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Above-ground forest carbon shows different responses to fire frequency in harvested and unharvested forests

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Running head: Logging and frequent fire reduce carbon

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24 Abstract

25 Sequestration of carbon in forest ecosystems has been identified as an effective strategy to
26 help mitigate the effects of global climate change. Prescribed burning and timber harvesting
27 are two common, co-occurring forest management practices that may alter forest carbon
28 pools. Prescribed burning for forest management, such as wildfire risk reduction, may shorten
29 inter-fire intervals and potentially reduce carbon stocks. Timber harvesting may further
30 increase the susceptibility of forest carbon to losses in response to frequent burning regimes,
31 by redistributing carbon stocks from the live pools into the dead pools, causing mechanical
32 damage to retained trees and shifting the demography of tree communities. We used a 27 year
33 experiment in a temperate eucalypt forest to examine the effect of prescribed burning
34 frequency and timber harvesting on above-ground carbon (AGC). Total AGC was reduced by
35 ~23% on harvested plots when fire frequency increased from zero to seven fires, but was not
36 affected by fire frequency on unharvested plots. The reduction in total AGC associated with
37 increasing fire frequency on harvested plots was driven by declines in large coarse woody
38 debris (≥ 10 cm diameter) and large trees (≥ 20 cm diameter). Small tree (< 20 cm DBH) AGC
39 increased with fire frequency on harvested plots, but decreased on unharvested plots. Carbon
40 in dead standing trees decreased with increasing fire frequency on unharvested plots, but was
41 unaffected on harvested plots. Small coarse woody debris (< 10 cm diameter) was largely
42 unaffected by fire frequency and harvesting. Total AGC on harvested plots was between 67%
43 and 82% of that on unharvested plots, depending on burning treatment. Our results suggest
44 that AGC in historically harvested forests may be susceptible to declines in response to
45 increases in prescribed burning frequency. Consideration of historic harvesting will be
46 important in understanding the effect of prescribed burning programs on forest carbon
47 budgets.

48 **Keywords:** above-ground carbon, eucalypt forest, fire regime, forest management, logging,
49 prescribed burning, temperate forest, timber harvesting

50 Introduction

51 Effective mitigation of global climate change requires a multitude of strategies aimed at
52 reducing carbon emissions and increasing carbon sequestration (IPCC 2014). Forest

ecosystems are influential in determining global carbon budgets, accounting for approximately 45% of terrestrial carbon stores (Bonan 2008). Consequently, forest management aimed at increasing carbon sequestration can play an important role in reducing atmospheric CO₂ concentrations, and mitigating the effects of anthropogenic climate change (McKinley et al. 2011, IPCC 2014). Forest resource use and management can affect forest carbon stocks by altering rates of carbon emission and sequestration (North et al. 2009, Bowman et al. 2013, Berenguer et al. 2014). Fire management and timber harvesting are two key management practices affecting forest carbon balances globally (Bryan et al. 2010, Aponte et al. 2014, Hurteau et al. 2016).

Fire alters ecosystem carbon pools through the consumption of dead organic material and mortality of plant material (Williams et al. 2012), with the latter resulting in the redistribution of carbon from the live to dead pools (Bassett et al. 2015). In forests, most above-ground carbon (AGC) is stored in live trees (Hubbard et al. 2004, Bennett et al. 2014, Gordon et al. 2018), consequently ecosystem carbon losses during a fire are generally relatively small (Volkova and Weston 2013, Keith et al. 2014). Redistribution of carbon from the live to dead pool will depend on fire response syndromes of plant species, with high redistribution occurring in forests dominated by obligate seeder and basal resprouter tree species (Keith et al. 2014, Fairman et al. 2017). AGC is less affected by a single fire event in forests dominated by tree species that resprout epicormically (e.g. Volkova and Weston 2013), except under extreme conditions that result in high rates of tree mortality (e.g. extreme fire intensity following drought; Bennett et al. 2016).

AGC in forests may be sensitive to shifts in fire frequency, due to effects on plant community demography and input/loss dynamics of dead woody debris (Aponte et al. 2014, Collins et al. 2014b, Stares et al. 2018). Short inter-fire intervals can inhibit plant recruitment, increase mortality and reduce growth rates of trees, leading to reduced basal area and biomass (e.g. Peterson and Reich 2001, Collins et al. 2014b). Reductions in tree recruitment and standing biomass will have flow on effects to dead carbon pools, potentially reducing dead carbon biomass in the long term (Bassett et al. 2015). Reductions in dead carbon pools will occur if the rate of decay and consumption by fire exceeds input (Bassett et al. 2015). Experiments examining the response of forest biomass to long-term regimes of frequent experimental burning have generally reported reductions in the biomass of trees and woody debris in

response to frequent fire (e.g. Ryan and Williams 2010, Aponte et al. 2014, Collins et al. 2014b).

