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Aboveground forest carbon shows different responses to fire frequency in harvested and unharvested forests

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2 **Received Date:**3 **Revised Date:**4 **Accepted Date:**5 **Article Type: Articles**6 **Above-ground forest carbon shows different responses to fire frequency in**  
7 **harvested and unharvested forests**8 Luke Collins<sup>1\*</sup>, Ross Bradstock<sup>1</sup>, Fabiano Ximenes<sup>2</sup>, Bronwyn Horsey<sup>1</sup>, Robert Sawyer<sup>1</sup>,  
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20 3086, Australia21 **Corresponding author:** Luke Collins, email: [lcollins241181@gmail.com](mailto:lcollins241181@gmail.com)22 **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 ( $\geq 10$  cm diameter) and large trees ( $\geq 20$  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

53 ecosystems are influential in determining global carbon budgets, accounting for  
54 approximately 45% of terrestrial carbon stores (Bonan 2008). Consequently, forest  
55 management aimed at increasing carbon sequestration can play an important role in reducing  
56 atmospheric CO<sub>2</sub> concentrations, and mitigating the effects of anthropogenic climate change  
57 (McKinley et al. 2011, IPCC 2014). Forest resource use and management can affect forest  
58 carbon stocks by altering rates of carbon emission and sequestration (North et al. 2009,  
59 Bowman et al. 2013, Berenguer et al. 2014). Fire management and timber harvesting are two  
60 key management practices affecting forest carbon balances globally (Bryan et al. 2010,  
61 Aponte et al. 2014, Hurteau et al. 2016).

62 Fire alters ecosystem carbon pools through the consumption of dead organic material and  
63 mortality of plant material (Williams et al. 2012), with the latter resulting in the redistribution  
64 of carbon from the live to dead pools (Bassett et al. 2015). In forests, most above-ground  
65 carbon (AGC) is stored in live trees (Hubbard et al. 2004, Bennett et al. 2014, Gordon et al.  
66 2018), consequently ecosystem carbon losses during a fire are generally relatively small  
67 (Volkova and Weston 2013, Keith et al. 2014). Redistribution of carbon from the live to dead  
68 pool will depend on fire response syndromes of plant species, with high redistribution  
69 occurring in forests dominated by obligate seeder and basal resprouter tree species (Keith et  
70 al. 2014, Fairman et al. 2017). AGC is less affected by a single fire event in forests  
71 dominated by tree species that resprout epicormically (e.g. Volkova and Weston 2013),  
72 except under extreme conditions that result in high rates of tree mortality (e.g. extreme fire  
73 intensity following drought; Bennett et al. 2016).

74 AGC in forests may be sensitive to shifts in fire frequency, due to effects on plant community  
75 demography and input/loss dynamics of dead woody debris (Aponte et al. 2014, Collins et al.  
76 2014b, Stares et al. 2018). Short inter-fire intervals can inhibit plant recruitment, increase  
77 mortality and reduce growth rates of trees, leading to reduced basal area and biomass (e.g.  
78 Peterson and Reich 2001, Collins et al. 2014b). Reductions in tree recruitment and standing  
79 biomass will have flow on effects to dead carbon pools, potentially reducing dead carbon  
80 biomass in the long term (Bassett et al. 2015). Reductions in dead carbon pools will occur if  
81 the rate of decay and consumption by fire exceeds input (Bassett et al. 2015). Experiments  
82 examining the response of forest biomass to long-term regimes of frequent experimental  
83 burning have generally reported reductions in the biomass of trees and woody debris in

84 response to frequent fire (e.g. Ryan and Williams 2010, Aponte et al. 2014, Collins et al.  
85 2014b).

