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Title: Assessing fire impacts on the carbon stability of fire-tolerant forests

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Abstract. The carbon stability of fire-tolerant forests is often assumed but less frequently assessed, limiting potential to anticipate threats to forest carbon posed by predicted increases in forest fire activity. Assessing the carbon stability of fire-tolerant forests requires multi-indicator approaches that recognise the myriad of ways that fires influence the carbon balance including combustion, deposition of pyrogenic material, and tree death, post-fire decomposition, recruitment, and growth. Five years after a large-scale wildfire in south-eastern Australia, we assessed the impacts of low- and high-severity wildfire, with and without prescribed fire (≤ 10 years before), on carbon stocks in multiple pools, and on carbon stability indicators (carbon stock percentages in live trees and in small trees, and carbon stocks in char and fuels) in fire-tolerant eucalypt forests. Relative to unburnt forest, high-severity wildfire decreased short-term (five-year) carbon stability by significantly decreasing live tree carbon stocks and percentage stocks in live standing trees (reflecting elevated tree mortality), by increasing the percentage of live tree carbon in small trees (those vulnerable to the next fire), and by potentially increasing the probability of another fire through increased elevated fine fuel loads. In contrast, low-severity wildfire enhanced carbon stability by having negligible effects on above-ground stocks and indicators, and by significantly increasing carbon stocks in char and, in particular, soils, indicating pyrogenic carbon accumulation. Overall, recent preceding prescribed fire did not markedly influence wildfire effects on short-term carbon stability at stand scales. Despite wide confidence intervals around mean stock differences – indicating uncertainty about the magnitude of fire effects in these natural forests – our assessment highlights the need for active management of carbon assets in fire-tolerant eucalypt forests under contemporary fire regimes. Decreased live tree carbon and increased reliance on younger cohorts for carbon recovery after high-severity wildfire, could increase vulnerabilities to imminent fires, leading to decisions about interventions to maintain the productivity of some stands. Our multi-indicator assessment also highlights the importance of considering all carbon pools, particularly pyrogenic reservoirs like soils, when evaluating the potential for prescribed fire regimes to mitigate the carbon costs of wildfires in fire-prone landscapes.

Key words: carbon stocks, eucalypt forest, fire severity, prescribed fire, regeneration, resprouter, temperate forest, soil carbon, tree mortality.

57 INTRODUCTION

58 Fire, as a global disturbance agent (Giglio et al. 2013), influences the carbon balance of
59 forests worldwide. In addition to immediate combustion losses, fires, and in particular severe
60 fires, can have long-lasting impacts on forest carbon sequestration and stocks through effects
61 on tree mortality and associated decomposition (Ghimire et al. 2012, Campbell et al. 2016),
62 recovery of forest productivity (Cai and Yang 2016, Hu et al. 2016), and changes in the form
63 of carbon through the production of pyrogenic carbon (Santín et al. 2016). Predictions of
64 increased fire activity in multiple forest biomes with climate change (Stephens et al. 2013)
65 make assessments of carbon stock changes under a range of fire regimes critical to
66 understanding and sustainably managing forest carbon into the future (Millar and Stephenson
67 2015, Wear and Coulston 2015, Schlesinger et al. 2016).

68 Understanding the many ways fire influences forest carbon requires multifaceted
69 assessments of impacts and responses. In the first instance, this typically involves post-fire
70 measurement of carbon stocks by forest pool in order to quantify fire impacts on stand-level
71 carbon density – the carbon stored per unit area (e.g. Hurteau et al. 2011, Bennett et al. 2014,
72 Yocom Kent et al. 2015, Hu et al. 2016). Increasing carbon density is a principal aim of
73 stand-level practices for climate change mitigation (Lemprière et al. 2013), and of ‘carbon
74 maximization’ approaches to managing fire in the dry temperate forests of the western United
75 States (Hurteau and Brooks 2011). However, carbon maximization, where all stands are ‘at
76 maximum stand-level carbon density’ often in the older growth stages (Lemprière et al.
77 2013), is largely theoretical in fire-prone landscapes particularly where regular wildfires
78 result in younger stands with lower carbon stocks (Lemprière et al. 2013). As such, fire and
79 forest carbon assessments might also consider ‘carbon stabilization’, broadly defined as the
80 maintenance of carbon stocks over time (Hurteau and Brooks 2011). For the dry forests of the
81 western United States where the concept has been mainly applied, carbon stabilization
82 involves managing forest structure and composition to reduce the likelihood of high-severity
83 wildfires that can lead to dramatic carbon losses and conversions to less productive states
84 (Hurteau and Brooks 2011, Earles et al. 2014, Hurteau et al. 2016). Thus, in addition to
85 immediate combustion losses, carbon stabilization considers post-fire net productivity over
86 decadal time scales, with stability indicated by strong potential for recovery of fire-induced
87 carbon losses before the next fire (Yue et al. 2016). Conversely, instability could be indicated
88 by proneness to conversion to a less productive or non-forest state after the next fire (e.g. age
89 of dominant trees less than their juvenile period; Fairman et al. 2016), or by other stand

90 'intrinsic factors' like high fuel loads that might increase the likelihood of high-severity fire
91 (Bowman et al. 2016).

92 Current conceptual models suggest that increased fire activity will have minimal impact
93 on the stability of carbon stocks in fire-tolerant forests (e.g. Lavorel et al. 2015), although
94 empirical data to support such assumptions are often scarce. Model projections indicate
95 increasing wildfire frequency in the temperate United States will decrease time-averaged
96 carbon stocks of fire-sensitive forests but have minimal impact on stocks of fire-tolerant
97 forests (Earles et al. 2014). Similarly, conceptual models of fire-tolerant eucalypt forests in
98 temperate Australia assume sustained live tree biomass (a principal carbon stock) irrespective
99 of increased wildfire frequency due to the strong resprouting capacity of the dominant
100 eucalypts (Bowman et al. 2013). This general understanding has led to assumptions of
101 sustained ecosystem service provision, including carbon sequestration, by fire-tolerant
102 eucalypt forests under future fire regimes (Lavorel et al. 2015, Colloff et al. 2016). However,
103 empirical data to assess the carbon stability of many fire-tolerant forests are lacking; in
104 particular, few studies have assessed wildfire effects on carbon stocks in fire-tolerant
105 eucalypt forests despite evidence of increased mortalities of fire-tolerant eucalypts (and, thus,
106 potential for decreased biomass carbon) after recent high-intensity wildfires in south-eastern
107 Australia (Bennett et al. 2016, Prior et al. 2016).

108 The stability of carbon stocks in fire-prone forests will not only be affected by
109 individual wildfires, but by the collective fire regime, including prescribed fire treatments to
110 reduce wildfire hazards. A recent review of fuel-reduction studies in the western United
111 States concluded that prescribed fire plus thinning treatments decreased wildfire-induced
112 carbon emissions, particularly those associated with tree mortality (Kalies and Yocom Kent
113 2016). However, the relative and combined effects of wildfire and prescribed fire on carbon
114 stocks in temperate Australia's fire-tolerant forests remain under-examined, despite ongoing
115 commitment to broad-scale prescribed burning programs (The State of Victoria 2015). This
116 lack of data hinders accurate quantification of mitigation effects by prescribed fire on wildfire
117 carbon losses, and of the combined effects of prescribed fire and wildfire on stand-level
118 carbon stocks when, for example, any mitigation of wildfire behaviour by prescribed fire is
119 overridden by extreme fire weather (e.g. Price and Bradstock 2012). In addition, studies of
120 fuel-treatment effects on post-wildfire forest carbon seldom consider all carbon pools, and
121 soils in particular are often overlooked (Kalies and Yocom Kent 2016). This represents a
122 significant data gap since over 40% of the world's forest organic carbon stocks are in soils (to
123 1-m depth; Pan et al. 2011), with a considerable proportion as organic carbon in the surface

layers, which, depending on fire conditions, can be vulnerable to combustion and post-fire erosion losses (Santín and Doerr 2016). On the other hand, soils are also a principal reservoir of pyrogenic carbon (a continuum of ‘partially charred biomass and charcoal to soot’; Santín et al. 2016), which has been noted as a significant and long-term forest carbon pool (Turcios et al. 2016) that considerably delays net carbon emissions from fires (Santín et al. 2015).

