-scale climate drivers. *Weather and Climate Extremes*, *32*, 100321.

Nicolle, D. (2006). A classification and census of regenerative strategies in the eucalypts (*angophora*, *Corymbia* and *eucalyptus*-Myrtaceae), with special reference to the obligate seeders. *Australian Journal of Botany*, *54*(4), 391–407.

Nolan, R. H. (2022). Tree mortality and carbon stocks following 2019-20 Australian fires. *Mendeley Data*, *V1*. https://doi.org/10.17632/4xdgbbf2tx.1

Nolan, R. H., Collins, L., Leigh, A., Ooi, M. K. J., Curran, T. J., Fairman, T. A., Resco de Dios, V., & Bradstock, R. (2021). Limits to post-fire vegetation recovery under climate change. *Plant*, *Cell & Environment*, *44*(11), 3471–3489.

Nolan, R. H., Gauthey, A., Losso, A., Medlyn, B. E., Smith, R., Chhajed, S. S., Fuller, K., Song, M., Li, X., Beaumont, L. J., Boer, M. M., Wright, I. J., & Choat, B. (2021). Hydraulic failure and tree size linked with canopy die-back in eucalypt forest during extreme drought. *The New Phytologist*, *230*(4), 1354–1365.

Nolan, R. H., Mitchell, P. J., Bradstock, R. A., & Lane, P. N. J. (2014). Structural adjustments in resprouting trees drive differences in post-fire transpiration. *Tree Physiology*, *34*(2), 123–136.

Nolan, R. H., Price, O. F., Samson, S. A., Jenkins, M. E., Rahmani, S., & Boer, M. M. (2022). Framework for assessing live fine fuel loads and biomass consumption during fire. *Forest Ecology and Management*, *504*, 119830.

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

Paul, K. I., Roxburgh, S. H., Chave, J., England, J. R., Zerihun, A., Specht, A., Lewis, T., Bennett, L. T., Baker, T. G., Adams, M. A., Huxtable, D., Montagu, K. D., Falster, D. S., Feller, M., Sochacki, S., Ritson, P., Bastin, G., Bartle, J., Wildy, D., … Sinclair, J. (2016). Testing the generality of above-ground biomass allometry across plant functional types at the continent scale. *Global Change Biology*, *22*(6), 2106–2124.

Pausas, J. G., & Bradstock, R. A. (2007). Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-East Australia. *Global Ecology and Biogeography*, *16*(3), 330–340.

Pausas, J. G., Pratt, R. B., Keeley, J. E., Jacobsen, A. L., Ramirez, A. R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I. N., & Davis, S. D. (2016).

