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### Timber harvest and frequent prescribed burning interact to affect the demography of Eucalypt species

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# Timber harvest and frequent prescribed burning interact to affect the demography of Eucalypt species

## Abstract

Ecosystem management can negatively affect the demography of plant communities through the introduction of novel disturbance regimes. Prescribed burning and timber harvesting are two common and widely applied management strategies across forest ecosystems. Despite this, little is known about the long-term effects that these interacting disturbances have on forest demography. This study examined the effect of timber harvesting and frequent prescribed burning on the mortality, growth and regeneration of trees in a temperate eucalypt forest of south-eastern Australia. The study took place at a long-term experimental site, where experimental coupes were subjected to a one-off selective harvesting treatment (harvested, not harvested), followed by regimes of experimental burning (no fire, ~4 year burn intervals or ~2 year burn intervals) over a 22 year period. Tree communities were surveyed at permanent monitoring sites prior to the application of experimental treatments (1985 – 1989), and resurveyed post treatment (2016) to assess mortality, growth rates and ingrowth of trees >10 cm diameter at breast height. Harvesting directly removed ~40% of trees and indirectly increased the mortality of retained trees through damage (e.g. crown and bole breakage) caused during the harvesting operation. The likelihood of harvesting damage was greater for small trees and increased with harvesting intensity (i.e. the amount of timber removed). Frequent burning increased the likelihood of tree mortality on harvested sites, with large, old trees being particularly vulnerable. Growth rate and ingrowth of trees was elevated at harvested sites, increasing almost linearly with harvesting intensity, which suggests that competitive release had occurred. Fire frequency had no effect on growth rates or ingrowth of trees. This study highlights that frequent prescribed burning and selective timber harvesting can have additive effects on the loss of large trees, reducing the availability of these keystone habitat structures in intensively managed forest ecosystems. Although the elevated rates of growth and ingrowth may hasten the replacement of lost large trees, recovery will require long time frames.

## Keywords

eucalypt, timber, demography, species, affect, interact, burning, prescribed, frequent, harvest

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1 **Timber harvest and frequent prescribed burning interact to affect the demography of**  
2 **Eucalypt species**

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15 **Running head:** Logging and fire affect tree demography

16

17

18 **ABSTRACT**

19 Ecosystem management can negatively affect the demography of plant communities through  
20 the introduction of novel disturbance regimes. Prescribed burning and timber harvesting are  
21 two common and widely applied management strategies across forest ecosystems. Despite  
22 this, little is known about the long-term effects that these interacting disturbances have on  
23 forest demography. This study examined the effect of timber harvesting and frequent  
24 prescribed burning on the mortality, growth and regeneration of trees in a temperate eucalypt  
25 forest of south-eastern Australia. The study took place at a long-term experimental site,  
26 where experimental coupes were subjected to a one-off selective harvesting treatment  
27 (harvested, not harvested), followed by regimes of experimental burning (no fire, ~4 year  
28 burn intervals or ~2 year burn intervals) over a 22 year period. Tree communities were  
29 surveyed at permanent monitoring sites prior to the application of experimental treatments  
30 (1985 – 1989), and resurveyed post treatment (2016) to assess mortality, growth rates and  
31 ingrowth of trees greater than 10 cm diameter at breast height. Harvesting directly removed  
32 ~40% of trees and indirectly increased the mortality of retained trees through damage (e.g.  
33 crown and bole breakage) caused during the harvesting operation. The likelihood of  
34 harvesting damage was greater for small trees and increased with harvesting intensity (i.e. the  
35 amount of timber removed). Frequent burning increased the likelihood of tree mortality on  
36 harvested sites, with large, old trees being particularly vulnerable. Growth rate and ingrowth  
37 of trees was elevated at harvested sites, increasing almost linearly with harvesting intensity,  
38 which suggests that competitive release had occurred. Fire frequency had no effect on growth  
39 rates or ingrowth of trees. This study highlights that frequent prescribed burning and selective  
40 timber harvesting can have additive effects on the loss of large trees, reducing the availability  
41 of these keystone habitat structures in intensively managed forest ecosystems. Although the

42 elevated rates of growth and ingrowth may hasten the replacement of lost large trees,  
43 recovery will require long time frames.