In this paper, we evaluate potential risks posed by recent fires to the carbon stability of fire-tolerant forests. Our study focuses on fire-tolerant mixed-eucalypt forests of south-eastern Australia five years after they were burned by wildfires that started under extreme weather conditions on ‘Black Saturday’, February 2009 (Cruz et al. 2012). To better understand the separate and combined effects of wildfire and prescribed fire on forest carbon, our sampling design includes factorial combinations of three 2009-wildfire severities (unburnt, low, high) and two times since last fire before 2009 (≤ 10 years since prescribed fire, >30 years since any fire). We use a multi-indicator approach to ask the questions: 1) what are the stand-level effects of low- and high-severity wildfire on above- and below-ground carbon stocks five years after the wildfire? 2) Are these stand-level effects modified by recent prescribed fire prior to the wildfire? and 3) Is there evidence – based on stock changes and on a novel set of carbon stability indicators – that wildfire combined with recent prescribed fire can influence the short-term carbon stability of fire-tolerant eucalypt forests? Our overarching aims are to highlight the importance of considering multiple pools and indicators when assessing fire regime effects on forest carbon stability, and to identify potential threats and mitigation opportunities associated with changing fire regimes in fire-prone landscapes.

METHODS

Overview

We examined the influences of wildfire severity and time since last preceding fire on carbon stocks in key forest pools (IPCC 2014), and on a novel set of stand-level carbon stability indicators (Table 1). Our assessment was made five years after the wildfire, which is a short term relative to the life cycle of the dominant trees, but sufficiently long to capture secondary fire effects including tree resprouting and death, seedling recruitment, and soil stabilisation or erosion (Morgan et al. 2014).

Our stock and indicator assessments of burnt versus comparable unburnt conditions

relate to three facets of the multidimensional concept that is ecological stability, namely: resistance (magnitude of stock change), resilience (rate of stock recovery), and persistence (maintenance of the same forest state; Donohue et al. 2016). That is, while our comparative carbon stocks at five years summarise the wildfire's short-term impacts (stock resistance), our stability indicators are designed to examine relative change in a stand's potential to recover and to maintain carbon stocks over subsequent years, particularly in the face of imminent fire, as is consistent with predictions of more frequent wildfire in south-eastern Australia (Clarke et al. 2011).

Our first stability indicator 'percentage live tree carbon' represents carbon stocks in established (>10 cm diameter) live trees as a proportion of total stocks in standing live and dead trees of the same size class (Table 1). In a fire-tolerant forest where most carbon is stored in the larger trees (Bennett et al. 2014), this post-fire indicator represents the balance between the retained carbon fixation capacity of surviving trees and ongoing decomposition losses associated with tree mortality (Ghimire et al. 2012). It thus provides a comparison of the stand-level potential to recover carbon stocks through net primary productivity before the next fire, consistent with longer-term assessments of fire impacts on forest carbon stability elsewhere (Earles et al. 2014, Yue et al. 2016). Note that while smaller trees and regeneration can also contribute to post-fire carbon sequestration, they are usually a relatively minor stock in multi-aged fire-tolerant eucalypt forests (Bennett et al. 2014), and are instead considered here mainly in the context of relative vulnerability to the next fire (see 'percentage small tree carbon' below). In addition to recovery of stocks through growth of established trees, forest carbon stability might also be enhanced by the on-site retention of carbon in more persistent forms. Thus, our second stability indicator (Table 1) provides a comparison of 'char carbon', which, as a relatively stable form of carbon with slower degradation than 'uncharred precursors' (Santín et al. 2015), can contribute to substantive long-term pyrogenic carbon stocks in some forests (Turcios et al. 2016). While our indicator focuses on visible char (>2 mm) in the litter and soil, pyrogenic carbon is produced as a continuum of size fractions from charcoal to fine soot (Santín et al. 2016), which can be incorporated into the soil profile in the post-fire period (Hobley et al. 2017). As such, while we did not characterise <2 mm pyrogenic carbon, we anticipated that its retention might be indicated by our assessments of soil carbon stocks to 30 cm depth.

Our final two stability indicators (percentage small tree carbon, fuel carbon; Table 1) relate to the vulnerability or proneness of stand-level carbon stocks to a subsequent fire. Here, 'percentage small tree carbon' presents the proportion of total live tree carbon that is

stored in the smallest trees including regeneration (Table 1). Since small rather than larger trees are often most prone to death by fire (Bennett et al. 2013), comparatively greater percentage small tree carbon could indicate reduced carbon stability since a greater proportion of the growing stock will likely be transferred to dead pools after the next fire. Similarly, the likelihood of carbon transfers from live to dead pools could be greater if a stand's 'intrinsic factors' (Bowman et al. 2016) increase the ignition potential or severity of the next fire. Such intrinsic factors could include 'fuel carbon', that is, carbon stocks (reflecting mass per unit area or 'fuel loading'; Keane 2013) in pools that represent fuel layers associated with fire behaviour in eucalypt forests (Gould et al. 2011). These include: litter as surface fine fuel (influencing ignition, flame height, and rate of spread), shrubs and eucalypt regeneration as elevated fine fuel (influencing flame height, rate of spread and spotting), and fallen dead wood as coarse fuel (influencing heat release and smouldering combustion; Tolhurst and Cheney 1999, Gould et al. 2011). Lower carbon stability might also be indicated for stands with both high relative fuel carbon and high percentage small tree carbon, since this represents heightened potential for ignition of a more vulnerable growing stock, and could portend changes to non-forest and/or less productive states (Lindenmayer et al. 2011, Fairman et al. 2016), thereby limiting future carbon-stock recovery.

Study area

Our study examines fire effects in a single, widespread forest type in the foothills of the Great Dividing Range in central Victoria, south-eastern Australia (study area centre: 37°28'S, 145°32'E). The forest type, known locally as 'Herb-rich Foothill Forest' (Department of Sustainability and Environment 2004), is a dry sclerophyll forest (Ashton 2000) or 'Open-forest' (tree heights 10-30 m, projective foliage cover 30-70%, Specht 1981) of mean basal area 29 m² ha⁻¹ (Bennett et al. 2016). It is dominated by a mix of fire-tolerant eucalypts of different bark types, such as *Eucalyptus obliqua* L'Hér (deep fibrous 'stringybark'), *E. radiata* Sieber ex DC. and *E. dives* Schauer (short fibrous bark), and *E. globulus* subsp. *bicostata* (Maiden, Blakely & Simmonds) J.B. Kirkp. (smooth 'gum' bark). Such eucalypts reliably survive most fires to resprout from epicormic buds on the stem and branches, and/or from basal buds of the lignotuber (Burrows 2013). The understorey is characterised by a diverse and well-developed herb layer beneath a sparse to continuous sclerophyll shrub layer (Ashton 2000), and contains both obligate seeder and resprouter fire-response traits (Cheal 2010). Wildfires are estimated to burn forests of this type every 5 to 20 years at low- to

medium-intensities (e.g. 1,000 – 5,000 kW m⁻¹), although much higher intensities (e.g. 10,000 – 50,000 kW m⁻¹) can occur at longer return intervals up to 100 years (Murphy et al. 2013). Time to recovery of fire-affected biomass in our forest type has not been quantified, although the estimated ‘tolerable fire interval’ based on the maturation time of all characteristic species, including short-lived shrubs and grasses, is 15 years (Cheal 2010). Nonetheless, intervals between low-intensity prescribed fires can be shorter given ongoing commitments to reduce forest fuel hazards in south-eastern Australia (The State of Victoria 2015), and evidence from comparable forest types that the influence of prescribed fires on wildfire behaviour will be largely confined to ≤10 years and have the greatest effects 1 to 5 years after prescribed fire (Fernandes and Botelho 2003, Price and Bradstock 2012, Tolhurst and McCarthy 2016).

The regional climate is temperate, characterised by hot dry summers, and cold wetter winters, with annual rainfall in the range 800 to 1200 mm (Ashton 2000). Mean daily minimum temperatures range from 4°C in July (winter) to 12°C in February (summer), and mean daily maximums from 9°C in July to 23°C in February (Toolangi weather station; Bureau of Meteorology 2015). Our forest type often occurs on yellow podzolic soils of relatively poor structure (Ashton 2000). More detailed descriptions of the study area’s soils are lacking, although particle-size analyses of soils from our sites indicate a fairly uniform texture to 30-cm depth dominated by silt (0.002 – 0.05 mm, 54%), with comparatively minor sand fractions (0.05 – 2 mm, 16%; data not shown). As detailed in Bennett et al. (2016), our study sites encompassed a range of aspects, elevations (165 – 890 m above sea level), and slopes (1 – 36°), representative of the area’s variable geomorphology (Ashton 2000).