86 Prescribed burning is widely applied across forest ecosystems to achieve a range of  
87 management objectives, including the reduction of wildfire risk to assets via fuel reduction  
88 and the manipulation of fire regimes for ecological purposes (Penman et al. 2011, Williams et  
89 al. 2012, Ryan et al. 2013). In Australian forests dominated by resprouting angiosperm trees  
90 (i.e. 'eucalypts'), prescribed burning is largely used for fuel reduction, with an objective of  
91 reducing wildfire risk at the wildland urban interface or within forests managed for economic  
92 timber assets (Penman et al. 2011). Effective fuel reduction typically requires the regular  
93 application of prescribed burning, which can increase overall fire frequency across treated  
94 landscapes (Penman et al. 2011). However, factors such as topographic heterogeneity,  
95 climate, fuels and ignition patterns will create unburnt patches within prescribed burns  
96 (Penman et al. 2007, McCarthy et al. 2017). Consequently, there will be spatial variability in  
97 the effect of a prescribed burning regime on forest ecosystems in response to environmental  
98 characteristics of the treated landscape (e.g. topography, vegetation) and weather conditions  
99 prior to and during burns. Although carbon sequestration has been identified as an objective  
100 of forest fire management (e.g. Victorian Department of Sustainability and Environment  
101 2012), burning prescriptions to achieve this are undefined or poorly understood.  
102 Consequently, it is unknown whether current burning prescriptions for asset protection will  
103 lead to desirable outcomes for carbon sequestration (e.g. Bradstock et al. 2012, Martin et al.  
104 2015).

105 Timber harvesting results in immediate changes to AGC within a forest, with losses in the  
106 live carbon pool that are directly proportional to harvesting intensity, and gains to the dead  
107 carbon pool in the form of harvesting residue or 'slash' (Ximenes et al. 2008). Post-harvest  
108 sequestration will occur with the regeneration of vegetation communities (Roxburgh et al.  
109 2006). Harvesting can increase the sensitivity of AGC stocks to fire by shifting tree size class  
110 distribution towards fire-sensitive juveniles (Collins et al. 2014b), converting live carbon to  
111 fallen dead debris that is susceptible to consumption (Knapp et al. 2005, Holland et al. 2017)  
112 and by causing mechanical damage to trees (Feldpausch et al. 2005, Thorpe et al. 2008)  
113 which increases the likelihood of fire related tree mortality and collapse (Whitford and  
114 Williams 2001, Gibbons et al. 2008). Despite the concurrent application of repeated

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

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

## 125 **Methods**

### 126 *Study area*

127 The study took place in the Eden Burning Study Area (EBSA) in Yambulla State Forest  
128 (37°14'S, 149°38'E) in south-eastern New South Wales, Australia (Figure 1). The EBSA  
129 covers approximately 1100 ha of dry sclerophyll forest (Penman et al. 2007). The forest  
130 community is predominantly Timbillica Dry Shrub Forest (Keith and Bedward 1999), an  
131 'open forest' community with tree heights between ~10 m and 30 m and canopy cover of  
132 30% - 70%. The tree canopy is comprised of a mix of eucalypt species (e.g. *E. agglomerata*,  
133 *E. globoidea*, *E. sieberi*, *E. consideriana*, *E. muelleriana*, *E. cypellocarpa*, *E. obliqua*) that  
134 resprout epicormically following wildfire, which is typical of eucalypts across dry sclerophyll  
135 forests of Australia (Gill and Catling 2002). The understorey is dominated by a diverse array  
136 of shrubs and ground cover, including *Allocasuarina littoralis*, *Banksia serrata*, *Daviesia*  
137 *buxifolia*, *Epacris impressa*, *Acacia terminalis*, *Acacia longifolia*, *Gonocarpus teucroides*,  
138 *Platysace lanceolata*, and *Lomandra filiformis* (Binns and Bridges 2003, Penman et al. 2008).  
139 Climate within the study region is temperate, with a maximum mean monthly temperature of  
140 24.9°C in January, a minimum mean monthly temperature of 4.1°C in July and average  
141 annual rainfall of 760 mm (Merimbula Airport AWS, [www.bom.gov.au](http://www.bom.gov.au), accessed 5<sup>th</sup> April  
142 2018).