44 **Keywords:** Eucalypt forest, fire frequency, fuel reduction burning, logging, recruitment, tree  
45 growth rate, tree mortality

46 **1 INTRODUCTION**

47 Forest ecosystems provide many important services, as they sustain a large portion of global  
48 biodiversity and contribute to biogeochemical cycles, water quality control, timber stocks and  
49 carbon sequestration (Bonan 2008, Pan et al. 2011, Crowther et al. 2015). The age and size  
50 class structure of tree communities is a key determinant of the ecosystem services that a  
51 forest provides (Nolan et al. 2015, Schall et al. 2018, Gordon et al. 2018). Natural disturbance  
52 is an intrinsic component of forest ecosystems and is important for regulating plant  
53 demography (Dale et al. 2001, Lindenmayer and McCarthy 2002). Management of forest  
54 ecosystems can introduce novel disturbances or shift disturbance regimes beyond the  
55 envelope of what is naturally experienced. Prescribed burning and timber extraction are two  
56 recurrent and widely applied management actions across forests globally (Alencar et al. 2004,  
57 Penman et al. 2011, Crowther et al. 2015, Hurteau et al. 2016). However, despite their global  
58 application, little is known about the interactive effects of prescribed burning and harvesting  
59 on plant population dynamics over long timeframes.

60 Prescribed burning is used for fuel hazard reduction in forests to reduce the threat of  
61 future wildfires to life, property and timber assets (Fernandes and Botelho 2003, Penman et  
62 al. 2011), and as a management tool for ecological purposes (Bowman et al. 2009, Hurteau et  
63 al. 2016). Prescriptions aimed at achieving effective fuel hazard reduction typically try to  
64 maintain fuels in young age classes, requiring the application of burning at short intervals  
65 (Penman et al. 2011). Reductions in inter-fire intervals associated with regular application of  
66 prescribed burning can alter plant demography by inhibiting post-fire recruitment (Peterson  
67 and Reich 2001, Ooi 2012), altering growth rates of fire resistant individuals (Murphy et al.  
68 2010) and increasing rates of adult mortality (Peterson and Reich 2001), resulting in changes  
69 to population structure and plant community composition (Morrison et al. 1995, He et al.

70 2019). Impacts of low intensity fire are typically more pronounced for understory species  
71 than tree species (Penman et al. 2008, Bennett et al. 2013, Collins et al. 2014).

72         The sensitivity of tree populations to regimes of frequent burning will be dependent  
73 on the combination of fire resilience and resistance traits a species possesses (Bellingham and  
74 Sparrow 2000, Clarke et al. 2013). Resilience traits facilitate population recovery following  
75 fire, and include fire stimulated seed release and germination, and vegetative recovery via  
76 resprouting (Lawes et al. 2016). Species capable of resprouting post fire (i.e. ‘resprouters’)  
77 are considered to be more tolerant to the shortening of inter-fire intervals than species that  
78 experience high rates of adult mortality and regenerate exclusively via post-fire seed  
79 germination (i.e. ‘obligate seeders’) (Bellingham and Sparrow 2000, Enright et al. 2014,  
80 Pausas et al. 2016, Pausas and Keeley 2017). Resistance traits are those attributes which  
81 protect tissues and buds from lethal temperatures during fire, such as thick bark or a tall  
82 crown (Lawes et al. 2016). The development of resistance traits are critical in determining  
83 resprouting success (Lawes et al. 2011, Catry et al. 2013, Charles-Dominique et al. 2015,  
84 Collins et al. 2019), and can facilitate the survival of seeder and resprouter trees during low  
85 intensity fire events (e.g. *Pinus ponderosa*; Hurteau et al. 2016).

86         Regular prescribed burning is generally targeted towards forest communities  
87 comprised of tree species that display strong fire resistance in their mature form (e.g. dry  
88 sclerophyll eucalypt forests, *Pinus ponderosa* forest; Bowman et al. 2013). The effect of  
89 frequent burning on tree mortality in these communities will vary across size and age classes  
90 (Gibbons et al. 2000, 2008, Whitford and Williams 2001). Frequent fire can lead to changes  
91 in demography, through increased seedling and sapling mortality, as there is insufficient time  
92 to develop resistance traits to survive subsequent burns (Guinto et al. 1999, Peterson and  
93 Reich 2001, Lawes et al. 2011, Bennett et al. 2013, Collins et al. 2014). Conversely, mature

94 or senescing trees may experience high rates of mortality owing to the loss of resistance or  
95 resilience with age, or through damage sustained during past fires (i.e. basal scaring) or other  
96 disturbances (e.g. timber extraction) (Gibbons et al. 2000, Clarke et al. 2013, Bennett et al.  
97 2013, Silvério et al. 2019, Collins 2020). Frequent prescribed burning can also affect growth  
98 rates, with positive, negative and no effect being reported across the literature (Murphy et al.  
99 2010, Bennett et al. 2013, Collins et al. 2014).