Prescribed burning is widely applied across forest ecosystems to achieve a range of management objectives, including the reduction of wildfire risk to assets via fuel reduction and the manipulation of fire regimes for ecological purposes (Penman et al. 2011, Williams et al. 2012, Ryan et al. 2013). In Australian forests dominated by resprouting angiosperm trees (i.e. 'eucalypts'), prescribed burning is largely used for fuel reduction, with an objective of reducing wildfire risk at the wildland urban interface or within forests managed for economic timber assets (Penman et al. 2011). Effective fuel reduction typically requires the regular application of prescribed burning, which can increase overall fire frequency across treated landscapes (Penman et al. 2011). However, factors such as topographic heterogeneity, climate, fuels and ignition patterns will create unburnt patches within prescribed burns (Penman et al. 2007, McCarthy et al. 2017). Consequently, there will be spatial variability in the effect of a prescribed burning regime on forest ecosystems in response to environmental characteristics of the treated landscape (e.g. topography, vegetation) and weather conditions prior to and during burns. Although carbon sequestration has been identified as an objective of forest fire management (e.g. Victorian Department of Sustainability and Environment 2012), burning prescriptions to achieve this are undefined or poorly understood. Consequently, it is unknown whether current burning prescriptions for asset protection will lead to desirable outcomes for carbon sequestration (e.g. Bradstock et al. 2012, Martin et al. 2015).

Timber harvesting results in immediate changes to AGC within a forest, with losses in the live carbon pool that are directly proportional to harvesting intensity, and gains to the dead carbon pool in the form of harvesting residue or 'slash' (Ximenes et al. 2008). Post-harvest sequestration will occur with the regeneration of vegetation communities (Roxburgh et al. 2006). Harvesting can increase the sensitivity of AGC stocks to fire by shifting tree size class distribution towards fire-sensitive juveniles (Collins et al. 2014b), converting live carbon to fallen dead debris that is susceptible to consumption (Knapp et al. 2005, Holland et al. 2017) and by causing mechanical damage to trees (Feldpausch et al. 2005, Thorpe et al. 2008) which increases the likelihood of fire related tree mortality and collapse (Whitford and Williams 2001, Gibbons et al. 2008). Despite the concurrent application of repeated

prescribed burning and timber harvesting across forest ecosystems globally, there have been few studies examining their interactive effects on AGC stocks (e.g. Berenguer et al. 2014).

The aim of this study was to examine the interactive effect of timber harvesting and prescribed burning frequency on forest AGC. We utilised a long-term burning experiment (the 'Eden Burning Study Area'), located in a temperate eucalypt forest in southern Australia, to assess the impact of timber harvesting and ~25 years of experimental prescribed burning regimes on AGC. We hypothesise that: (i) AGC will be reduced by timber harvesting and frequent prescribed burning; (ii) that the effect of fire frequency will be greatest on harvested plots, and; (iii) that heterogeneity of burn patterns imposed by topography and ignition patterns may moderate these effects at a landscape scale.

Methods

Study area

The study took place in the Eden Burning Study Area (EBSA) in Yambulla State Forest (37°14'S, 149°38'E) in south-eastern New South Wales, Australia (Figure 1). The EBSA covers approximately 1100 ha of dry sclerophyll forest (Penman et al. 2007). The forest community is predominantly Timbillica Dry Shrub Forest (Keith and Bedward 1999), an 'open forest' community with tree heights between ~10 m and 30 m and canopy cover of 30% - 70%. The tree canopy is comprised of a mix of eucalypt species (e.g. *E. agglomerata*, *E. globoidea*, *E. sieberi*, *E. consideriana*, *E. muelleriana*, *E. cypellocarpa*, *E. obliqua*) that resprout epicormically following wildfire, which is typical of eucalypts across dry sclerophyll forests of Australia (Gill and Catling 2002). The understorey is dominated by a diverse array of shrubs and ground cover, including *Allocasuarina littoralis*, *Banksia serrata*, *Daviesia buxifolia*, *Epacris impressa*, *Acacia terminalis*, *Acacia longifolia*, *Gonocarpus teucroides*, *Platysace lanceolata*, and *Lomandra filiformis* (Binns and Bridges 2003, Penman et al. 2008). Climate within the study region is temperate, with a maximum mean monthly temperature of 24.9°C in January, a minimum mean monthly temperature of 4.1°C in July and average annual rainfall of 760 mm (Merimbula Airport AWS, www.bom.gov.au, accessed 5th April 2018).

Fire regimes in the dry sclerophyll forests of south-eastern Australia are characterised by mixed severity fires (Bradstock 2008), with typical inter-fire intervals ranging from 5 to 20

years, though intervals up to 100 years may occur in some cases (Bradstock 2010, Murphy et al. 2013). Prescribed burning is used extensively to manage fuels for asset protection, with effective fuel management requiring burning targeted at short rotations (~4 - 8 years) (Penman et al. 2011). Timber harvesting has been undertaken extensively across these forests over the past century (Raison and Squire 2008). Recent harvesting rates in forests of south-eastern Australia (New South Wales, Victoria and Tasmania) have been ~60, 000 ha per annum (2001 - 2010), with selective and variable retention harvesting being the dominant silvicultural systems (Montreal Process Implementation Group for Australia and National Forest Inventory Steering Committee 2013).

The EBSA was largely inaccessible prior to the 1970s, due to limited access roads (Binns and Bridges 2003). There was no evidence of timber harvesting (i.e. no cut stumps) and a low level of recorded prescribed burning (~15% of the study area between 1979 and 1981) prior to the commencement of the experiment (Binns and Bridges 2003). A large wildfire burnt the entire study area at low intensity in January 1973, ~12 years prior to study establishment and commencement of initial measurements (Binns and Bridges 2003). Therefore, prior to the commencement of the study, the EBSA represented an ecosystem functioning largely in the absence of contemporary anthropogenic management.