Study sites

Our study sites were located within a 60 x 120 km² area, which was within and around the perimeter of two 2009 wildfires collectively known as the Kilmore East-Murrindindi fire complex. The complex, centred some 100 km northeast of the state capital of Melbourne, started on ‘Black Saturday’, 7 February 2009, and went on to burn about 400,000 ha over the following three weeks (Teague et al. 2010, Cruz et al. 2012). As indicated by the Forest Fire Danger Index (FFDI; Noble et al. 1980), the complex included three short and one longer period of contrasting fire weather (Price and Bradstock 2012). The first ~ 6-hour period was classified as ‘catastrophic’ fire weather (FFDI ~ 100; Price and Bradstock 2012), when ‘exceedingly dry fuel combined with near-gale to gale force winds’ resulted in rapid crown-

fire propagation, extreme fire-line intensities (70,000 to 85,000 kW m⁻¹), and multiple short- and long-range spot fires (Cruz et al. 2012). The next 6 hours included a period of ‘very high’ fire weather (FFDI ~ 50) associated with a southerly change, followed by a period of ‘moderate’ fire weather after the change (FFDI ~ 10; Price and Bradstock 2012). Thereafter, in the days and weeks following 7 February, the fire weather was classified as ‘low’ (FFDI ~ 3; Price and Bradstock 2012). This variable fire weather resulted in a range of fire severities, although highly erratic fire behaviour in the first three periods, including long-range spotting up to 33 km (Cruz et al. 2012), meant that it was not possible to accurately determine what burnt when (Price and Bradstock 2012). In general, however, the ‘High’ fire severities assessed in our study (see below) were associated with the catastrophic, very high, and moderate fire-weather periods, whereas the ‘Low’ fire severities were principally associated with the moderate and low fire-weather periods (Price and Bradstock 2012).

Our field assessments in 2013/2014 involved 71 sites (large-tree carbon only, as below) or a subset of 42 sites (all other carbon stocks; Table 1), which were 9 to 17 replicates of each of six combinations of two times since the last preceding fire (‘Recently burnt’, ‘Long unburnt’), and three 2009 wildfire-severity classes (‘Unburnt’, ‘Low’, ‘High’; Appendix S1: Table S1). According to the state environment department’s spatial data-layer of fire history (unpublished data), which is considered most accurate after 1972, Long unburnt sites had no records of any fire (wildfire or prescribed fire) for more than 30 years prior to 2009. In contrast, Recently burnt sites had been burnt 1 to 10 years before 2009 by a prescribed fire, which was presumably of low intensity to meet management objectives (The State of Victoria 2015) although supporting fire-intensity data were not available. Of the ~ 68,119 ha of Herb-rich Foothill Forest burnt by the Kilmore East-Murrindindi fire complex (Bennett et al. 2016), just 9% (5,986 ha) was classified as Recently burnt, which limited the area available for selecting sites within a narrower time-since-prescribed-fire period. In particular, the Recently burnt – High severity combination included just 357 ha (Appendix S1: Table S1), which was apparently due to the low encounter rate of recent prescribed fire with the wildfire rather than effective mitigation by prescribed fire of the wildfire’s severity at landscape scales (Price and Bradstock 2012).

The 2009 wildfire-severity classes were obtained from a 1:25,000 spatial data-layer, which was based on the Normalised Burn Ratio (dNBR), as estimated from pre- and post-fire remote sensing data, and extensive ground truthing within two months of the wildfires (Department of Sustainability and Environment 2009). The 2009 wildfire-severity assessment included five classes relevant to forests (1 to 5; Appendix S1: Table S1), with our study

focusing on two contrasting conditions: ‘High’ severity, class 1, 70 – 100% crowns burnt, understorey entirely consumed; and ‘Low severity’, classes 4 and 5, <1 – 35% crowns scorched, mostly light ground fire (Department of Sustainability and Environment 2009). We focused on these contrasting conditions to assess the full range of wildfire effects, and to minimise uncertainties associated with the mapping of severity classes 2 and 3, which could include a spatially variable mix of fire impacts on the crown and understorey (Appendix S1: Table S1). Prior to our assessments in 2013/2014, we checked each site for consistency with its 2009 wildfire-severity class using clear signs of wildfire impacts, namely: stem and branch charring and dense epicormic resprouts dominating the crowns of most surviving mature trees at High severity sites; and stem charring below the crowns, which showed no evidence of fire, at Low severity sites. Similarly, we confirmed that there were no signs of fire in the tree crowns at ‘Unburnt’ sites, which were clearly beyond the wildfire-complex boundary, but as evenly spread and as close as possible (~ 30 km) to that boundary to ensure comparability with burnt sites.

We assessed large trees (≥ 20 cm diameter at breast height overbark, ‘dbhob’ at 1.3 m height) at 71 sites from October 2013 to March 2014 (Appendix S1: Table S1). We then assessed all other carbon stocks (in small- and medium-sized trees, regeneration, stumps, shrubs, fallen dead wood, litter, soil; Table 1) at a subset of 42 sites (7 replicates of each of the six wildfire severity by time-since-fire combinations) from April to October 2014.

Carbon stocks in above-ground biomass and standing dead wood

Live trees were the principal component of carbon stocks in above-ground biomass (plus a minor live woody shrub component), and dead trees the main component of stocks in standing dead wood (plus a minor stump component; Table 1). Tree carbon stocks were assessed as live and dead standing trees of all species in three size classes: large ≥ 20 cm, medium 10 – <20 cm, and small 2.5 – <10 cm dbhob. In addition, eucalypt seedlings and saplings (<2.5 cm basal or breast height diameter, c. 0.5 to 4.0 m tall) were counted to estimate carbon in the main form of post-fire regeneration. Basal resprouts (i.e. from eucalypt lignotubers) were also assessed but were hereafter ignored as a very minor component (<2% of live and dead small stems) of the post-fire regrowth at all sites (Bennett et al. 2016).

Our tree measurements follow those described in Bennett et al. (2016). In brief, at each of the 71 sites (Appendix S1: Table S1), we assessed large trees in two 10 x 50 m plots (total plot area 0.1 ha). Large trees were classified as ‘live’ if live leaves were present in the canopy

(unburnt, and/ or epicormic resprouts) or on the stem (epicormic resprouts), and ‘dead’ if the canopy and stem held no live leaves. Live large trees were assessed for species, dbhob, and bark thickness at 1.3 m height, whereas dead trees were only assessed for dbhob because species was usually not discernible. At the subset of 42 sites (Appendix S1: Table S1) and within the large-tree plots, we counted live and dead small- and medium-sized trees in two 10 x 25 m sub-plots (total area 0.05 ha), and live and dead eucalypt regeneration (as seedlings and saplings) in two 2 x 25 m sub-plots (total area 0.01 ha). In addition, in the 250-m² sub-plots we counted small stumps (<20 cm diameter at 30-cm height, <1.3 m total height), and measured large stumps (≥20 cm diameter) for diameter, predominant height, and % cylindrical volume remaining.

Total above-ground biomass (stems, bark, branch, foliage) of live large trees in the dbh range 20 to 50 cm was estimated using extant dbhob-based allometric equations that were specific to species for most eucalypts (which comprised 98% of all live trees), or generic for less common eucalypt and non-eucalypt species (Appendix S1: Table S2). Larger trees (>50 cm to maximum 158 cm dbhob) were often beyond the diameter range used to construct individual allometric equations. Thus, to minimise extrapolation errors, we used a conservative ‘large eucalypt’ equation (Dean et al. 2012), including a decay modifier for internal rot (Roxburgh et al. 2006), for biomass estimates beyond 50 cm dbhob. To minimise disparities in tree biomass estimates above and below 50 cm dbhob, we used a weighted average of the assigned allometric equation and the large eucalypt equation for individual stems in the dbhob range 35 to 50 cm. In addition, we used an adjusted dbhob for estimating biomass of live large *E. obliqua* stems at Recently burnt, and Low and High wildfire severity sites on the basis that burning significantly reduced bark thickness of this species creating the potential for dbhob-based equations to underestimate biomass (Bennett et al. 2013). Here, adjusted dbhob of each stem was calculated from dbh under-bark (‘dbhub’) using a very strong relationship (R^2 0.99) between dbhob and dbhub of large *E. obliqua* stems at unburnt sites.