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

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

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

### 162 *Experimental treatments*

163 The EBSA was established in 1985 by the Forestry Commission of New South Wales  
164 (currently the Forest Corporation of New South Wales) to examine the long-term ecological  
165 impacts of frequent burning and timber harvesting. The study area was divided into 18  
166 experimental blocks (8–56 ha, mean = 32 ha), which were timber harvesting coupes (Binns  
167 and Bridges 2003) (Figure 1). Three replicate coupes were randomly allocated to each of the  
168 6 treatments: unharvested and not burned (UN); unharvested and routinely burned (burning at  
169 4-year intervals, UR); unharvested and frequently burned (burning at 2-year intervals, UF);  
170 harvested and not burned (HN); harvested and routinely burned (burning at 4-year intervals  
171 commencing 10 years post harvesting, HR); and harvested and frequently burned (burning at  
172 2-year intervals, HF). Six permanent plots (108 plots in total) were randomly located and  
173 established in each experimental coupe to measure forest attributes including overstorey trees  
174 and coarse woody debris (CWD) (Binns and Bridges 2003).

175 Harvesting occurred in 1987 and 1988 and was an integrated operation, targeting both  
176 sawlogs and pulpwood. A proportion of mature trees were retained for habitat, seed trees,  
177 visual amenity and future sawlogs (Binns and Bridges 2003). Additionally, trees with an  
178 under-bark stump diameter <20 cm or with substantial defect or deformity were not felled  
179 because they did not meet product specifications (Binns and Bridges 2003). Harvesting  
180 removed ~60% of the original overstorey tree basal area (Binns and Bridges 2003). The  
181 intensity of harvesting varied considerably across the permanent monitoring plots, with the  
182 basal area of timber removed on plots ranging from 0 to 35.4 m<sup>2</sup> ha<sup>-1</sup> (mean = 15.38 m<sup>2</sup> ha<sup>-1</sup>).  
183 The mean (± S.E.) basal area of timber removed (m<sup>2</sup> ha<sup>-1</sup>) across the survey plots was 12.04 ±  
184 1.73, 18.06 ± 2.11 and 16.04 ± 1.68 in the harvesting no burning (HN), harvesting routine  
185 burning (HR) and harvesting frequent burning (HF) treatments respectively. Harvesting slash  
186 (i.e. felled tree crowns) was left onsite following harvesting (Bridges 2005). A post-harvest  
187 burn was conducted in coupes allocated to burning treatments (HR, HF) within 8 months  
188 following harvest, to reduce dead fuel biomass created by harvesting slash (Binns and  
189 Bridges 2003).

190 Prescribed fires were conducted in Autumn during periods when weather conditions were  
191 considered suitable. Ignition lines and points were implemented by ground crews with drip  
192 torches and the ignition patterns used varied depending on weather conditions and fuels  
193 (Penman et al. 2007). The most recent prescribed burns occurred in 2009, four years prior to  
194 our study, in all burning coupes. Four plots within the UN treatment were accidentally burnt at  
195 this time due to fires escaping containment lines. One plot (28, UF) was burnt by a small low  
196 intensity unplanned fire ignited by a lightning strike in November 1997 (Binns and Bridges  
197 2003). These accidental fires were incorporated into plot-scale measures of fire frequency.  
198 We did not exclude the fire affected plots that were assigned to the 'No fire' treatment (i.e.  
199 UN) when assessing the effect of the factorial coupe level treatments.

200 Ten 4 m<sup>2</sup> fire evaluation quadrats were established within each plot and surveyed three  
201 months before and after each prescribed burn to assess fuel conditions and burn extent (Binns  
202 and Bridges 2003). Cumulative burn coverage was calculated by summing the proportion of  
203 fire evaluation quadrats burnt in each prescribed fire over the entire study period. The number  
204 of fires experienced at a sample plot was calculated as the number of burns in which ≥ 20%  
205 of the fire evaluation quadrats were burnt. Assessment of fire frequency data showed there  
206 was considerable differences in the number of fires applied at the coupe scale and the number