Towards understanding resprouting at the global scale. *The New Phytologist*, *209*(3), 945–954.
Peters, J. M. R., López, R., Nolf, M., Hutley, L. B., Wardlaw, T., Cernusak, L. A., & Choat, B. (2021). Living on the edge: A continental-scale assessment of forest vulnerability to drought. *Global Change Biology*, *27*(15), 3620–3641.
Peterson, D. A., Fromm, M. D., McRae, R. H., Campbell, J. R., Hyer, E. J., Taha, G., Camacho, C. P., Kablick, G. P., Schmidt, C. C., & DeLand, M. T. (2021). Australia's black summer pyrocumulonimbus super outbreak reveals potential for increasingly extreme stratospheric smoke events. *npj Climate and Atmospheric Science*, *4*(1), 1–16.
Prichard, S. J., Kennedy, M. C., Wright, C. S., Cronan, J. B., & Ottmar, R. D. (2017). Predicting forest floor and woody fuel consumption from prescribed burns in southern and western pine ecosystems of the United States. *Forest Ecology and Management*, *405*, 328–338.
Rodriguez-Cubillo, D., Prior, L. D., & Bowman, D. M. J. S. (2020). Variation in *Eucalyptus delegatensis* post-fire recovery strategies: The Tasmanian subspecies is a resprouter whereas the mainland Australian subspecies is an obligate seeder. *Forest Ecology and Management*, *473*, 118292.
Roxburgh, S. H., Wood, S. W., Mackey, B. G., Woldendorp, G., & Gibbons, P. (2006). Assessing the carbon sequestration potential of managed forests: A case study from temperate Australia. *Journal of Applied Ecology*, *43*(6), 1149–1159.
Santín, C., Doerr, S. H., Kane, E. S., Masiello, C. A., Ohlson, M., de la Rosa, J. M., Preston, C. M., & Dittmar, T. (2016). Towards a global assessment of pyrogenic carbon from vegetation fires. *Global Change Biology*, *22*(1), 76–91.
Strasser, M. J., Pausas, J. G., & Noble, I. R. (1996). Modelling the response of eucalypts to fire, Brindabella ranges, ACT. *Australian Journal of Ecology*, *21*(3), 341–344.
Sun, Q., Meyer, W. S., Koerber, G. R., & Marschner, P. (2020). Rapid recovery of net ecosystem production in a semi-arid woodland after a wildfire. *Agricultural and Forest Meteorology*, *291*, 108099.
Trouvé, R., Oborne, L., & Baker, P. J. (2021). The effect of species, size, and fire intensity on tree mortality within a catastrophic bushfire complex. *Ecological Applications*, *31*(6), e02383.
van der Velde, I. R., van der Werf, G. R., Houweling, S., Maasakkers, J. D., Borsdorff, T., Landgraf, J., Tol, P., van Kempen, T. A., van Hees, R., Hoogeveen, R., Veefkind, J. P., & Aben, I. (2021). Vast CO2 release from Australian fires in 2019–2020 constrained by satellite. *Nature*, *597*(7876), 366–369.
van der Werf, G. R., Randerson, J. T., Giglio, L., van Leeuwen, T. T., Chen, Y., Rogers, B. M., Mu, M., van Marle, M. J. E., Morton, D. C., Collatz, G. J., Yokelson, R. J., & Kasibhatla, P. S. (2017). Global fire emissions estimates during 1997–2016. *Earth System Science Data*, *9*(2), 697–720.
Van Wagner, C. E. (1968). The line intersect method in forest fuel sampling. *Forest Science*, *14*(1), 20–26.
Volkova, L., Bi, H. Q., Murphy, S., & Weston, C. J. (2015). Empirical estimates of aboveground carbon in open eucalyptus forests of South-Eastern Australia and its potential implication for national carbon accounting. *Forests*, *6*(10), 3395–3411.
Volkova, L., Meyer, C. P. M., Murphy, S., Fairman, T., Reisen, F., & Weston, C. (2014). Fuel reduction burning mitigates wildfire effects on forest carbon and greenhouse gas emission. *International Journal of Wildland Fire*, *23*(6), 771–780.
Volkova, L., Weiss Aparicio, A. G., & Weston, C. J. (2019). Fire intensity effects on post-fire fuel recovery in *eucalyptus* open forests of South-Eastern Australia. *Science of the Total Environment*, *670*, 328–336.
Volkova, L., & Weston, C. J. (2015). Carbon loss from planned fires in southeastern Australian dry eucalyptus forests. *Forest Ecology and Management*, *336*, 91–98.
Williams, R. J., Bradstock, R., Barrett, D., Beringer, J., Boer, M., Cary, G., Cook, G., Gill, A., Hutley, L., Keith, H., Maier, S. W., Meyer, C., Price, O., Roxburgh, S., & Russell-Smith, J. (2012). Fire regimes and carbon in Australian vegetation. In R. A. Bradstock, A. M. Gill, & R. J. Williams (Eds.), *Flammable Australia, fire regimes, biodiversity and ecosystems in a changing world* (pp. 273–292). CSIRO Publishing.
Yin, C., He, B., Yebra, M., Quan, X., Edwards, A. C., Liu, X., & Liao, Z. (2020). Improving burn severity retrieval by integrating tree canopy cover into radiative transfer model simulation. *Remote Sensing of Environment*, *236*, 111454.
Zhang, Y., Beggs, P. J., McGushin, A., Bambrick, H., Trueck, S., Hanigan, I. C., Morgan, G. G., Berry, H. L., Linnenluecke, M. K., Johnston, F. H., Capon, A. G., & Watts, N. (2020). The 2020 special report of the MJA-lancet countdown on health and climate change: Lessons learnt from Australia's "black summer". *Medical Journal of Australia*, *213*, 490–492.e10.

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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