Experimental treatments

The EBSA was established in 1985 by the Forestry Commission of New South Wales (currently the Forest Corporation of New South Wales) to examine the long-term ecological impacts of frequent burning and timber harvesting. The study area was divided into 18 experimental blocks (8–56 ha, mean = 32 ha), which were timber harvesting coupes (Binns and Bridges 2003) (Figure 1). Three replicate coupes were randomly allocated to each of the 6 treatments: unharvested and not burned (UN); unharvested and routinely burned (burning at 4-year intervals, UR); unharvested and frequently burned (burning at 2-year intervals, UF); harvested and not burned (HN); harvested and routinely burned (burning at 4-year intervals commencing 10 years post harvesting, HR); and harvested and frequently burned (burning at 2-year intervals, HF). Six permanent plots (108 plots in total) were randomly located and established in each experimental coupe to measure forest attributes including overstorey trees and coarse woody debris (CWD) (Binns and Bridges 2003).

Harvesting occurred in 1987 and 1988 and was an integrated operation, targeting both sawlogs and pulpwood. A proportion of mature trees were retained for habitat, seed trees, visual amenity and future sawlogs (Binns and Bridges 2003). Additionally, trees with an under-bark stump diameter <20 cm or with substantial defect or deformity were not felled because they did not meet product specifications (Binns and Bridges 2003). Harvesting removed ~60% of the original overstorey tree basal area (Binns and Bridges 2003). The intensity of harvesting varied considerably across the permanent monitoring plots, with the basal area of timber removed on plots ranging from 0 to 35.4 m² ha⁻¹ (mean = 15.38 m² ha⁻¹). The mean ($\pm$ S.E.) basal area of timber removed (m² ha⁻¹) across the survey plots was 12.04 $\pm$ 1.73, 18.06 $\pm$ 2.11 and 16.04 $\pm$ 1.68 in the harvesting no burning (HN), harvesting routine burning (HR) and harvesting frequent burning (HF) treatments respectively. Harvesting slash (i.e. felled tree crowns) was left onsite following harvesting (Bridges 2005). A post-harvest burn was conducted in coupes allocated to burning treatments (HR, HF) within 8 months following harvest, to reduce dead fuel biomass created by harvesting slash (Binns and Bridges 2003).

Prescribed fires were conducted in Autumn during periods when weather conditions were considered suitable. Ignition lines and points were implemented by ground crews with drip torches and the ignition patterns used varied depending on weather conditions and fuels (Penman et al. 2007). The most recent prescribed burns occurred in 2009, four years prior to our study, in all burning coupes. Four plots within the UN treatment were accidentally burnt at this time due to fires escaping containment lines. One plot (28, UF) was burnt by a small low intensity unplanned fire ignited by a lightning strike in November 1997 (Binns and Bridges 2003). These accidental fires were incorporated into plot-scale measures of fire frequency. We did not exclude the fire affected plots that were assigned to the 'No fire' treatment (i.e. UN) when assessing the effect of the factorial coupe level treatments.

Ten 4 m² fire evaluation quadrats were established within each plot and surveyed three months before and after each prescribed burn to assess fuel conditions and burn extent (Binns and Bridges 2003). Cumulative burn coverage was calculated by summing the proportion of fire evaluation quadrats burnt in each prescribed fire over the entire study period. The number of fires experienced at a sample plot was calculated as the number of burns in which $\geq$ 20% of the fire evaluation quadrats were burnt. Assessment of fire frequency data showed there was considerable differences in the number of fires applied at the coupe scale and the number

of times a plot burnt (Figure 2a). There was also considerable burn patchiness within plots, as shown by the variability in cumulative burn coverage (Figure 2b).

Assessment of carbon

Complete surveys of live trees ≥ 10 cm diameter at breast height (DBH) and fallen CWD (diameter ≥ 2.5 cm) were undertaken across all plots prior to the implementation of experimental treatments (1986-1988). Twelve of the original 108 plots were excluded from sampling in 2013 because they contained extensive rock outcropping or were dominated by shrubby thickets of *Meleuca* spp. and did not meet our definition of forest (i.e. the pre-treatment tree canopy cover was estimated at $<30\%$). An adjusted methodology was utilised across the 96 plots surveyed in 2013 to allow for a rapid assessment of carbon stocks. The methodology was designed to match the previous approaches, enhance the quality of the data and quantify new carbon pools (i.e. trees <10 cm DBH and stags ≥ 10 cm DBH).

Living trees with a DBH ≥ 10 cm were recorded within 25.2 m radius plots (0.2 ha) between July 1985 to April 1989 prior to the application of experimental treatments. Species, DBH and any damage or deformities were recorded for each tree (Binns and Bridges 2003). In the 2013 measurements, the DBH of all living and dead trees greater than 20 cm DBH were recorded across these 25.2 m radius plots. DBH of living and dead trees between 10 cm and 20 cm DBH were recorded across 11.3 m radius plots (0.04 ha) nested within the larger plot. Species, DBH and height were recorded for each tree. Height of the tallest trees onsite was recorded using a laser range finder (Nikon Forestry Pro), to obtain the maximum canopy height, and estimated for the remaining trees, using the maximum canopy height as a reference. Tallies of trees between 2.5 cm and 10 cm DBH were recorded on the 11.3 m radius plots. The DBH of dead trees and stumps was only recorded if they were greater than 1.3 m tall (i.e. breast height).