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

### 209 *Assessment of carbon*

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

219 Living trees with a DBH  $\geq 10$  cm were recorded within 25.2 m radius plots (0.2 ha) between  
220 July 1985 to April 1989 prior to the application of experimental treatments. Species, DBH  
221 and any damage or deformities were recorded for each tree (Binns and Bridges 2003). In the  
222 2013 measurements, the DBH of all living and dead trees greater than 20 cm DBH were  
223 recorded across these 25.2 m radius plots. DBH of living and dead trees between 10 cm and  
224 20 cm DBH were recorded across 11.3 m radius plots (0.04 ha) nested within the larger plot.  
225 Species, DBH and height were recorded for each tree. Height of the tallest trees onsite was  
226 recorded using a laser range finder (Nikon Forestry Pro), to obtain the maximum canopy  
227 height, and estimated for the remaining trees, using the maximum canopy height as a  
228 reference. Tallies of trees between 2.5 cm and 10 cm DBH were recorded on the 11.3 m  
229 radius plots. The DBH of dead trees and stumps was only recorded if they were greater than  
230 1.3 m tall (i.e. breast height).

231 Above-ground live tree biomass was estimated using equations presented in Bi et al. (2004)  
232 to account for inter-species variation in allometry. If species specific equations were not  
233 available, analogous species in terms of growth form and wood properties were used (Stewart  
234 et al. 1979, Boland et al. 2006). Generic equations for native forest presented in Keith et al.  
235 (2000) were used for any other species ( $< 5\%$  of trees surveyed) (Appendix S1). The  
236 concentration of carbon in above-ground living tree biomass was taken to be 50% of  
237 estimated above-ground biomass (Gifford 2000). Adjustments to tree biomass estimates were

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

243 Standing dead tree (i.e. stag) biomass was calculated using the generic equation in Keith et al.  
244 (2000) (Appendix S1) as the species of stags and stumps could not be reliably identified.  
245 Biomass estimates were corrected for bark, leaf, twig and stem loss. Measured live tree bole  
246 heights recorded for a subset of trees in the pre-treatment measurements were used to  
247 calculate mean bole height for a range of DBH classes (10-20, 20-40, 40-60, 60-80, >80).  
248 Dead trees exceeding the mean bole height for their diameter class were assumed to only be  
249 missing bark, leaves and small twigs, which make up approximately 23% of tree biomass for  
250 common species in the study region (Stewart et al. 1979). Therefore, a correction multiplier  
251 of 0.77 was applied to biomass estimates of these trees. If dead tree height was less than the  
252 mean bole height for their diameter class, biomass was first multiplied by 0.6 (i.e. the  
253 proportion of tree that is the bole) (Stewart et al. 1979, Ximenes et al. 2008) and then  
254 multiplied by the dead tree height to mean bole height ratio (i.e. the estimated proportion of  
255 the bole that remains). A decay function of 0.85 was used to convert predicted biomass to an  
256 estimate of dead biomass (Bennett et al. 2013). Carbon content was taken as 50% of dead tree  
257 biomass (Woldendorp et al. 2002).

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

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

$$271 \quad V = \pi^2 / (8 \times L) \times \sum(D)^2 \quad (1)$$

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

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

## 281 *Analysis*

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

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

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

305 Models for the harvested dataset included fire frequency, harvesting intensity and pre-  
306 treatment AGC as additive effects. Models for the unharvested dataset included fire  
307 frequency and pre-treatment AGC. Pre-treatment AGC was included as a covariate in the  
308 models to account for the effects of spatial variability in carbon storage due to landscape  
309 factors (e.g. topography, soil characteristics). Pre-treatment large CWD and small CWD and  
310 total AGC were used as predictors for their respective post-treatment measures. Total pre-  
311 treatment tree AGC ( $\geq 10$  cm DBH) was used as a predictor for large trees, small trees and  
312 stags. We do not present results on the effects of pre-treatment AGC in the manuscript as this  
313 was not a primary objective of the study, though a predicted relationship between AGC and  
314 predictor variables is provided in Appendix S2. Predictor variables with  $P \leq 0.05$  were  
315 considered statistically significant, though  $P$ -values between 0.1 and 0.01 have been  
316 interpreted with caution due to uncertainty associated with deriving  $P$  – values from mixed  
317 effect models (Zuur et al. 2009). Due to the confounded nature of fire frequency and time  
318 since fire, models containing effects of fire frequency that were significant or close to  
319 significance ( $P < 0.1$ ) were refitted to a subset of the dataset containing plots that had burnt 4  
320 – 8 years prior to sampling. In all cases the effect of fire frequency was found to be consistent  
321 across the two analyses (Appendix S3).