100           Timber harvesting modifies the age class distribution of tree communities via the  
101 removal of mature trees and subsequent ingrowth of seedlings, though effects will vary  
102 depending on the silvicultural system implemented (Sebbenn et al. 2008). For example, clear  
103 felling simplifies stand age distribution, often creating a single cohort of homogenously-aged  
104 regrowth, whilst selective harvesting promotes a multi-aged population through the retention  
105 of a proportion of the original stand for seed, habitat and future timber (Lindenmayer and  
106 McCarthy 2002). Selective harvesting operations will typically target trees that are free of  
107 defects and exceed a minimum size determined by product specifications (Kotwal et al. 2008,  
108 Binns and Bridges 2003). The retention of small sized trees and senescent, deformed or  
109 damaged large trees during selective timber harvesting may give rise to populations that have  
110 impaired resistance and resilience to regimes of frequent prescribed burning (Gibbons et al.  
111 2000, Whitford and Williams 2001). Retained trees that sustain damage during timber  
112 extraction operations, as well as coppice stems regenerating from the stumps of felled trees,  
113 may also be susceptible to fire related mortality and collapse (Gibbons et al. 2000). However,  
114 elevated growth rates due to competitive release created by timber removal or fire related  
115 mortality could potentially reduce the time required for seedlings and saplings to reach fire-  
116 tolerant size classes (Bailey and Tappeiner 1998, Yamada et al. 2013). Therefore, selective  
117 timber harvesting and frequent prescribed burning may have both synergistic and antagonistic  
118 effects on tree populations.



119 In this study we examined the interactive effects of selective timber harvesting and  
120 regimes of prescribed burning on three elements of tree demography: mortality, growth and  
121 regeneration (i.e. coppicing and ingrowth). Our study utilised a long term (1986 – 2016)  
122 landscape scale manipulative experiment, the Eden Burning Study Area (EBSA) (Binns and  
123 Bridges 2003), to examine the effects of one-off timber harvesting and ~25 years of  
124 prescribed burning regimes. The study took place in a temperate forest dominated by tree  
125 species from the genera *Angophora*, *Corymbia* and *Eucalyptus*, collectively referred to as  
126 ‘eucalypts’, which display strong resistance to low intensity fire upon maturity (Denham et  
127 al. 2016, Collins 2020). We predicted that prescribed burning and timber harvesting would  
128 have: (i) synergistic effects on eucalypt tree mortality and regeneration, with the combination  
129 of frequent burning and harvesting resulting in highest rates of mortality and ingrowth; and  
130 (ii) opposing effects on tree growth, with harvesting and fire frequency having positive and  
131 negative effects, respectively.

## 132 **2 METHODS**

### 133 *Study Area*

134 The Eden Burning Study Area (EBSA) is located within Yambulla State Forest, 29  
135 km south west of Eden in south eastern Australia (37°21’S, 149°64’E) (Figure 1). The  
136 Yambulla State Forest is situated within the Yuin Nation. The EBSA extends across 1080 ha  
137 of eucalypt forest, with the dominant community classified as Timbillica Dry Shrub forest  
138 (Keith and Bedward 1999, Binns and Bridges 2003). The overstorey is comprised of a mix of  
139 eucalypt species, including *Eucalyptus agglomerata*, *E. consideriana*, *E. cypellocarpa*, *E.*  
140 *globoidea*, *E. muelleriana*, *E. radiata* and *E. sieberi*. Non-eucalypt tree species (e.g.  
141 *Allocasuarina littoralis*, *Banksia serrata*) are present in the sub-canopy, though they  
142 infrequently form a dominant layer. The study area falls within a temperate climatic zone,

143 with a mean monthly maximum temperature of 24.6 °C in summer (February) and a  
144 minimum of 4.4 °C in winter (July). Rainfall in the region is not seasonal, with an average  
145 mean annual rainfall of 829.3 mm (Station 069147, Bureau of Meteorology 2016,  
146 [www.bom.gov.au](http://www.bom.gov.au), accessed 19<sup>th</sup> December 2016). The sites are situated upon granitoid  
147 Devonian Wallagaraugh Ademellite parent material and have broadly homogenous geology  
148 and climate (Binns and Bridges 2003).

149 [Figure 1]

150 The temperate forests of southern Australia characteristically experience large mixed  
151 severity wildfires (Bradstock 2008, Collins et al. 2018), which are associated with periods of  
152 drought (Bradstock 2010, Murphy et al. 2013). Prescribed burning is a widely used  
153 management tool for fuel hazard reduction and wildfire management in these forests, with  
154 contemporary prescriptions aiming to maintain fuels in a young seral stage (e.g. < 10 years  
155 since fire; Penman et al. 2011). The combination of wildfire and prescribed burning results in  
156 typical fire return intervals of ~5 – 20 years across these dry eucalypt forests, with extremes  
157 of >100 years (Murphy et al. 2013).

158 The study area was largely inaccessible to vehicles prior to the establishment of the  
159 EBSA, hence there was little historic evidence of timber harvesting before the experiment  
160 commenced. Records indicate that a small portion (~15%) of the study area was treated by  
161 fuel reduction burning between 1979 and 1981 (Binns and Bridges 2003). Indigenous people  
162 inhabiting south eastern Australia implemented burning for cultural and management  
163 purposes (Bowman 2008, McKemey et al. 2019) though written accounts of these practices  
164 for the study area are lacking. The study area was burnt at low intensity by a large wildfire in  
165 January 1973, approximately 12 years prior to the establishment of the EBSA (Binns and  
166 Bridges 2003).