Above-ground live tree biomass was estimated using equations presented in Bi et al. (2004) to account for inter-species variation in allometry. If species specific equations were not available, analogous species in terms of growth form and wood properties were used (Stewart et al. 1979, Boland et al. 2006). Generic equations for native forest presented in Keith et al. (2000) were used for any other species ($<5\%$ of trees surveyed) (Appendix S1). The concentration of carbon in above-ground living tree biomass was taken to be 50% of estimated above-ground biomass (Gifford 2000). Adjustments to tree biomass estimates were

made to account for decay and hollows using published size specific equations (pg 1151, Roxburgh et al. 2006). Trees between 2.5 cm to 10 cm DBH were each assigned a carbon stock of 2.5 kg, a value that was calculated by Bennett et al. (2013) using a generic equation for small eucalypts, assuming an average tree height of 2 m (which is consistent with field observations at the EBSA).

Standing dead tree (i.e. stag) biomass was calculated using the generic equation in Keith et al. (2000) (Appendix S1) as the species of stags and stumps could not be reliably identified. Biomass estimates were corrected for bark, leaf, twig and stem loss. Measured live tree bole heights recorded for a subset of trees in the pre-treatment measurements were used to calculate mean bole height for a range of DBH classes (10-20, 20-40, 40-60, 60-80, >80). Dead trees exceeding the mean bole height for their diameter class were assumed to only be missing bark, leaves and small twigs, which make up approximately 23% of tree biomass for common species in the study region (Stewart et al. 1979). Therefore, a correction multiplier of 0.77 was applied to biomass estimates of these trees. If dead tree height was less than the mean bole height for their diameter class, biomass was first multiplied by 0.6 (i.e. the proportion of tree that is the bole) (Stewart et al. 1979, Ximenes et al. 2008) and then multiplied by the dead tree height to mean bole height ratio (i.e. the estimated proportion of the bole that remains). A decay function of 0.85 was used to convert predicted biomass to an estimate of dead biomass (Bennett et al. 2013). Carbon content was taken as 50% of dead tree biomass (Woldendorp et al. 2002).

The volume of CWD was estimated prior to experimental treatments using two 25 m long line transects offset 5 m from the plot centre. Transects were located using random bearings with a minimum separation of 10 degrees. Transect ends and mid-points were marked using steel posts to enable accurate relocation of transects (Bridges 2005). In the 2013 measurements, the original transects were extended by 25 m along the opposite bearing and offset 5 m from the plot centre. This resulted in 100 m of transect per plot, the recommended minimum transect length for CWD biomass estimation in Australian forests (Woldendorp et al. 2004). If the original transects were at approximately opposite bearings (i.e. between 170° and 190° apart) an alternate 50 m transect was established perpendicular to the original transects.

All CWD with a diameter ≥ 2.5 cm at the point of transect intersection was recorded. The intersected diameter and decay state (Table 1) of each piece of CWD was recorded. The volume of CWD was calculated for each plot using equation 1 (van Wagner 1968):

$$V = \pi^2 / (8 \times L) \times \sum (D)^2 \quad (1)$$

Where V is volume ($\text{m}^3 \text{ ha}^{-1}$), L is the transect length in metres and D is the intersected diameter (cm) of a piece of CWD. CWD biomass was obtained by multiplying CWD volume for each decay class (Table 1) by a decay specific wood density (Decay 1: 0.78 Mg m^{-3} ; Decay 2: 0.70 Mg m^{-3} ; Decay 3: 0.41 Mg m^{-3}) (Roxburgh et al. 2006). Carbon biomass was then calculated by multiplying CWD biomass by specific conversion factors for each decay class (Decay 1: 0.478; Decay 2: 0.481; Decay 3: 0.480) (Roxburgh et al. 2006).

Live plants and debris < 2.5 cm in diameter were not considered in this study as they typically make a relatively small contribution to total AGC in temperate eucalypt forests (Roxburgh et al. 2006, Jenkins et al. 2016).

Analysis

Analysis focused on AGC of large trees (≥ 20 cm DBH), small trees (2.5 - 20 cm DBH), stags, large CWD (≥ 10 cm diameter), small CWD (2.5 - 10 cm diameter) and all pools combined. Trees were separated into large and small size classes in order to assess the effects of treatments on mature trees and potential recruits respectively. We considered large and small CWD separately because of differences in consumption rates by fire (Holland et al. 2017).

The effects of fire frequency and harvesting intensity experienced at the sampling plot scale were the focus of our analysis, as this data can be more easily interpreted and applied elsewhere than coupe scale treatments. Generalised additive mixed models (GAMMs) were used to capture linear and non-linear responses of AGC pools to fire frequency and harvesting intensity. GAMMs link response and predictor variables via smoothing functions, allowing for estimation of non-linear relationships (Zuur et al. 2009). We used cubic regression splines with the number of knots limited to four, which is appropriate for datasets with between 30 and 100 observations (Zuur et al. 2009). Experimental coupe was specified as a random effect in the GAMMs to account for the nesting of sample plots within coupes.