322 Data analysis was conducted using the statistical package R v3.2 (R Development Core Team  
323 2016). The ‘gamm4’ package was used to fit GAMMs (Wood and Scheipl 2016).

## 324 **Results**

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

327 77% of total AGC, with large live trees ( $\geq 20$  cm DBH) storing  $107.7 \pm 4.2$  Mg C ha<sup>-1</sup> and  
328 small trees ( $< 20$  cm DBH) storing  $16.8 \pm 1.5$  Mg C ha<sup>-1</sup>. Large CWD ( $\geq 10$  cm diameter) was  
329 the primary component of the dead carbon pool ( $26.0 \pm 1.9$  Mg C ha<sup>-1</sup>), followed by stags  
330 ( $6.5 \pm 0.8$  Mg C ha<sup>-1</sup>) and small CWD ( $< 10$  cm diameter) ( $3.6 \pm 0.2$  Mg C ha<sup>-1</sup>).

### 331 *Individual Carbon Pools*

332 Harvesting intensity was found to have opposing effects on the large and small tree AGC  
333 pools (Figure 3). Large tree AGC decreased linearly as the basal area of timber removed  
334 increased ( $P < 0.001$ ), with AGC being reduced by  $\sim 103$  Mg C ha<sup>-1</sup> over the range of  
335 harvesting intensities experienced across the sample plots ( $0$  m<sup>2</sup> ha<sup>-1</sup> to  $35.4$  m<sup>2</sup> ha<sup>-1</sup>; Figure  
336 3a). These losses were partially offset by a linear increase ( $\sim 26$  Mg C ha<sup>-1</sup>) in small tree AGC  
337 with increasing timber harvesting ( $P = 0.013$ ; Figure 3b). The dead carbon pools did not  
338 show a significant ( $P > 0.1$ ) response to harvesting intensity, though there were differences in  
339 stag and large CWD AGC between harvested and unharvested plots that experienced no fire  
340 or low fire frequency, which are described below.

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

351 Differences in small tree AGC between unharvested and harvested plots were only evident if  
352 there had been three or more fires, with harvested plots experiencing average harvesting  
353 intensity having up to  $\sim 21$  Mg C ha<sup>-1</sup> more AGC than unharvested plots (Figure 4b).

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

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

### 365 **Total Carbon**

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

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

### 383 **Discussion**

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

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

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

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

419 Numerous manipulative burning experiments have found reduced tree biomass under regimes  
420 of frequent, low intensity fire in Australia (Bennett et al. 2013, Collins et al. 2014b) and  
421 globally (Peterson and Reich 2001, Ryan and Williams 2010). In our study, there was ~20%  
422 less carbon stored in the large tree pool on harvested plots burnt six times compared to those  
423 that experienced no fires during the experiment, which is similar to differences reported in  
424 another frequent burning experiment conducted in eucalypt forest that was historically  
425 managed for timber extraction (i.e. ~14% reduction; Bennett et al. 2014). Elevated mortality  
426 and collapse of large trees on frequently burnt plots was most likely driving the decline in  
427 AGC on harvested plots, as has been shown in other experiments (Bennett et al. 2013, Collins  
428 et al. 2014b). The sensitivity of resprouting trees to fire related damage, mortality and  
429 collapse can be elevated following harvesting and thinning, due to mechanical harvesting  
430 damage to retained trees and elevated dead fuel loads (McCaw et al. 1997, Gibbons et al.  
431 2000). Furthermore, reducing stand basal area increases wind speed in forests and the  
432 likelihood of tree wind throw (Scott and Mitchell 2005), elevating the risk of collapse for  
433 retained trees with basal fire scarring (Gibbons et al. 2008). Although losses of large tree  
434 carbon were partially offset by increased recruitment on frequently burnt plots, sustained  
435 frequent burning may inhibit the transition of saplings to canopy trees (Guinto et al. 1999,  
436 Peterson and Reich 2001, Collins et al. 2014b), potentially leading to further losses of large  
437 tree AGC. Reductions in tree density due to fire related mortality will reduce competition,  
438 potentially resulting in increased growth (Guinto et al. 1999), though findings from long-term  
439 studies have frequently reported negative or no effects of frequent burning on growth rates  
440 for many eucalypt species (Abbott and Loneragan 1983, Guinto et al. 1999, Collins et al.  
441 2014b).