Mass of dead large trees was estimated as for live trees (allometrics assigned using the most common live large species in that plot), but adjusted using two multipliers – 0.75 of total biomass to adjust for bark, branch and leaf losses (based on biomass proportions in Feller 1980, and Grierson et al. 1992), and then 0.80 to account for wood decay (Bennett et al. 2013, Fedrigo et al. 2014).

Total aboveground biomass of small- and medium-sized live trees and of live eucalypt regeneration at each site was estimated by multiplying individual stem counts by the biomass

of a single representative stem in each size class. For small- and medium-sized trees, the representative stem was estimated using the average of biomass estimates for each 1 cm-increment within the relevant diameter range (i.e. 2 to 10 cm, 10 to 20 cm) from an Australian allometric equation for understorey tree species (Dean et al. 2012). Similarly, the mass of a live representative eucalypt seedling/ sapling was assumed to be 0.70 kg, based on a mean of 1-mm diameter increments in the same equation, and our limited weighing of field samples. Mass of dead small- and medium-sized trees was then estimated using the above-mentioned multipliers, and mass of dead eucalypt regeneration was estimated using an individual mass of 0.56 kg (i.e. 0.70 kg multiplied by 0.80 decay modifier, as above). Total mass of small stumps was the product of stump counts by a representative volume (cylinder, 10 cm diameter, 80 cm height) and average density of sound-dead wood (0.459 g cm^{-3} ; Bennett et al. 2013). Large stump mass was estimated in a similar way, although individual volumes were calculated from the measured diameter and height, and corrected for remaining volume.

Woody understorey shrubs were $<2.5 \text{ cm}$ in maximum diameter, typically multi-stemmed, and were classified as 'prostrate/ short' ($<1.3 \text{ m}$ height) or 'medium' ($\geq 1.3 \text{ m}$ height). Estimates of understorey shrub biomass were based on foliage projective cover (FPC) because variable, multi-stemmed form, and inter-locking crowns, precluded the use of standardised individual shrub measures. Cover measurements involved measuring the length (to the nearest 5 cm) of each 1-m interval along two 25 m transects (each a side of the 250-m^2 tree sub-plots) that was intercepted by a vertical projection of the crowns, irrespective of species, of the two shrub categories (prostrate/ short, and medium). FPC per shrub category was the total cover as a proportion of the total 50-m transect length, which was converted to total biomass (Mg ha^{-1}) using FPC as a dependent variable in Australian shrub allometric equations (Grierson et al., 2000; Appendix S1: Table S2).

Components of above-ground biomass (live trees in all size classes, live shrubs), and of standing dead-wood mass (dead trees in all size classes, stumps) were summed for each site, and converted to carbon content using a 0.50 multiplier (Penman et al. 2003, Aponte et al. 2014). These data were converted to carbon (C) in Mg ha^{-1} by dividing by total plot area, which was corrected for slope.

Carbon stocks in fallen dead wood

Carbon stocks in fallen dead wood were assessed using the methods of Aponte et al. (2014). This involved recording the diameter, remaining cross-sectional area, and decay class (D1, no decay to D5, substantially decayed) of all fallen-wood pieces that intersected a central 50-m side of each large-tree plot (total c. 100 m). The mass of pieces was then calculated using a modified version of the van Wagner (1968) volume equation, and wood density values by decay class (Aponte et al. 2014), then summed by site, and converted to total carbon (Mg ha^{-1}) using a 0.5 multiplier (Aponte et al. 2014).

Carbon stocks in litter and soil

Litter (dead plant material on the forest floor, <2.5 cm minimum cross-sectional diameter) was sampled from within six 0.1 m^2 quadrats per site, which were located at three set points within each of the two 250-m^2 sub-plots (i.e. at 6, 12 and 18 m along a line running 2 m from, and parallel to, the sub-plot's central 25-m side). Soil was sampled from the centre of two quadrats per sub-plot (6 and 18-m points; total of four per site) to two depths: 0 – 10 cm, collecting all soil within a core of known volume (425 cm^3), and 10 – 30 cm using an auger (because time and labour constraints prevented mass by volume sampling of soil at depth).

After removal of fallen wood (≥ 2.5 cm diameter, as above), rooted plants, and non-plant material, litter was sampled by using a spatula to cut along the inside edge of the quadrat, then collecting all visible litter fragments after gentle scraping to expose the mineral soil. Field-moist samples were stored in a cold room (4°C) before being placed, within three days of collection, in a low-humidity glasshouse to air dry. Individual samples were then sieved without mass loss to provide a >2 mm component, and a <2 mm component, which was treated as soil (below; Bennett et al. 2014). The >2 mm component was sorted to remove any further non-litter material, and to provide two litter fractions: visible char ('litter char'), and all other dead plant material ('litter'). The fractions were oven-dried (40°C) to a recorded constant mass, and then the six samples per site were combined, thoroughly mixed, and shredded to provide a single composite sample per fraction per site. Representative sub-samples of each fraction were finely ground (1 min, Standard Ring Mill, Rocklabs Ltd, New Zealand), and analysed for total C concentration by dry combustion using a LECO TruMac CNS Analyser (LECO Corp., St Joseph, MI, USA). Litter and litter-char C stocks (Mg ha^{-1}) were then calculated as the C concentration of the composite fraction sample multiplied by the mean areal mass per site.

All soil samples were air-dried as per the litter samples before oven drying (40°C) to constant mass. Cored soil samples (0 – 10 cm depth) were carefully sieved to remove roots and >2 mm rock fragments, and to separate <2 mm mineral soil from >2 mm ‘soil char’. Volumetric mass (‘VM’, g cm⁻³) of the <2 mm soil and >2 mm soil char components were calculated as oven-dried (40°C) mass divided by total core volume to 10 cm depth. Auger samples at 10 to 30 cm depth were dried, sieved and sorted as above, with only the <2 mm mineral soil component retained for C analysis. Replicate soil samples were combined to provide one composite sample of each soil component (<2 mm soil to 10 cm, <2 mm soil 10 to 30 cm, and >2 mm soil char) per site. These were thoroughly mixed, and a representative sub-sample was finely ground, checked to confirm the absence of carbonates (i.e. no visible effervescence in response to drops of 1 M hydrochloric acid), and analysed for total C concentrations as per the litter samples. A site’s soil C stock to 10 cm depth was calculated as the sum of C in the <2 mm soil and >2 mm char components (each the product of VM and C concentration), plus C in the above-mentioned <2 mm litter component (mean mass multiplied by C concentration). A site’s soil C stock at 10 – 30 cm depth was calculated as the product of the <2 mm soil C concentration and VM, which was estimated from the mean 0 – 10 cm VM for that site using a strong relationship (R^2 0.70) between 0 – 10 cm and 10 – 30 cm VM based on 75 profiles in the same forest type elsewhere (Bennett et al. 2014). This calculation might have marginally overestimated soil carbon stocks at 10 – 30 cm depth at High severity relative to Low severity sites since mean 0 – 10 cm VM was significantly greater at the former, although neither was significantly different from 0 – 10 cm VM at Unburnt sites (see Results).

Statistical analyses

Our four carbon stability indicators were calculated from measured carbon stocks as described in Table 1. Effects of 2009 wildfire-severity class and of time since last fire on the carbon stocks, and on the stability indicators were then tested using the two-way Analysis of Variance models of GenStat (15th edition, VSN International Ltd, Hemel Hempstead, UK). These models cater for unbalanced designs by automatically using regression analyses (Payne 2012). In addition, given that soil carbon stocks in particular can vary with soil type and topographic position, we tested a range of covariates in our fire-effects models, including variables representing location, topography, and climate (Appendix S1: Table S3). Effects of non- normality and variance heterogeneity on model outcomes were checked using

transformed dependent variables as necessary (natural logarithm for stocks, arcsine for percentages; Quinn and Keough 2002). Differences in dependent variables among wildfire severity classes and between time-since-fire classes were considered significant if the 95% confidence interval of the predicted difference between the two means did not include zero.