Approximately half the plots in the dataset were unharvested ($n = 49$), thus having a harvesting intensity of zero, which meant the dataset had insufficient replication of harvesting intensity across the range of fire frequency to reliably model interactions between the two variables. To overcome this limitation, we conducted the analysis on harvested and unharvested plots separately, using model estimates and 95% confidence intervals to compare the effect of fire frequency between harvesting treatments. The approach of splitting the analysis into harvested and unharvested plots is also ecologically justifiable, as harvesting impacts are not limited to just timber removal (e.g. soil compaction and mechanical injury to trees by machinery).

Models for the harvested dataset included fire frequency, harvesting intensity and pre-treatment AGC as additive effects. Models for the unharvested dataset included fire frequency and pre-treatment AGC. Pre-treatment AGC was included as a covariate in the models to account for the effects of spatial variability in carbon storage due to landscape factors (e.g. topography, soil characteristics). Pre-treatment large CWD and small CWD and total AGC were used as predictors for their respective post-treatment measures. Total pre-treatment tree AGC (≥ 10 cm DBH) was used as a predictor for large trees, small trees and stags. We do not present results on the effects of pre-treatment AGC in the manuscript as this was not a primary objective of the study, though a predicted relationship between AGC and predictor variables is provided in Appendix S2. Predictor variables with $P \leq 0.05$ were considered statistically significant, though P -values between 0.1 and 0.01 have been interpreted with caution due to uncertainty associated with deriving P – values from mixed effect models (Zuur et al. 2009). Due to the confounded nature of fire frequency and time since fire, models containing effects of fire frequency that were significant or close to significance ($P < 0.1$) were refitted to a subset of the dataset containing plots that had burnt 4 – 8 years prior to sampling. In all cases the effect of fire frequency was found to be consistent across the two analyses (Appendix S3).

Data analysis was conducted using the statistical package R v3.2 (R Development Core Team 2016). The ‘*gam4*’ package was used to fit GAMMs (Wood and Scheipl 2016).

Results

Total AGC per plot ranged from 70.3 Mg C ha⁻¹ to 264.5 Mg C ha⁻¹ across the study plots, with a mean ($\pm$ S.E.) of 160.6 $\pm$ 3.9 Mg C ha⁻¹. Across all plots, the live carbon pool comprised

77% of total AGC, with large live trees (≥ 20 cm DBH) storing 107.7 ± 4.2 Mg C ha⁻¹ and small trees (< 20 cm DBH) storing 16.8 ± 1.5 Mg C ha⁻¹. Large CWD (≥ 10 cm diameter) was the primary component of the dead carbon pool (26.0 ± 1.9 Mg C ha⁻¹), followed by stags (6.5 ± 0.8 Mg C ha⁻¹) and small CWD (< 10 cm diameter) (3.6 ± 0.2 Mg C ha⁻¹).

Individual Carbon Pools

Harvesting intensity was found to have opposing effects on the large and small tree AGC pools (Figure 3). Large tree AGC decreased linearly as the basal area of timber removed increased ($P < 0.001$), with AGC being reduced by ~ 103 Mg C ha⁻¹ over the range of harvesting intensities experienced across the sample plots (0 m² ha⁻¹ to 35.4 m² ha⁻¹; Figure 3a). These losses were partially offset by a linear increase (~ 26 Mg C ha⁻¹) in small tree AGC with increasing timber harvesting ($P = 0.013$; Figure 3b). The dead carbon pools did not show a significant ($P > 0.1$) response to harvesting intensity, though there were differences in stag and large CWD AGC between harvested and unharvested plots that experienced no fire or low fire frequency, which are described below.

The effect of fire frequency on the AGC pools varied between harvested and unharvested plots (Figure 4). Large tree AGC decreased linearly by ~ 22 Mg C ha⁻¹ as fire frequency increased from zero to seven fires on harvested plots ($P = 0.062$), but was not affected by fire frequency on unharvested plots ($P = 0.211$; Figure 4a). Consequently, the difference in large tree AGC on unharvested and harvested plots increased with increasing fire frequency, with unharvested plots storing $\sim 31 - 67$ Mg C ha⁻¹ more than harvested plots experiencing an average harvesting intensity (Figure 4a). Small trees showed the opposite trend to large trees, whereby AGC increased linearly by ~ 13 Mg C ha⁻¹ as fire frequency increased from zero to seven fires on harvested plots ($P = 0.035$) and decreased linearly by ~ 11 Mg C ha⁻¹ as fire frequency increased from zero to six fires on unharvested plots ($P = 0.080$; Figure 4b).

Differences in small tree AGC between unharvested and harvested plots were only evident if there had been three or more fires, with harvested plots experiencing average harvesting intensity having up to ~ 21 Mg C ha⁻¹ more AGC than unharvested plots (Figure 4b).