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

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

454 Landscape scale effects of prescribed burning on forest carbon pools will be dependent upon  
455 the extent of burning within the treatment area (i.e. patchiness), as the loss of material in the  
456 live and dead carbon pools will increase with decreasing burn patchiness (e.g. Holland et al.  
457 2017). Average burn extent recorded within the planned treatment areas in the EBSA was  
458 ~40% (Penman et al. 2007), which falls towards the lower end of the range typically recorded  
459 in temperate eucalypt forests (25% - 90%; Bennett et al. 2013, Holland et al. 2017, McCarthy  
460 et al. 2017). This suggests that the effect size of burning treatments on AGC reported in our  
461 study may be somewhat conservative, though we note that losses reported at the EBSA are  
462 generally consistent with experiments from other eucalypt forests (Bennett et al. 2014,  
463 Collins et al. 2014b).

464 Recent work has shown that soil carbon is sensitive to shifts in fire regimes (Bennett et al.  
465 2014, Pellegrini et al. 2017, Sawyer et al. 2018), though assessment of this carbon pool was  
466 beyond the scope of our paper. Surface soil carbon (<20 - 30 cm depth) has been found to  
467 decline in response to long term frequent burning in many ecosystems (Pellegrini et al. 2017),  
468 including temperate eucalypt forests (Bennett et al. 2014). However, it is possible that the  
469 response of soil carbon to frequent burning will be influenced by timber harvesting, as the  
470 incomplete combustion of harvesting slash may create a source of long-lived pyrogenic  
471 carbon, that may bolster soil carbon stocks (Aponte et al. 2014, Jenkins et al. 2016). Our  
472 surveys also excluded live and dead AGC less than 2.5 cm in diameter and short stumps (<  
473 1.3 m tall), though these components make only a relatively small contribution to the total  
474 AGC pool (Ximenes et al. 2008, Jenkins et al. 2016, Gordon et al. 2018), and are unlikely to  
475 have influenced our results.

#### 476 ***Management implications***

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

483 the likelihood of large tree mortality (e.g. coarse fuels, mechanical damage during harvesting)  
484 (Thorpe et al. 2008, Collins et al. 2012b, Collins et al. 2014b). The majority of the current  
485 forested area in temperate regions of Australia, both under public and private ownership,  
486 have been subjected to timber harvesting over the past the 100 years (Raison and Squire  
487 2008), a management history that is analogous to many North and South American forests  
488 (Armesto et al. 2010, McKinley et al. 2011). Regeneration of historically harvested forests  
489 that are now managed in the public reserve system represents a large potential future carbon  
490 sink (Roxburgh et al. 2006), and will contribute to the mitigation of global climate change  
491 (McKinley et al. 2011). However, our results suggest that the sequestration potential of  
492 regenerating forests dominated by trees that resprout following fire may be compromised  
493 under frequent prescribed burning regimes, and that these effects may not be obvious over  
494 short time frames (e.g. <10 years).