167 *Experimental Design*

168           The EBSA was established to examine the interactive effect of prescribed burning and  
169 timber harvest on forest ecosystems. There were three prescribed burning treatments  
170 implemented in the study: no fire, fire at two-year intervals ('frequent' burning) and fire at  
171 four-year intervals (i.e. 'routine' burning). Two harvesting treatments were examined,  
172 including no harvesting and a single harvesting event prior to the implementation of burning  
173 regimes. Treatments were applied in a balanced factorial design, resulting in six combinations  
174 of burning and harvesting. Three replicate operational coupes were randomly assigned to  
175 each of the six treatment combinations, resulting in 18 experimental coupes that were  
176 between 8 ha and 56 ha in size. Six sites were randomly assigned within each coupe to  
177 monitor overstory tree response to prescribed burning and harvesting treatments, resulting in  
178 108 permanent long-term monitoring sites (Binns and Bridges 2003). We surveyed two thirds  
179 of the sites in each coupe ( $n = 72$ ), targeting those sites that were located on mid- to upper-  
180 slopes, in order to control for topographic position. For those sites within the experimental  
181 treatments assigned to routine or frequent burning, we selected sites that had been most  
182 recently burnt, between 2005 – 2009, to minimise the confounding effect of time since fire on  
183 fire frequency.

184           Timber harvesting treatments took place between November 1987 and April 1988, in  
185 accordance with plans prepared by Forestry NSW, Eden District (formerly State Forests of  
186 New South Wales) (Binns and Bridges 2003). Harvesting was an integrated operation,  
187 targeting both sawlogs and pulpwood. Approximately 60% of the basal area of mature trees  
188 (>20 cm diameter) was harvested, resulting in  $\sim 90 \text{ t ha}^{-1}$  of timber removal (Binns and  
189 Bridges 2003). Trees with extensive deformities or decay were retained as they did not meet  
190 product specifications (Bridges 2009). A post-harvest burn was implemented in June 1988

191 (Austral Winter) to remove fine and coarse fuels created by harvest debris. The post-harvest  
192 burn affected ~50% of trees on the 36 monitoring sites treated, with crown scorch reported on  
193 just 16% of surveyed trees. Few trees experienced cambium damage (~1%) or fell (~1%) as a  
194 results of the post-harvest burn (Bridges 2009).

195 Prescribed burns were applied during Autumn (March – May) of the programmed  
196 years, when prevailing weather conditions permitted, in accordance with the operational  
197 standards at the time of the experiment (Penman et al. 2007). Burning treatments commenced  
198 in 1990 across the coupes assigned to the frequent burning (HF, UF) and unharvested routine  
199 burning treatments (UR). Burning in the coupes assigned to the harvested routine burning  
200 treatment (HR) did not commence until 13 years after the post-harvest burn (2001), to allow  
201 for post-harvest regeneration, as was practice at the time (Bridges 2009). Burning treatments  
202 were not conducted in 1998 and 2000 due to unfavourably wet conditions, a situation  
203 contextually reflective of any long-term prescribed burning regime (Guinto et al. 1999).  
204 Burning recommenced in 2001 and continued as planned until the most recent round of  
205 prescribed burns in 2009. Four sites within the unharvested unburnt treatment (UN) were  
206 accidentally burnt in 2009 when experimental burns broke containment lines (three of these  
207 sites were included in our study). One site was burnt by a small low intensity fire ignited by  
208 lightning in November 2007 (Binns and Bridges 2003). These unplanned fires were  
209 incorporated into subsequent fire frequency calculations.

210 Low intensity prescribed burns show considerable variation in spatial patchiness  
211 (McCarthy et al. 2017), hence not all sites in a coupe burnt during each round of planned  
212 burning (Penman et al. 2007). The occurrence of fire was assessed on each site within 8  
213 weeks of burning, using ten 4 m<sup>2</sup> circular quadrats located within a 25 m radius of the site  
214 centre (Penman et al. 2007). A site was considered burnt during the prescribed burn if  $\geq 2$  fire

215 assessment quadrats were affected by fire. Fire frequency was calculated as the number of  
216 times a site was burnt, including both planned and unplanned fire, across the duration of the  
217 study. The number of fires experienced at a site ranged from 0 to 7 fires, with the realised fire  
218 frequency being ~40% - 60% of the intended frequency on average across the experimental  
219 treatments (Collins et al. 2019).