RESULTS

Effects of wildfire severity on carbon stocks

Effects of wildfire severity and time since last fire on carbon stocks are presented separately (Fig. 1) since interactive effects on the main stocks were not significant. For wildfire severity, mean total carbon stocks – the sum of stocks in all above-ground pools plus soil to 30 cm depth – did not significantly differ among Unburnt (UB, 230 Mg C ha⁻¹), Low severity (LS, 251 Mg C ha⁻¹), and High severity sites (HS, 232 Mg C ha⁻¹; Fig. 1a). However, 95% confidence intervals of the mean differences were very wide (e.g. -28 – 32 Mg C ha⁻¹ for the difference between UB and HS sites; Fig. 1a), reflecting high spatial variability typical of these natural forests (Bennett et al. 2014). In addition, mean total stocks masked both significant negative and positive effects of wildfire severity on stocks in the main pools, particularly in above-ground biomass and soil (Fig. 1a).

On average, carbon stocks in above-ground biomass (ABGB) were lower at both LS (104 Mg C ha⁻¹) and HS (105 Mg C ha⁻¹) sites than UB sites (117 Mg C ha⁻¹; Fig. 1a). However, mean differences in ABGB carbon stocks based on 42 sites were not significant due, in part, to high variability, but also to both decreases and increases in component carbon stocks. That is, lower stocks at HS than UB sites in live large trees (significant based on the 71 sites assessed for large trees only; Appendix S2: Fig. S1a) and in medium live trees (Appendix S2: Fig. S1d) were partially counterbalanced by increases at HS sites in stocks in small trees and eucalypt regeneration (Appendix S2: Fig. S1d). The latter reflected prolific post-wildfire eucalypt regeneration at HS sites (some of which progressed to saplings and small trees in the five years before our assessment) that was not evident at LS and UB sites (Bennett et al. 2016).

Consistent with transfers from live to dead tree pools, carbon stocks in standing dead wood were significantly greater at HS (21 Mg C ha⁻¹) than LS (10 Mg C ha⁻¹) and UB sites (9 Mg C ha⁻¹; Fig. 1a), mainly reflecting significantly greater carbon stocks in standing dead large trees (Appendix S2: Figs S1b, e). In contrast, mean total carbon stocks in fallen dead

wood were not significantly different among wildfire-severity classes ($12 - 15 \text{ Mg C ha}^{-1}$; Fig. 1a), partly reflecting high variability in stocks in large fallen wood ($\geq 75 \text{ mm}$ diameter; Fig. 2d). Nonetheless, carbon stocks in small fallen wood were significantly lower at HS than UB sites (Fig. 2c), indicating that combustion losses, as indicated by significantly lower carbon stocks in rotten fallen wood of both size classes (which was presumably present before the wildfire; Figs 2c, d), were not fully counterbalanced by transfers between the standing and fallen dead wood pools. Significantly lower mean carbon stocks in rotten small fallen wood at HS than LS sites (Fig. 2c) was consistent with greater consumption of surface fuels at HS sites, which was also reflected in significantly lower carbon stocks in litter at HS (3 Mg C ha^{-1}) than LS sites (5 Mg C ha^{-1}), although neither was significantly different from litter carbon at UB sites (Figs 1a, 2a).

In contrast to the above-ground pools, soil carbon stocks were more clearly affected by low- than high-severity wildfire. Soil carbon stocks to 10 cm depth (including $<2 \text{ mm}$ soil, $>2 \text{ mm}$ char, and $<2 \text{ mm}$ litter) were significantly greater at Low severity (49 Mg ha^{-1}) than both Unburnt (41 Mg ha^{-1}) and High severity sites (40 Mg ha^{-1} ; Fig. 3a). This effect to 10 cm depth was largely due to significant effects both on the mean carbon concentration of $<2 \text{ mm}$ mineral soil (6.0% LS versus 5.1% UB and 4.1% HS), and its volumetric mass, which was significantly greater at High severity (0.90 g cm^{-3}) than Low severity sites (0.77 g cm^{-3}), and was negatively correlated with carbon concentration ($r -0.77$; Appendix S2: Fig. S2a). As for the top 10 cm, estimated soil carbon stocks from 10 to 30 cm depth were significantly greater at Low severity (68 Mg ha^{-1}) than Unburnt (44 Mg ha^{-1}) and High severity sites (52 Mg ha^{-1} ; Fig. 3b), reflecting differences in soil carbon concentrations, which were significantly correlated with carbon concentrations to 10 cm depth ($r 0.75$; Appendix S2: Fig. S2b). Combining the 0-10 cm and 10-30 cm depths, mean soil carbon stocks to 30 cm depth were significantly greater at Low severity than Unburnt sites by an estimated 31 Mg C ha^{-1} (no effect of high-severity wildfire; Fig. 1a).

Inclusion of site-level covariates, many of which were non-significant, did not markedly influence the highly significant effect of wildfire severity on soil carbon stocks at depth; that is, carbon stocks from 10 to 30 cm depth were consistently significantly greatest at Low severity sites (Appendix S1: Table S3). However, inclusion of different covariates led to sometimes non-significant differences between Low severity and Unburnt sites for soil carbon stocks to 10 cm depth (Appendix S1: Table S3). These variable effects reflected very wide 95% confidence intervals around all soil carbon mean differences (Appendix S1: Table S3) consistent with high spatial variability of soil carbon stocks in these natural forests.

513 *Effects of time since last fire on carbon stocks*

514 Overall, mean total carbon stocks were greater at Recently burnt (RB, 249 Mg C ha⁻¹)
515 than Long unburnt sites (LUB, 226 Mg C ha⁻¹), although the mean difference had a wide 95%
516 confidence interval and was not significant (Fig. 1b). The greater overall mean reflected
517 positive, albeit non-significant, differences in most of the main carbon stocks between RB
518 and LUB sites (Fig. 1b). Of the component stocks, only soil carbon at 10 to 30 cm depth was
519 significantly greater at Recently burnt (60 Mg C ha⁻¹) than Long unburnt sites (50 Mg C ha⁻¹;
520 Fig. 3b). However, the significance of this difference was marginal (i.e. 95% confidence
521 interval of the mean difference nearly included zero), and the effect was often non-significant
522 with the inclusion of site-level covariates (Appendix S1: Table S3).

523 *Fire effects on carbon stability indicators*

524 Wildfire severity clearly influenced three of our four carbon stability indicators.
525 Reflecting significant trends in both live tree and dead tree carbon (above), ‘percentage live
526 tree carbon’ (representing carbon in established fire-tolerant trees; Table 1) was significantly
527 lower at HS than both LS and UB sites in both large trees (means 85% HS, 93% UB, 94%
528 LS; Fig. 4a), and, particularly, medium-sized trees (17% HS, 65% LS, 73% UB; Fig. 4b). In
529 contrast, ‘percentage small tree carbon’ (proportional live tree carbon in potentially fire-
530 sensitive smaller trees; Table 1) was significantly greater at HS (9.6%) than LS (4.8%) and
531 UB sites (4.2%; Fig. 5). This increased vulnerability of the growing stock to the next fire at
532 HS sites was accompanied by a heightened potential for fire ignition as indicated by
533 significant increases, relative to LS and UB sites, in elevated fine fuel carbon (largely as live
534 and dead tree regeneration; Fig. 2b) that more than counterbalanced significant but relatively
535 minor decreases in litter (Fig. 2a) and small fallen dead wood (Fig. 2c).

536 The remaining carbon stability indicator, ‘char carbon’ (>2 mm char; Table 1), was
537 minimally influenced by wildfire severity. Significantly greater litter char at LS than UB sites
538 (Fig. 6a) was consistent with low-severity wildfire effects on soil carbon stocks (Fig. 3) but
539 of a much smaller magnitude (mean difference of 0.23 Mg C ha⁻¹ between LS and UB sites;
540 Fig. 6a). Unlike mineral soil carbon, wildfire severity did not clearly influence carbon stocks
541 in soil char to 10 cm depth, which was a minor carbon stock with means in the range 2.3
542 (UB) to 3.0 Mg ha⁻¹ (HS; Fig. 6b).

543 Compared with wildfire severity, the effects of recent (≤10 years) prescribed fire prior
544 to 2009 on our carbon stability indicators were negligible. That is, with the exception of

minor or variable interactive effects with wildfire severity on some components of fuel carbon (Figs 2b, 2d), time since last preceding fire had no significant effects on percentage live tree carbon (Fig. 4), on percentage small tree carbon (Fig. 5), or on char carbon (Fig. 6).