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

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

515 (Bennett et al. 2017). While prescribed burning can reduce canopy fire occurrence in eucalypt  
516 forests, the window of effectiveness is typically short (i.e. up to 5 years after a prescribed  
517 burn, Price and Bradstock 2012, Collins et al. 2014a). Thus high frequency burning (e.g. < 5  
518 year intervals) over large scales may be required to mitigate crown fire potential. Such a rate  
519 of treatment, however, has the potential to reduce AGC stocks, as shown in this study (in  
520 previously harvested areas), and others (Bennett et al. 2013, Collins et al. 2014b), even if  
521 burning is heterogeneous across landscapes. Similar conclusions have been reached for  
522 forests in the Western United States (Campbell et al. 2012). Understanding ecosystem scale  
523 effects of prescribed burning, and other fuel treatments (e.g. mechanical fuel reduction,  
524 timber harvesting), on carbon stocks may require the use of landscape models (e.g. Hurteau et  
525 al. 2016) that have been parameterised and validated using data derived from experiments  
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772

### 773 **Data availability**

774 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.

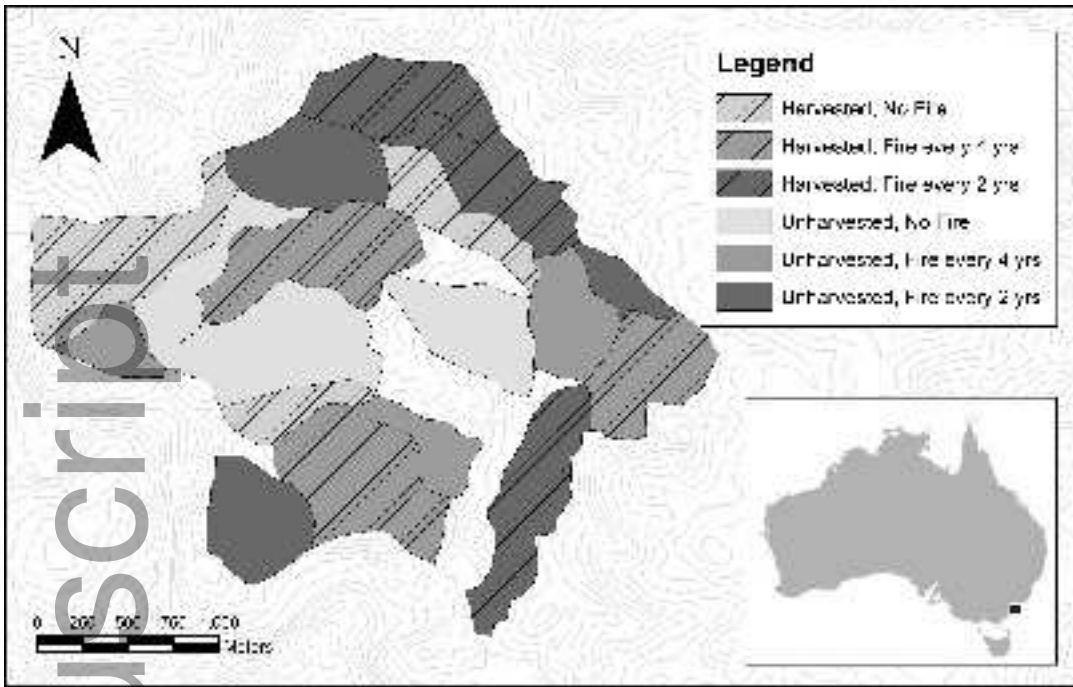
788 **Figure 3** The effect of harvesting intensity (basal area of timber removed) on above-ground  
789 carbon ( $\pm$ 95% CI) of a) large trees ( $\geq$  20 cm DBH) and b) small trees ( $<$ 20 cm DBH). Values  
790 are predictions derived from GAMMs, whereby fire frequency has been held constant at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