Stag AGC decreased by ~ 10 Mg C ha⁻¹ with increasing fire frequency on unharvested plots, but remained low on harvested plots (~ 3 Mg C ha⁻¹), resulting in greater stag AGC (up to ~ 10 Mg C ha⁻¹) on unharvested plots than harvested plots when fires were not frequent (i.e. $0 - 3$ fires) (Figure 4c). Large CWD had a non-linear relationship with fire frequency on harvested

plots ($P = 0.001$), decreasing by $\sim 21 \text{ Mg C ha}^{-1}$ between zero and three fires, then increasing ($\sim 10 \text{ Mg C ha}^{-1}$) at higher fire frequency (≥ 5 fires; Figure 4d). Large CWD did not respond to fire frequency on unharvested plots ($P = 0.566$; Figure 4d). Large CWD AGC was $\sim 16 \text{ Mg C ha}^{-1}$ greater in the harvested, no fire treatment plots than in the unharvested, no fire treatment plots (Figure 4d). Despite evidence of a non-linear effect of fire frequency on small CWD in unharvested plots ($P = 0.074$), model estimates suggested that there was little effect of fire frequency or harvesting on this carbon pool (Figure 4e).

Total Carbon

The effect of fire frequency on total AGC varied as a function of harvesting (Figure 5). Total AGC decreased linearly with the number of fires on harvested plots ($P = 0.013$), with a $\sim 34 \text{ Mg C ha}^{-1}$ reduction in AGC from zero to seven fires (Figure 5a), which was driven by losses in the large tree and large CWD pools (Figure 4). Fire frequency had no effect on total AGC on unharvested plots ($P = 0.780$; Figure 5a), as gains in large tree AGC were offset by losses in the small tree and stag pools (Figure 4). There was a negative linear relationship between harvesting intensity and total AGC ($P = 0.005$), with a $\sim 69 \text{ Mg C ha}^{-1}$ reduction across the range of harvesting intensities experienced (Figure 5b). Total AGC on harvested plots was between 67% and 82% of that of unharvested plots with a comparable burning history, representing a $\sim 30 - 60 \text{ Mg C ha}^{-1}$ difference (Figure 5a).

At the coupe scale, experimental treatments had a significant effect on total AGC ($P < 0.001$), indicating that burning and harvesting treatments were leading to detectable changes in AGC stocks at the landscape scale, despite within coupe heterogeneity in both burn patchiness and harvesting intensity. Harvested coupes generally had lower AGC stocks than unharvested coupes (e.g. UR>HR, UF>HF). Harvested, frequently burned (HF) coupes stored less AGC than harvested, not burned coupes (HN) (Figure 5c). There was no effect of burning treatments within the unharvested coupes (Figure 5c).

Discussion

Our study provides a long-term experimental assessment of the interactive effects of timber harvesting and frequent prescribed burning on AGC in forest ecosystems. We found that both timber harvesting and frequent prescribed burning can reduce AGC stocks, though the effect of fire frequency was only evident on harvested plots and coupes, providing support for our

initial hypotheses. Such effects of harvesting and fire frequency on AGC stocks were robust to spatial heterogeneity of burning patterns induced by landscape heterogeneity and ignition patterns. Thus our hypothesis, concerning the moderation of the potential effect of these disturbance regimes on carbon stocks via landscape heterogeneity, was rejected. Our work highlights the need to consider the impacts of multiple concurrent forest management actions when managing carbon stocks, as has been demonstrated in other forest ecosystems globally (e.g. Berenguer et al. 2014, Hurteau et al. 2016). In particular, fire management prescriptions aimed at managing forest carbon will need to account for historic timber extraction and stand management practices.

Timber harvesting had the greatest impact on total AGC stocks, with AGC storage on harvested plots being between 67% and 82% of that of unharvested plots with a comparable burning history. These differences were largely driven by AGC losses due to timber extraction in the large tree (≥ 20 cm DBH) pool, which were only partially offset by regeneration in the small tree pool (< 20 cm DBH) and redistribution of material to the dead carbon pool. Depending on the amount of timber removal, centuries of post-harvest tree growth may be required for tree AGC to reach carbon carrying capacity i.e. the peak carbon storage under typical climatic conditions and disturbance regimes (Roxburgh et al. 2006). However, it is important to note that the carbon storage reductions reported here do not directly translate to emissions, as a considerable amount of material removed from the living tree pool is converted to timber products (Ximenes et al. 2008).

The decline in above-ground carbon on harvested plots in response to frequent burning was driven by the decline of the large CWD (≥ 10 cm diameter) and large live tree carbon pools, consistent with previous experiments conducted in historically harvested temperate eucalypt forest (Bennett et al. 2014, Collins et al. 2014b). Harvesting results in the pulse input of CWD in the form of harvesting residue (Grove 2001). Post-harvest burns and prescribed burns will remove harvesting residue, though material is unlikely to be completely consumed during a single burn due to inherent fire patchiness and incomplete consumption of CWD (Knapp et al. 2005, Holland et al. 2017). Consequently, large CWD carbon stocks will be elevated following harvesting, decreasing as the number of post-harvest prescribed burns increases, until a balance between the consumption and input of CWD occurs, which appeared to be after $\sim 3 - 4$ fires at the EBSA (Figure 4d).