DISCUSSION

Stand-level carbon stocks influenced by wildfire severity rather than preceding prescribed fire

Wildfire severity, rather than preceding prescribed fire, had the greatest influence on the main carbon stocks in our fire-tolerant forests five years after the Black Saturday wildfire. Significant decreases in live large tree carbon and increases in standing dead wood carbon associated with high-severity wildfire reflected elevated tree mortalities in all size classes, particularly the medium-sized cohort (Bennett et al. 2016). Greater tree mortalities were counteracted by significantly greater seedling recruitment at High severity sites, indicating an increased reliance on seedlings in post-fire recovery akin to more fire-sensitive forests (Bennett et al. 2016). Time to recovery of tree carbon stocks will depend on post-fire net ecosystem productivity (NEP), particularly the balance between losses associated with the ongoing decomposition of dead trees and gains from growth of both surviving trees and new recruits (Campbell et al. 2016). Evidence from stand-replacing disturbances elsewhere (Wang et al. 2008, Anderson-Teixeira et al. 2013) suggests that High severity sites were initially a net carbon source (negative NEP), and could switch to a net carbon sink as the ratio of gross primary productivity to ecosystem respiration increases in the first decade after wildfire. However, predicting source-sink dynamics in fire-tolerant eucalypt forests remains problematic since, while we have some understanding of NEP trajectories of comparable even-aged forests (Attiwill 1979), very little is known about the NEP of mixed-aged eucalypt forests with time since fire including the relative contributions of established and juvenile trees to carbon uptake, and the ongoing emissions associated with decomposition of fire-killed biomass.

In contrast to tree carbon, soil carbon stocks were more clearly influenced by low-severity than high-severity wildfire. Mean soil increases of 8 Mg ha⁻¹ to 10 cm depth at Low severity relative to Unburnt sites were consistent with deposition of pyrogenic organic matter (Mastrolonardo et al. 2014, Hobbey et al. 2017), and were within the range of ash carbon loads assessed two months after the 2009 Black Saturday wildfire in a similar forest type (4

to 10 Mg ha⁻¹; Santín et al. 2012). That a similar effect was not detected at High severity sites could be due to a number of factors including greater production of partly burnt material at Low severity sites that is often carbon enriched relative to more combusted residues (Santín et al. 2012), an effect consistent with the significantly greater litter char at Low severity than Unburnt sites. In addition, significantly lower soil carbon stocks to 10-cm depth at High than Low severity sites could be due to greater soil erosional losses at High severity sites (Bormann et al. 2008). This is consistent with qualitative observations five months after Black Saturday of ash redistribution via overland flow at severely burnt forest (Santín et al. 2012), and with the significantly greater soil volumetric mass (and bulk density, data not shown) of 0-10 cm soils at High than Low severity sites, which could indicate sampling of deeper soils after erosion of more carbon enriched surface soils (Bormann et al. 2008).

Carbon stocks deeper in the soil profile were also influenced by low-severity wildfire and, less reliably, by preceding prescribed fire. Elevated soil carbon stocks at 10 to 30 cm depth at Low severity sites is consistent with evidence elsewhere of vertical movement of pyrogenic carbon down the soil profile through percolation, bioperturbation, and physical processes (Santín et al. 2016, Hobley et al. 2017). Vertical accessions of incompletely combusted pyrogenic residues at our Low severity sites were also indicated by independent analyses of soil organic matter (SOM) content to 30 cm depth (loss on ignition, 375°C, data not shown). Increases in mean carbon and SOM stocks at 10 to 30 cm depth were also associated with burning by prescribed fire up to 10 years before the wildfire, suggesting that deep soil carbon stocks could be influenced by a succession of low-intensity fires. While covariate analyses indicated this effect was not reliably significant, it is consistent with evidence from a prescribed fire experiment in a similar eucalypt forest where soil carbon content at 20 to 30 cm was increased by repeated burning over 27 years relative to long-unburnt controls, particularly at 10-yearly intervals (Shrestha 2015). Nonetheless, a total mean increase in soil carbon to 30 cm depth of 31 Mg ha⁻¹ at Low severity relative to Unburnt sites is difficult to reconcile given minimal effects of both low-severity wildfire and recent preceding prescribed fire on the other carbon pools. Indeed, very wide 95% confidence intervals around this mean difference (16 to 47 Mg ha⁻¹) and all soil carbon stock differences suggest considerable uncertainty around the magnitude of fire effects on soil carbon at depth. In addition to naturally high spatial variability, this could be due to a number of factors including overestimation of soil volumetric mass at depth, a bias in the selection of Low severity and Recently burnt sites (although covariate analyses indicated few significant effects of location, topography, and climate), and/or variable deposition of off-site pyrogenic

carbon via water and wind vectors (Santín et al. 2016). Whatever the reasons, our data provide support for arguments that pyrogenic carbon can be a quantitatively important ‘sink’ (Santín et al. 2015) at least in the short-term, and certainly worthy of further investigations to better understand its origins and fate (Hobley et al. 2017).

Indications of changes in short-term carbon stability associated with wildfire severity

The short-term carbon stability of our fire-tolerant forests was variously influenced by wildfire severity. Overall, wildfire severity did not significantly affect the resistance component of stability at five years. That is, the magnitude of change in mean total carbon stocks (in all live and dead above-ground pools plus soil to 30 cm depth) was not significantly different among Low severity, High severity and Unburnt sites. This could in part be due to insufficient power in our sampling design given high spatial variability of stocks in these natural forests (e.g. decreases in live large tree carbon at High severity sites were significant for 71 sites but not for the subset of 42 sites). However, no overall carbon-stock effect was also due to carbon stock decreases in above-ground biomass being counterbalanced by increases in either standing dead wood (High severity sites), or in soil (Low severity sites). As such, our multi-pool assessment highlights how transfers between live and dead pools in fire-tolerant forests can buffer total stand-level carbon losses in the first five years after even high-severity wildfire.

Beyond the first few years after wildfire, maintenance of carbon stocks in our fire-tolerant forests will in part depend on the persistence of carbon in dead pools. As indicated by our assessment of litter char carbon and soil carbon (discussed above), low-severity wildfire could have the potential to increase the carbon stability of our fire-tolerant forests by increasing the carbon stored in more persistent pyrogenic forms, particularly if stored at depth (Hobley et al. 2017). Nonetheless, how long pyrogenic products will persist in our forest soils remains largely unknown, and could vary from decades to centuries (Singh et al. 2012) depending on its physico-chemical nature (a focus of our ongoing research) and on its interactions with the decomposing environment and with soil properties (Singh et al. 2012, Butnor et al. 2017). Similarly, the persistence of carbon stocks in standing dead wood, which were significantly greater at our High severity than Low severity and Unburnt sites, remains largely unknown for our forests, and will require quantitative understanding of the rates at which standing eucalypt trees both decompose and collapse in the coming decades (Ghimire et al. 2012).

While carbon stocks in dead pools will decrease with time, carbon stocks in the live pools, particularly in the dominant trees, will determine the rate of stock recovery – that is, the resilience component of forest carbon stability. Here, high-severity but not low-severity wildfire led to significant decreases in our stability indicator ‘percentage live tree carbon’ in surviving large- and medium-sized trees. This decreased carbon fixation capacity of established trees was at least partially offset by prolific tree regeneration at High severity sites. However, while small trees can grow quickly in the immediate post-fire environment, competition from established trees can markedly reduce growth of smaller trees in these multi-aged forests (Griebel et al. 2017), so that they are unlikely to become substantive carbon stores in the longer term (e.g. <4% of total live tree carbon; Bennett et al. 2013). Indeed, proportionally more live tree carbon in small trees (our ‘percentage small tree carbon’ indicator) after high-severity wildfire could indicate greater vulnerability of tree carbon at High severity sites to an impending fire, since small trees are less likely to survive the next fire (Gill and Ashton 1968, Lawes et al. 2001), and to be replaced by new growing stock if the fire interval is less than the tree’s primary or secondary juvenile phase (Fairman et al. 2016). Loss of small trees in a subsequent fire could portend decreases in forest productivity at High severity sites where mortalities of large trees were already relatively high (Bennett et al. 2016), and where growth rates will likely be compromised by repeated fires (Bennett et al. 2013). Nonetheless, while the potential for demographic changes has been noted (Fairman et al. 2016), empirical data to examine effects of recurrent wildfires on the productivity of fire-tolerant eucalypt forests are currently lacking.