## 220 *Eucalypt Surveys*

221 Overstory vegetation monitoring sites of 25 m radius (0.2 ha) were established in 1985  
222 prior to harvesting and burning. Trees that had a diameter at breast height over bark (DBH)  $\geq$   
223 10 cm were surveyed between 1985 – 1989 and the DBH, species, distance and bearing from  
224 the site centre were recorded for each tree (Binns and Bridges 2003). A second round of surveys  
225 was undertaken on the harvested sites shortly after harvesting, but before the commencement  
226 of burning treatments, to determine whether a tree had been felled and to assess damage to the  
227 stem cambium or crown of retained trees caused by harvesting. Harvesting damage was  
228 initially scored on a scale of 1 – 8 to reflect different degrees of damage (Binns and Bridges  
229 2003), though insufficient observations across most of the damage classes necessitated the  
230 categorisation of trees into classes of damaged or not damaged for statistical analysis. In 2016,  
231 all trees originally surveyed were relocated and their DBH and state (i.e. alive or dead) was  
232 recorded. Trees were considered dead if there was no evidence of photosynthetically active  
233 foliage or regrowth/resprouting on the stem or extending from the tree base. The stumps of  
234 felled trees (>10 cm DBH) were assessed for the presence of coppicing (i.e. resprouting stems),  
235 though all felled stems were excluded from the analysis of tree mortality.

236 The growth rate of trees that survived through the experiment was calculated using  
237 DBH measurements taken before harvesting and burning (i.e. pre-treatment) and during the  
238 survey in 2016 (i.e. post-treatment). Relative growth rate (RGR), which is the change in the

239 basal area of the main stem at breast height, in proportion to the initial basal area, was  
240 calculated as follows:

$$241 \quad \text{RGR} = (\text{BA}_{\text{post}} - \text{BA}_{\text{pre}}) / \text{BA}_{\text{pre}} \quad \text{Eqn. 1}$$

242 Where  $\text{BA}_{\text{pre}}$  and  $\text{BA}_{\text{post}}$  are the basal area before and after the burning treatments, respectively.

243 The potential replacement of trees was assessed by measuring ingrowth, i.e. the number  
244 of trees that had grown past 10 cm DBH between the pre- and post-treatment measurements.  
245 We did not include coppicing in these assessments. Ingrowth of trees > 10 cm DBH was  
246 measured at each site (i.e. within the 0.2 ha survey site) using one randomly located 5 m radius  
247 subplot (0.0078 ha). All trees > 10 cm DBH that were not recorded in the initial pre-treatment  
248 survey were counted.

#### 249 *Statistical Analysis*

250 The effect of harvesting on the size class distribution of trees was assessed by  
251 comparing histograms of DBH distribution both pre- and post-harvest. DBH was categorised  
252 in 10 cm intervals and the amount of tree removal (% removed) was calculated for each.  
253 Harvesting intensity was calculated as the amount (i.e. % removed) of basal area removed by  
254 timber harvesting. The likelihood of coppicing from the stumps of felled trees was assessed  
255 using a generalised additive mixed model (GAMM). A GAMM was used as they handle both  
256 linear and non-linear relationships between response and predictor variables (Zuur et al.  
257 2009). We modelled the likelihood of coppicing using a binomial distribution. DBH prior to  
258 felling was included as a fixed effect in all models, as tree size affects eucalypt resprouting  
259 success (Collins 2020). Site and coupe were included as nested random effects in all models,  
260 to account for trees being nested within sites and sites being nested within coupes. Models  
261 containing the interactive and additive effects of fire frequency and DBH (Table S1) were

262 assessed using Akaike Information Criterion (AIC), with the model with the lowest AIC  
263 considered as having the most support (Zuur et al. 2009). Models within 2 AIC points were  
264 considered as plausible alternatives.

265         The effect of burning and harvesting on mortality of retained trees was examined at  
266 the scale of the individual tree. The probability of mortality was modelled with GAMMs  
267 using a binomial distribution. Tree DBH prior to treatment and bark type were included in all  
268 models, as they have been found to influence the likelihood of tree topkill and mortality  
269 during fire (Collins 2020). Tree species were assigned to one of three bark types based on  
270 bark characteristics at the base of the stem (see Collins 2020). Bark groupings were as  
271 follows: (i) ‘Dense’ - hard compact bark (*E. sieberi*, *E. cypellocarpa*); (ii) ‘Stringy’ - thick  
272 long fibred bark (*E. agglomerata*, *E. globoidea*, *E. muelleriana*, *E. obliqua*), and; (iii)  
273 ‘Fibrous’ - thin short fibred bark (*E. consideniana*, *E. radiata*, *Corymbia gummifera*,  
274 *Angophora floribunda*). Site and coupe were included as random effects in all models. We  
275 first examined the effects of different disturbance regimes of fire (no fire, repeat burning) and  
276 harvesting (unharvested, harvested) on the relationship between mortality and DBH, to  
277 understand how the introduction of novel disturbances affects size related mortality (Coomes  
278 et al. 2003). Candidate models included bark type and (i) unique fitted relationships (i.e.  
279 smooth terms) between DBH and mortality for each disturbance regime, (ii) the additive  
280 effect of DBH and disturbance regime, and (iii) the additive effect of DBH (Table S2). The  
281 set of candidate models were assessed using AIC as described above.