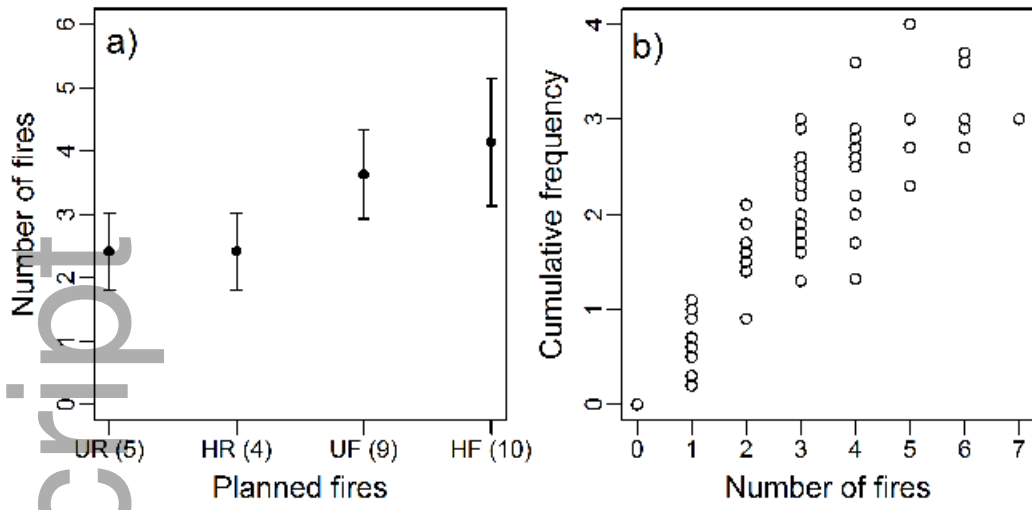
797 harvesting intensity ( $16.4 \text{ m}^2 \text{ ha}^{-1}$ ) and pre-treatment AGC ( $122.9 \text{ Mg C ha}^{-1}$ ) have been used  
798 to make predictions. The points are the observations used to fit the GAMM.

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

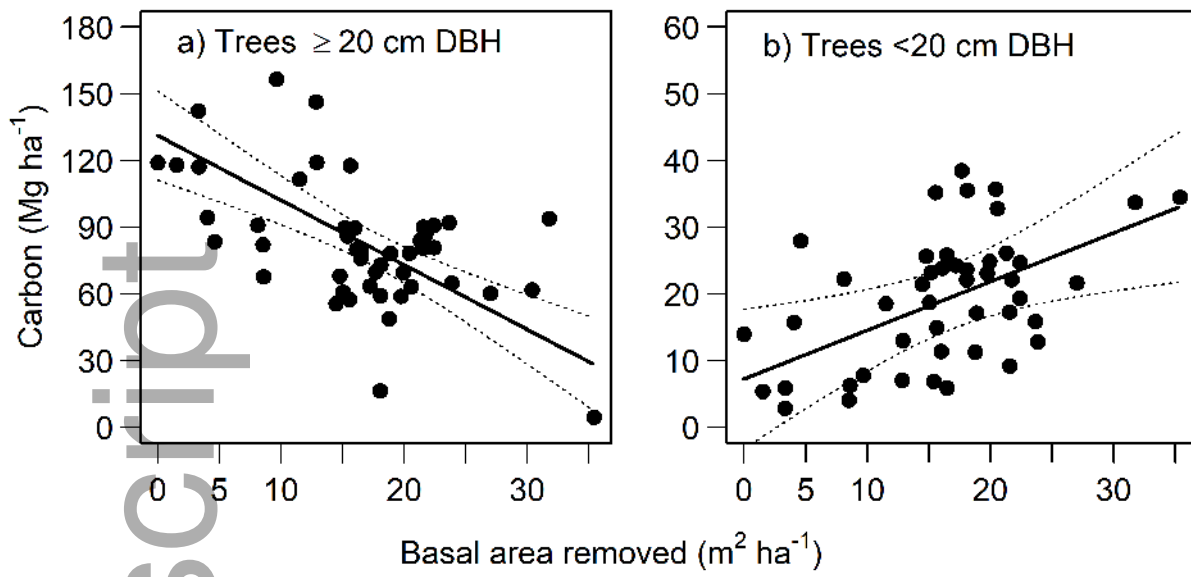
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