Numerous manipulative burning experiments have found reduced tree biomass under regimes of frequent, low intensity fire in Australia (Bennett et al. 2013, Collins et al. 2014b) and globally (Peterson and Reich 2001, Ryan and Williams 2010). In our study, there was ~20% less carbon stored in the large tree pool on harvested plots burnt six times compared to those that experienced no fires during the experiment, which is similar to differences reported in another frequent burning experiment conducted in eucalypt forest that was historically managed for timber extraction (i.e. ~14% reduction; Bennett et al. 2014). Elevated mortality and collapse of large trees on frequently burnt plots was most likely driving the decline in AGC on harvested plots, as has been shown in other experiments (Bennett et al. 2013, Collins et al. 2014b). The sensitivity of resprouting trees to fire related damage, mortality and collapse can be elevated following harvesting and thinning, due to mechanical harvesting damage to retained trees and elevated dead fuel loads (McCaw et al. 1997, Gibbons et al. 2000). Furthermore, reducing stand basal area increases wind speed in forests and the likelihood of tree wind throw (Scott and Mitchell 2005), elevating the risk of collapse for retained trees with basal fire scarring (Gibbons et al. 2008). Although losses of large tree carbon were partially offset by increased recruitment on frequently burnt plots, sustained frequent burning may inhibit the transition of saplings to canopy trees (Guinto et al. 1999, Peterson and Reich 2001, Collins et al. 2014b), potentially leading to further losses of large tree AGC. Reductions in tree density due to fire related mortality will reduce competition, potentially resulting in increased growth (Guinto et al. 1999), though findings from long-term studies have frequently reported negative or no effects of frequent burning on growth rates for many eucalypt species (Abbott and Loneragan 1983, Guinto et al. 1999, Collins et al. 2014b).

Prescribed burning frequency had no effect on total AGC on historically unharvested plots, suggesting that total AGC in these forests is either resistant to frequent prescribed burning or has a lagged response. AGC stocks are strongly influenced by large live trees, which are the dominant biomass component of the live vegetation pool that directly feeds dead carbon pools (Hubbard et al. 2004, Roxburgh et al. 2006). Eucalypts capable of epicormic resprouting characteristically experience low rates of mortality during a low severity fire (Vivian et al. 2008, Collins et al. 2014b), with tree collapse being a common cause of mortality (Bowman and Kirkpatrick 1986). Burning may increase the likelihood of eucalypt collapse by creating basal fire-scars (McCaw et al. 1997, Collins et al. 2012a), though long time frames, including multiple fires, may be required following fire scar formation before

trees collapse. Consequently, we cannot discount future declines in large tree density and biomass due to frequent burning on unharvested plots.

Landscape scale effects of prescribed burning on forest carbon pools will be dependent upon the extent of burning within the treatment area (i.e. patchiness), as the loss of material in the live and dead carbon pools will increase with decreasing burn patchiness (e.g. Holland et al. 2017). Average burn extent recorded within the planned treatment areas in the EBSA was ~40% (Penman et al. 2007), which falls towards the lower end of the range typically recorded in temperate eucalypt forests (25% - 90%; Bennett et al. 2013, Holland et al. 2017, McCarthy et al. 2017). This suggests that the effect size of burning treatments on AGC reported in our study may be somewhat conservative, though we note that losses reported at the EBSA are generally consistent with experiments from other eucalypt forests (Bennett et al. 2014, Collins et al. 2014b).

Recent work has shown that soil carbon is sensitive to shifts in fire regimes (Bennett et al. 2014, Pellegrini et al. 2017, Sawyer et al. 2018), though assessment of this carbon pool was beyond the scope of our paper. Surface soil carbon (<20 - 30 cm depth) has been found to decline in response to long term frequent burning in many ecosystems (Pellegrini et al. 2017), including temperate eucalypt forests (Bennett et al. 2014). However, it is possible that the response of soil carbon to frequent burning will be influenced by timber harvesting, as the incomplete combustion of harvesting slash may create a source of long-lived pyrogenic carbon, that may bolster soil carbon stocks (Aponte et al. 2014, Jenkins et al. 2016). Our surveys also excluded live and dead AGC less than 2.5 cm in diameter and short stumps (< 1.3 m tall), though these components make only a relatively small contribution to the total AGC pool (Ximenes et al. 2008, Jenkins et al. 2016, Gordon et al. 2018), and are unlikely to have influenced our results.

Management implications

The contrasting response of AGC to frequent prescribed burning in harvested and unharvested areas suggests that consideration of historic land management will be important in determining the effects of prescribed burning regimes on carbon budgets. Although our burning treatments took place soon after harvesting, it is likely that the sensitivity of harvested forests to fire will persist for years to decades post-harvest, due to the time required for juvenile trees to reach fire resistant size classes and the persistence of factors that increase

the likelihood of large tree mortality (e.g. coarse fuels, mechanical damage during harvesting) (Thorpe et al. 2008, Collins et al. 2012b, Collins et al. 2014b). The majority of the current forested area in temperate regions of Australia, both under public and private ownership, have been subjected to timber harvesting over the past the 100 years (Raison and Squire 2008), a management history that is analogous to many North and South American forests (Armesto et al. 2010, McKinley et al. 2011). Regeneration of historically harvested forests that are now managed in the public reserve system represents a large potential future carbon sink (Roxburgh et al. 2006), and will contribute to the mitigation of global climate change (McKinley et al. 2011). However, our results suggest that the sequestration potential of regenerating forests dominated by trees that resprout following fire may be compromised under frequent prescribed burning regimes, and that these effects may not be obvious over short time frames (e.g. <10 years).