282         The second mortality analysis examined the effect of fire frequency, DBH, bark type  
283 and harvesting damage, including interactions between fire frequency and DBH. Models  
284 were fitted independently for harvested and unharvested sites, to avoid complex interactions  
285 between harvesting, fire frequency and DBH. GAMMs were fitted with DBH and bark type

286 included as fixed effects in all models and site and coupe included as random effects.  
287 Candidate models examined the interactive and additive effects of fire frequency and DBH,  
288 and the additive effects of harvesting damage. Interactions involving harvesting damage and  
289 fire frequency were not considered due to insufficient replication for large (>60 cm DBH)  
290 damaged trees on frequently burnt (>4 fires) sites. GAMMs considered for the unharvested  
291 sites included the interactive and additive effects of DBH and fire frequency. Candidate  
292 models (Table S3) were assessed using AIC. Variation in the occurrence of harvesting  
293 damage with DBH and harvesting intensity (both % and basal area removed) was also  
294 examined using GAMM and AIC (Table S4).

295 Examination of the growth rate data revealed a small number of negative RGR values  
296 ( $n = 38$  out of 1700 trees), suggesting shrinking of DBH over time. Negative RGR values  
297 were likely measurement errors and were removed. They may also be a result of the  
298 consumption of bark during burns, however, given the low severity of the experimental burns  
299 (Binns and Bridges 2003) and the even spread of the negative growth rates across recorded  
300 bark thicknesses (Fig S1), it is unlikely that these were artefacts of bark consumption . We  
301 used GAMMs with a Gaussian distribution to analyse the effect of fire frequency and timber  
302 harvesting on the relative growth rate (RGR) of individual trees. Site and coupe were  
303 included as random effects. Tree species was included in all models as an additive effect, due  
304 to known inter-specific differences in eucalypt growth rates (Guinto et al. 1999). We  
305 excluded any species with fewer than 50 observations (i.e. *A. floribunda*, *C. gummifera*, *E.*  
306 *obliqua*) from the analysis to allow for the calculation of reliable RGR. A  $\log(x + 0.1)$   
307 transformation was applied to RGR to meet assumptions. Alternative models testing the  
308 interactive and additive effects of both harvesting and fire frequency were examined and  
309 compared using AIC (Table S5).



310 We looked for evidence of increased tree growth rates through competitive release by  
311 modelling the effect of harvesting intensity on RGR. The basal area of trees present before  
312 harvesting ( $BA_{pre}$ ) was included as an additive covariate, and in interaction with basal area  
313 removed ( $BA_{pct}$ ), to account for spatial variation in potential tree density across sites. Tree  
314 species was included as an additive covariate in all models to account for known differences in  
315 eucalypt species growth rates. Log RGR was modelled using a GAMM and assessed using  
316 AIC.

317 The interactive effect of fire frequency and harvesting on ingrowth (i.e. the number of  
318 new trees >10 cm DBH) was analysed using a GAMM. Treatment coupe was included in the  
319 model as a random effect to account for sites being nested within treatment coupes. A GAMM  
320 with a negative binomial distribution was used to model the data. Models containing both the  
321 additive and interactive effects of fire frequency and harvesting were assessed using AIC  
322 (Table S7). We also looked for evidence of competitive release by comparing models with  
323 additive and interactive combinations of  $BA_{pre}$  and  $BA_{pct}$  using AIC (Table S8).

324 Data analysis was undertaken using the statistical software R v3.6.2 (R Development  
325 Core Team 2019). GAMMs were fitted using the package 'gamm4' (Wood and Scheipl  
326 2017).

327 **3 RESULTS**328 *Harvesting effect on eucalypt population structure*

329 A total of 2944 eucalypts were surveyed across the 72 sites prior to the experimental  
330 treatments, with average ( $\pm$  S.E.) stocking rates of  $204.4 \pm 9.9$  trees  $\text{ha}^{-1}$  and average basal area  
331 of  $29.4 \pm 0.8$   $\text{m}^2$   $\text{ha}^{-1}$  per site. Harvesting removed 42% of trees  $> 10$  cm DBH recorded, with  
332 the greatest reduction of trees in the 30 cm to 60 cm DBH classes (Figure 2). The average  
333 percentage of basal area removed per site was  $61.3 \pm 3.1\%$ . Of the stumps that were surveyed  
334 ( $n=626$ ), 32% had live coppicing in 2016. The likelihood of coppicing was greatest for those  
335 trees that were between 30 cm to 60 cm DBH prior to harvest, but decreased for smaller and  
336 larger size classes ( $p < 0.001$ ; Figure 3). Coppicing was not affected by fire frequency,  
337 irrespective of whether it was considered as an additive effect or in interaction with DBH  
338 ( $\Delta\text{AIC} > 2$ ; Table S1).