While signs from our live- and small-tree carbon stability indicators seemed clear, fire effects on our final carbon stability indicator, fuel carbon, were mixed. Lower stocks of fine surface and small woody fuels at High severity sites could reduce the likelihood of subsequent fire ignitions and/or fire intensity in the first five years after wildfire. However, the functional importance of these relatively minor decreases in terms of fire behaviour is difficult to gauge since our fine surface fuel loads were universally low (mean *mass* range of 6 to 10 Mg ha⁻¹), and well below the 12 Mg ha⁻¹ fine fuel (mass) threshold in eucalypt-dominated forests for ‘fire control problems under conditions of severe fire weather’ (Raison et al. 1983), despite including an additional fuel component from 6 to 25 mm thickness. In addition, and consistent with effects in more productive fire-sensitive eucalypt forests (Bowman et al. 2014), decreases in surface fine and small woody carbon after high-severity fire, were counterbalanced by significant increases in elevated fine fuels principally as

eucalypt regeneration. Thus, the scope for high-severity wildfire to markedly decrease fuel hazards beyond the immediate post-fire period seems limited in these forests.

Consistent with minimal effects of low-severity wildfire, our tree- and fuel-based indicators of carbon stability were not significantly influenced by recent preceding prescribed fire. No effect of preceding prescribed fire on percentage live tree carbon and percentage small tree carbon is consistent with negligible effects of prescribed fire regimes on tree mortality in comparable forest types (Bennett et al. 2013). Similarly, no effect of both recent prescribed fire and low-severity wildfire on carbon in surface fine fuels (litter) just five years after the wildfire fits with evidence of quick recovery of fine fuels in eucalypt forests after low-intensity fire (Raison et al. 1983, Jenkins et al. 2016), and with general findings that prescribed fire effects on wildfire behaviour in eucalypt forests are greatest within about five years of the prescribed fire (Fernandes and Botelho 2003, Tolhurst and McCarthy 2016). Sustained decreases in some fuel components after low-severity wildfire, like rotten small fallen wood, could help explain observations of ameliorated wildfire severity up to ten years after low-intensity prescribed fire in eucalypt-dominated landscapes (Price and Bradstock 2012, Tolhurst and McCarthy 2016). However, given that Unburnt sites supported minimal elevated fuels (as shrubs and eucalypt regeneration), which appear to influence the occurrence of crown fires elsewhere in eastern Australia (Storey et al. 2016), there seems little scope for marked changes with time in the amounts of fuel carbon in our forests. This is in contrast to the fire-tolerant forests of the temperate United States where understory fuel loads and tree density increase and persist for decades after wildfire, thereby increasing vulnerability of carbon stocks to subsequent fire over time (Hurteau and Brooks 2011).

Management implications

Resprouter eucalypt forests are presented as a reliable option in adaptation management frameworks for sustained carbon sequestration under increasing fire activity (Lavorel et al. 2015, Colloff et al. 2016) due to the capacity of the dominant eucalypts to ‘recover within a few years from even high intensity fire’ (Lavorel et al. 2015). Our assessment of the short-term carbon stability of resprouter eucalypt forests after a high-severity wildfire provides a cautionary note to this assumption. High-severity wildfire had clear impacts on both the size and distribution of live tree carbon – decreased live tree carbon stocks, decreased percentage live tree carbon, and increased percentage small tree carbon – without clearly reducing fuel hazards five years after the wildfire. These impacts could be atypical given that fire

intensities during the ‘catastrophic’ period of the Black Saturday wildfire were beyond even the extreme range for this type of forest (Murphy et al. 2013). However, without accurate knowledge of what burnt when during the first 12 hours of the wildfire (Price and Bradstock 2012), we cannot be certain how many of our High severity sites burnt under catastrophic fire weather in the first 6 hours as opposed to very high and moderate fire weather in the next. Moreover, while post-wildfire tree mortalities might have been elevated by an extended drought that preceded Black Saturday (Bennett et al. 2016), we suggest that our study will be increasingly relevant to future conditions in south-eastern Australia given predictions of more frequent high-severity wildfire (Clarke et al. 2011), and of more frequent severe droughts (CSIRO and Bureau of Meteorology 2015).

While a single high-severity wildfire impacted on the live tree carbon stocks of our fire-tolerant forests, their ongoing carbon stability will depend on what happens next. If the next high-severity wildfire occurs towards the upper limit of fire intervals for this forest type (20 to 100 years; Murphy et al. 2013), then live tree carbon stocks could well recover through growth of surviving established trees, and contributions from new recruits. However, a shorter wildfire interval (c. <15 years) will likely kill regrowth, which might not be replaced due to insufficient seed, and potentially kill more established trees since protective mechanisms like bark thickness would have been compromised in the first fire (Bennett et al. 2013, Fairman et al. 2016). While such short intervals were not common in the past, they now seem more likely given a recent spate of short-interval wildfires (Fairman et al. 2016), highlighting the importance – as elsewhere (Buma et al. 2014, Seidl et al. 2014) – to both anticipate and manage the potential impacts of compounded disturbances on forest carbon stability. Multiple short-interval wildfires could, for example, convert resprouter eucalypt forests to fragmented and non-eucalypt states (Fairman et al. 2016), necessitating decisions about interventions to restore current states including aerial seeding programs that have already been trialled for fire-sensitive eucalypt forests (Bassett et al. 2015).

Contrary to recent assumptions (Lavorel et al. 2015), our study indicates that carbon stability of fire-tolerant eucalypt forests might indeed need active management. In an emerging environment of more wildfire in southeastern Australia (Fairman et al. 2016), stability of live tree carbon stocks in fire-tolerant forests will increasingly depend on minimising the extent, and particularly the frequency, of high-severity wildfire. Potential options include comprehensive wildfire suppression as has been suggested for fire-sensitive eucalypt forests (Bowman et al. 2013), and increased use of fuel reduction treatments like low-intensity prescribed fire (Adams 2013). Considerable evidence indicates potential for

prescribed fires to mitigate wildfire extent in eucalypt forest landscapes (Fernandes and Botelho 2003), although effectiveness is limited after 10 years, and under severe ‘weather-dominated’ fire conditions (Price and Bradstock 2012, Tolhurst and McCarthy 2016). Our study was not designed to examine landscape-scale mitigation of wildfire by prescribed fire since we made stand-level assessments of contrasting severity classes after the fact, when any potential mitigation of wildfire behaviour by preceding prescribed fire was largely a moot point. However, non-significant effects of preceding prescribed fire on nearly all of our carbon stocks and stability indicators did demonstrate that a single prescribed fire ≤ 10 years before will not markedly exacerbate mean carbon losses due to either low- or high-severity wildfire. Indeed, elevated soil carbon at Low severity sites that was further increased at depth, if not reliably so, at Recently burnt sites, indicated scope for low-intensity fires to increase carbon stocks through the accumulation of pyrogenic carbon in soil carbon reserves.

While providing much needed empirical evidence of fire effects in fire-tolerant eucalypt forests, our study could only consider a limited range of fire conditions. Ongoing knowledge gaps include effects of prescribed-wildfire sequences that involve more sites burnt within shorter timeframes than were possible here (i.e. ≤ 5 versus ≤ 10 years), and that involve moderate wildfire severities (e.g. Volkova et al. 2014). In addition, comparative impacts of multiple low-intensity prescribed fires compared with less frequent wildfires requires more extensive examination in southeastern Australia (Bennett et al. 2014), so that we can better weigh up the carbon ‘outlays’ and ‘savings’ of fuel treatment practices at broad temporal and spatial scales (Bradstock et al. 2012). Here, our multi-indicator study highlights the importance of going beyond comparisons of fuel consumption in prescribed versus wildfires (Bradstock et al. 2012) – since fine fuels like litter store very little carbon in fire-tolerant eucalypt forests – to consider potential carbon savings (decreased decomposition, increased uptake) if low-intensity prescribed fires reduce the extent of tree mortality due to high-severity wildfire. Our study also highlights the importance of better integrating soils in fire carbon assessments not only in terms of their vulnerability to combustion and erosion losses (including potential feedbacks to post-fire forest productivity; Bormann et al. 2008), but also in terms of their potential to act as reservoirs of what could be substantial pyrogenic carbon.

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Supporting Information

1038 Additional supporting information may be found in the online version of this article

1039 at <http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/supinfo>

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Data Availability

1042 Data available from Figshare: <https://doi.org/10.4225/49/59a7541053aed>

Author Manuscript

1043 **Table 1.** Stand-level carbon stocks and carbon stability indicators that were assessed for each wildfire severity by time-since-fire combination
 1044 five years after the 2009 wildfire.