Recent socially destructive wildfires in temperate regions of southern Australia have resulted in policy aimed at increasing the use of broad-scale prescribed burning for the purpose of fuel reduction (Clode and Elgar 2014). Prescribed burning regimes aimed at reducing fuels for asset protection in temperate eucalypt forests (e.g. 5 – 10 year inter-fire interval) will potentially result in up to a 10 – 20 % reduction in total AGC in recently harvested areas, if applied for a few decades (Figure 5a). However, inherent burn patchiness across treatment areas (Penman et al. 2007, McCarthy et al. 2017) will lead to spatial variation in fire effects on carbon, which may be particularly evident in topographically heterogeneous landscapes. Carbon losses will tend to be localised and somewhat predictable, as upper slopes and ridgetops will burn more often than gullies (Penman et al. 2007), and repeated prescribed burning may be concentrated in key strategic areas (e.g. the interface between forests and urban areas). Targeted protection of trees with high carbon storage potential (e.g. >40 cm DBH) may be an effective approach to minimising carbon losses in small areas most at risk. For example, the mechanical removal of coarse and fine fuels around the base of large trees immediately prior to prescribed burns could help reduce rates of fire related large tree mortality and collapse (Bluff 2016).

Prescribed burning has been identified as a potential management strategy to increase carbon storage in forests globally, by reducing wildfire size and/or severity, and thus the amount of carbon emitted (Williams et al. 2012, Hurteau et al. 2016). Evidence from southern Australia suggests that crown fires may destabilise carbon stocks in resprouting eucalypt forests

(Bennett et al. 2017). While prescribed burning can reduce canopy fire occurrence in eucalypt forests, the window of effectiveness is typically short (i.e. up to 5 years after a prescribed burn, Price and Bradstock 2012, Collins et al. 2014a). Thus high frequency burning (e.g. < 5 year intervals) over large scales may be required to mitigate crown fire potential. Such a rate of treatment, however, has the potential to reduce AGC stocks, as shown in this study (in previously harvested areas), and others (Bennett et al. 2013, Collins et al. 2014b), even if burning is heterogeneous across landscapes. Similar conclusions have been reached for forests in the Western United States (Campbell et al. 2012). Understanding ecosystem scale effects of prescribed burning, and other fuel treatments (e.g. mechanical fuel reduction, timber harvesting), on carbon stocks may require the use of landscape models (e.g. Hurteau et al. 2016) that have been parameterised and validated using data derived from experiments such as ours.

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Data availability

Data available from Figshare: <https://doi.org/10.6084/m9.figshare.7138307>

775

776 Tables

777 **Table 1** Description of the decay scores measured for coarse woody debris (CWD). Scores
778 are taken from Roxburgh et al. (2006).

Variable	Class	Description
Decay	1.	CWD sound and intact
	2.	Decomposition of CWD confined to the outer layers and sapwood
	3.	Decomposition of CWD extend to the heartwood

779

780 Figures

781 **Figure 1** Location of the study area and arrangement of the experimental treatment blocks.

782 **Figure 2** (a) The mean ($\pm$ 95% CI) number of fires experienced in each experimental
783 treatment. The number of attempted prescribed burns is included in parentheses next to the
784 treatment code. Treatment codes are: unharvested and routine burning (UR); unharvested and
785 frequent burning (UF); harvested and routine burning (HR); harvested and frequent burning
786 (HF). (b) The cumulative burn extent at a plot (i.e. number of fire assessment quadrats
787 burnt/10) plotted against the number of times a plot experienced a fire.

788 **Figure 3** The effect of harvesting intensity (basal area of timber removed) on above-ground
789 carbon ($\pm$ 95% CI) of a) large trees ($\geq$ 20 cm DBH) and b) small trees ($<$ 20 cm DBH). Values
790 are predictions derived from GAMMs, whereby fire frequency has been held constant at 3
791 fires and pre-treatment AGC has been held constant at the mean value ($122.9 \text{ Mg C ha}^{-1}$).
792 The points are the observations used to fit the GAMM. One point ($x = 30.39 \text{ m}^2 \text{ ha}^{-1}$, $y =$
793 $95.98 \text{ Mg C ha}^{-1}$) in plot b) falls outside the plotting region.

794 **Figure 4** The effect of fire frequency on above-ground carbon ($\pm$ 95% CI) of a) large trees ($\geq$
795 20 cm DBH), b) small trees ($<$ 20 cm DBH), c) stags, d) large CWD ($\geq$ 10 cm diameter) and e)
796 small CWD ($<$ 10 cm diameter). Values are derived from GAMMs, whereby mean values of

harvesting intensity ($16.4 \text{ m}^2 \text{ ha}^{-1}$) and pre-treatment AGC ($122.9 \text{ Mg C ha}^{-1}$) have been used to make predictions. The points are the observations used to fit the GAMM.

Figure 5 Total above-ground carbon ($\pm 95\%$ CI) in response to a) fire frequency, b) harvesting intensity and c) coupe-scale experimental treatments. Values are derived from GAMMs. All predictions used mean values of pre-treatment AGC ($122.9 \text{ Mg C ha}^{-1}$). Mean values of harvesting intensity ($16.4 \text{ m}^2 \text{ ha}^{-1}$) were used for predictions in a). Fire frequency was held at 3 fires in b). The points in a) and b) are the observations used to fit the GAMM.

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