339 [Figure 2]

340 [Figure 3]

341 *Mortality*

342 A total of 2303 live and dead trees were surveyed in 2016, with an average of  $159.93$   
343  $\pm 10.88$  trees  $\text{ha}^{-1}$ . The average mortality rate across sites was  $25.9\% \pm 1.5\%$ , irrespective of  
344 treatment. Mortality rates were 40% for trees with harvesting damage and 22% for trees  
345 without damage. The relationship between tree diameter and likelihood of tree mortality  
346 varied depending on the disturbance regime experienced (Table S2). There was no  
347 relationship between the likelihood of mortality and tree diameter on sites that remained  
348 unburnt (Figure 4a & b). A U-shaped relationship was observed between diameter and

349 mortality on sites that were unharvested and burnt at least once (Figure 4c), whereas a  
350 positive linear relationship was observed between mortality and diameter on sites that were  
351 both harvested and burnt (Figure 4d).

352 [Figure 4]

353 The likelihood of mortality on harvested sites was dependent on the interaction  
354 between fire frequency and tree diameter, as well as the additive effect of harvesting damage  
355 (Table S3). There was a general trend of greater mortality rates with increasing tree size and  
356 increasing fire frequency (Figure 5). Consequently, large trees (>80 cm DBH) exposed to  
357 frequent fire (>5 fires) were at greatest risk of mortality (Figure 5). Trees damaged during  
358 harvesting operations had a greater likelihood of mortality ( $\Delta P \sim 0.2$ ) than undamaged trees  
359 (Figure 5; Figure S2). Bark type had little effect on mortality (Figure S3). On unharvested  
360 sites, the model containing the interaction between fire frequency and DBH had the most  
361 support (Table S3), though model predictions indicate that likelihood of mortality showed  
362 little change across DBH and fire frequency (Figure S4). Bark type also had little effect on  
363 mortality in unharvested sites.

364 [Figure 5]

365 The likelihood that a tree was damaged during harvesting was related to both tree  
366 DBH and the basal area of timber removed (Table S4). There was a linear negative effect of  
367 DBH and harvesting damage, whereby trees with a small DBH were more likely to sustain  
368 damage than large trees (Figure 6a). The likelihood of harvesting damage for a tree smaller  
369 than 20 cm DBH was between 0.4 – 0.5 on sites with average timber removal (17 m<sup>2</sup>/ha).  
370 Harvesting damage increased ( $\Delta P = 0.4$ ) across the range of harvesting intensities present

371 across the study sites, though this effect was greater for small trees than large trees (Figure  
372 6b).

373 [Figure 6]

#### 374 *Relative growth rate (RGR)*

375 A total of 1622 surviving eucalypt trees were recorded, with an average RGR of 1.396  
376  $\pm 0.040$ , representing on average a 140% increase in tree basal area over the ~30 year  
377 duration of the experiment. The RGR of eucalypts differed between trees on harvested and  
378 unharvested sites but were not affected by fire frequency (Table S5). Trees on harvested sites  
379 grew at twice the rate of trees on unharvested sites (Figure 7a). There was little variation in  
380 RGR across species (Figure S5). There was strong support for the model containing the  
381 additive effect of the amount (%) of original stand basal area extracted ( $T_{\text{pct}}$ ) (Table S6),  
382 which supports the hypothesis that harvesting was increasing RGR through competitive  
383 release. RGR more than doubled over the range of harvesting intensities present across the  
384 study sites (Figure 7b).

385 [Figure 7]

#### 386 *Ingrowth*

387 The amount of ingrowth ranged from zero to forty six trees per subplot (5 m radius),  
388 with an overall average ( $\pm$  S.E.) of  $7.0 \pm 1.1$  trees (i.e.  $887.7 \pm 146.1$  trees  $\text{ha}^{-1}$ ). The model  
389 containing only timber harvesting had more support than those that also included the additive  
390 or interactive effects of fire frequency (Table S7). The number of new trees  $>10$  cm DBH  
391 was ~5 times greater on harvested sites (~10 trees per subplot) than unharvested sites (~2  
392 trees per subplot; Figure 8a). Ingrowth was affected by the amount of timber removed from a

393 site (Table S8), which supports the hypothesis that harvesting was increasing ingrowth  
394 through competitive release. The amount of ingrowth increased with the percent of the stand  
395 basal area felled (Figure 8b).