Stock or indicator	Units	Description	Notes and assumptions
<i>Stock</i> ^a			
Above-ground biomass	Mg C ha ⁻¹	Standing live trees in all size classes (large, medium, small, regeneration) plus live shrubs (42 sites), or standing live large trees only (71 sites)	Tree sizes: large ≥20 cm dbhob ^b , medium 10 – <20 cm dbhob; small: 2.5 – <10 cm dbhob; regeneration as saplings (<2.5 cm dbhob) and seedlings (<2.5 cm basal diameter)
Dead wood: standing	Mg C ha ⁻¹	Standing dead trees in all size classes (large, medium, small, and regeneration) plus stumps (42 sites), or standing dead large trees only (71 sites)	Tree sizes as above; stumps <1.3 m height (small <20 cm, large ≥20 cm diameter at 30-cm height)
Dead wood: fallen	Mg C ha ⁻¹	Coarse woody debris in all size and decay classes	≥2.5 cm minimum cross-sectional diameter
Litter	Mg C ha ⁻¹	Dead plant material on forest floor above the mineral soil	0.2 – <2.5 cm cross-sectional dimension including >0.2 cm litter char
Soil	Mg C ha ⁻¹	Soil organic carbon to 30 cm depth	Mineral soil (<0.2 cm) to 30 cm depth, including <0.2 cm litter component, and >0.2 cm soil char to 10 cm depth

Stability indicator: positive relationship with stability

Percentage live tree carbon	%	Carbon stocks in surviving live trees as a percentage of total carbon stocks in standing live and dead trees of the same size class (large or medium, defined above)	Stability assumed to increase with increasing percentage live carbon; i.e., capacity to recover post-fire carbon stocks is comparatively greater if proportionally more carbon is stored in actively growing than decomposing large- and medium-sized trees
Char carbon	Mg C ha ⁻¹	Carbon stocks in visible char in litter and in soil to 10 cm depth	Stability assumed to increase with increasing char carbon; i.e. more carbon stored in more persistent forms than ‘uncharred precursors’ ^c ; char >0.2 cm min. dimension

Stability indicator: negative relationship with stability

Percentage small tree carbon	%	Carbon stocks in live small trees and regeneration as a percentage of carbon stocks in live trees of all size classes	Stability assumed to decrease with increasing percentage small tree carbon; i.e. vulnerability of live tree carbon stocks to an imminent fire is comparatively greater if more carbon is stored in the smallest trees, which are more likely to be killed by fire than larger trees
Fuel carbon	Mg C ha ⁻¹	Carbon stocks by fuel class (litter, elevated fine fuel, coarse fuel)	Stability assumed to decrease with increasing fuel carbon; i.e. ignition potential and/or intensity of an imminent fire presumably increased by greater mass of litter, elevated fine fuels, and coarse fuel ^d ; litter represents surface fine

fuels (as defined above but excludes litter char); elevated fine fuels include shrubs, and live and dead tree regeneration; coarse fuel includes small fallen dead wood ≥ 2.5 cm – < 7.5 cm, and large fallen dead wood ≥ 7.5 cm diameter

1045 ^a Stocks by pool or pool components as identified by the Intergovernmental Panel on Climate Change (IPCC 2014) with the exception of carbon in below-ground biomass,
1046 which could not be adequately assessed within the study's logistical and time constraints

1047 ^b dbhob = diameter at breast height over-bark (breast height = 1.3 m)

1048 ^c Santin et al. 2015

1049 ^d Fuel carbon classes represent fuel layers associated with fire behavior in eucalypt-dominated forests (Tolhurst and Cheney 1999; Gould et al. 2011). Eucalypt bark, an
1050 additional potential fuel, was not considered because previous research indicated that changes in bark carbon would be minor irrespective of fire type in this forest type
1051 (Bennett et al. 2013)

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FIGURE LEGENDS

FIG. 1. Mean carbon stock differences between (a) Low and High wildfire severity sites and Unburnt sites, and (b) Recently burnt (by prescribed fire within 10 years before the wildfire) sites and Long unburnt sites. Values in italics are the mean stocks in the unburnt condition (across both time-since-preceding-fire classes in (a), and all severity classes in (b)). Values are means of (a) 14, and (b) 21 sites. Error bars are the 95% confidence interval of the difference (i.e. inclusion of zero indicates not significantly different from the unburnt condition). Stocks are as described in Table 1 ('ABG Biom' Above-ground biomass; 'DW' Dead wood). Asterisks indicate a significant difference ($P < 0.05$) between Low and High severity classes. Circles represent the mean differences in live large tree carbon or dead large tree carbon (only) using data from all 71 sites that were assessed for large trees (hatches indicate significantly different from the unburnt condition).

FIG. 2. Effects of 2009 wildfire severity class, and time since preceding fire (grey bars, Recently burnt by prescribed fire; white bars, Long unburnt) on stocks contributing to 'Fuel carbon' (Table 1): (a) litter (surface fine fuel, < 25 mm min. cross-sectional diam.); (b) elevated fine fuel as live woody shrubs and live and dead tree regeneration (< 25 mm diameter); and coarse fuel as (c) small fallen dead wood (DW, < 75 mm diameter); and (d) large fallen DW (≥ 75 mm). Values are the means of 7 sites ($\pm$ SE), with black bars representing woody shrubs in panel (b) and hatched bars representing rotten coarse fuel (Decay classes 4 and 5) in the lower panels. Asterisks indicate significant effects (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) of severity (S; abbreviations: Unburnt, UB; Low severity, LS; High severity, HS), and of the interaction between severity and time since fire (S x TSF) in two-way Analysis of Variance (ANOVA) models (Time since fire effects were not significant). Significant effects in square brackets relate to either shrubs or rotten coarse fuel. ANOVA results are summarised in Appendix S1: Table S4.

FIG. 3. Soil carbon stocks to 10 cm depth (a), and between 10 and 30 cm depth (b), by combinations of 2009 wildfire-severity class, and time since preceding fire (grey bars: Recently burnt by prescribed fire; white bars: Long unburnt). Values are means of 7 sites ($\pm$ SE). Asterisks indicate significant effects (* $P < 0.05$, *** $P < 0.001$) of severity (S; abbreviations: Unburnt, UB; Low severity, LS; High severity, HS), and of time since fire (TSF; abbreviations: Recently burnt,

RB; Long unburnt, LUB) in two-way Analysis of Variance (ANOVA) models. ANOVA results are summarised in Appendix S1: Table S4.

FIG. 4. Effects of 2009 wildfire severity class, and time since preceding fire (grey bars, Recently burnt by prescribed fire; white bars, Long unburnt) on 'percentage live tree carbon' (Table 1) in each of two tree size classes: (a) large (>20 cm dbhob), and (b) medium (10 to 20 cm). Values are the means ($\pm$ SE) of 9 to 17 sites (large trees) or 7 sites (medium trees). Asterisks indicate significant effects ($***P<0.001$) of severity (S; abbreviations: Unburnt, UB; Low severity, LS; High severity, HS) in two-way Analysis of Variance (ANOVA) models (Time since fire effects were not significant). ANOVA results are summarised in Appendix S1: Table S4.

FIG. 5. Effects of 2009 wildfire severity class, and time since preceding fire (grey bars, Recently burnt by prescribed fire; white bars, Long unburnt) on 'percentage small tree carbon' (the proportion of total live tree carbon in live small trees and regeneration). Asterisks indicate significant effect ($***P<0.001$) of severity (S; abbreviations: Unburnt, UB; Low severity, LS; High severity, HS) in a two-way Analysis of Variance (ANOVA) models (Time since fire effects were not significant). ANOVA results are summarised in Appendix S1: Table S4.

FIG. 6. Carbon stocks in char (>2 mm) in (a) litter and (b) soil to 10 cm depth by combinations of 2009 wildfire severity class, and time since preceding fire (grey bars, Recently burnt by prescribed fire; white bars, Long unburnt). Asterisks indicate significant effect ($*P<0.05$) of severity (S; abbreviations: Unburnt, UB; Low severity, LS; High severity, HS) in a two-way Analysis of Variance (ANOVA) model (Time since fire effects were not significant). ANOVA results are summarised in Appendix S1: Table S4.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

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