396 [Figure 8]

#### 397 **4 DISCUSSION**

398 Our study provides a long-term experimental assessment of the interactive effects of  
399 frequent prescribed burning and timber harvesting on the demography of a fire resilient  
400 eucalypt community. The greatest change in the demography of trees within these forests was  
401 the loss of large trees, which was associated with both harvesting and burning. Harvesting  
402 directly removed ~70% of trees greater than 50 cm DBH (upper 25<sup>th</sup> percentile) and was also  
403 indirectly responsible for elevated mortality rates of retained trees through harvesting  
404 damage. While the probability of mortality did not change with tree size in unburnt sites,  
405 increased mortality of larger size classes was seen in both unharvested and harvested sites  
406 that had been burnt at least once, indicating the importance of burning on mortality. The  
407 effect of fire frequency on tree mortality was greater on harvested sites, with large trees that  
408 had been burnt frequently being at greatest risk. Our findings highlight the importance of  
409 multiple interacting disturbances in determining mortality rates in fire resilient tree species  
410 (Hood et al. 2018).

411 Retained trees that suffered damage during harvesting operations had an elevated  
412 likelihood of mortality, which is consistent with findings from a range of broadleaf forests  
413 (Sist and Nguyen-Thé 2002, Tatsumi et al. 2014). Forty percent of the trees damaged by  
414 harvesting operations succumbed to mortality over the duration of the experiment, which was  
415 surprising given that these eucalypts show high resilience to complete crown defoliation and  
416 crown mortality (Collins 2020). However, stem damage may be a more important factor than

417 crown damage in determining mortality, as found in *Acacia karoo* (Balfour and Midgely  
418 (2006). The predominant type of mechanical damage recorded was complete loss of the tree  
419 crown and/or breakage of the bole (66% of damaged trees), which disproportionately affected  
420 smaller trees. Unsurprisingly, extensive crown damage has been found to substantially reduce  
421 the likelihood of tree survival post-harvest (Solarik et al. 2012) as well as the likelihood of  
422 mortality during fire (Strasser et al. 1996), which likely explains the high rates of mortality in  
423 damaged trees observed in our study.

424         The loss of large old trees will have important and lasting implications for  
425 biodiversity and carbon sequestration in temperate forests. Large, old trees are keystone  
426 structures which play unique ecological roles, providing critical nesting sites (e.g. hollow  
427 cavities) and food resources (van Pelt 2007, Remm and Löhmus 2011, Lindenmayer et al.  
428 2012b, Lindenmayer and Laurance 2017). In Australia's eucalypt forests and woodlands,  
429 ~300 native animal species depend on hollows in old eucalypts (>120 years old) for habitat,  
430 thus preserving these keystone structures is of high conservation priority (Gibbons and  
431 Lindenmayer 2002). Large old trees also store a considerable proportion of above-ground  
432 carbon (Fedrigo et al. 2014), which may take centuries to sequester following major  
433 ecological disturbances such as clearfelling and low retention harvesting (Roxburgh et al.  
434 2006). The combined impact of harvesting and frequent fire has led to ~20 - 30% reduction in  
435 carbon stocks at the EBSA, which partially reflects the loss of large trees identified in our  
436 study (Collins et al. 2019). The management of forests for commercial benefit needs to  
437 accommodate the maintenance of forest structure by ensuring enough trees advance to the  
438 large class cohort to maintain future structure and habitat value.

439         Competitive release was evident at harvested sites where both ingrowth and RGR  
440 were elevated relative to unharvested controls, a trend that has been reported across broadleaf  
441 forests globally (e.g. Sist and Nguyen-Thé 2002, Peña-Claros et al. 2008). There was a

442 positive relationship between harvesting intensity and both growth rate and ingrowth, which  
443 likely reflects the influence of increased light availability (Peña-Claros et al. 2008). The  
444 elevated growth rates and ingrowth on harvested sites will facilitate the replacement of large  
445 trees and recovery of stand biomass, though this will take considerable time depending on the  
446 intensity of timber extraction (Roxburgh et al. 2006). Enhanced growth rates associated with  
447 harvesting may hasten the development of fire resistance traits (i.e. bark thickness, canopy  
448 height) in saplings and small trees (Lawes et al. 2011) which could explain the tendency for  
449 reduced mortality of small stems (< 20 cm DBH) in harvested and burnt sites compared to  
450 unharvested and burnt sites (Figure 4c & d).

451         We found no effect of fire frequency on RGR, rejecting our initial prediction that  
452 frequent prescribed burning would be detrimental to the growth rate of eucalypts. This  
453 finding is in contrast to a number of studies that reported negative effects of frequent low  
454 intensity burning on eucalypt growth in temperate, sub-tropical and tropical forest and  
455 woodlands (Murphy et al. 2010, Bennett et al. 2013, Collins et al. 2014). The contrasting  
456 findings can likely be explained by the patchy and low-intensity prescribed burns applied at  
457 the EBSA (Penman et al. 2007), which were unlikely to be severe enough to cause  
458 widespread and extensive damage to the cambium and bark of eucalypts greater than 10 cm  
459 DBH (Collins 2020). Guinto, *et al.* (1999) similarly found no effect of burn frequency on tree  
460 growth rates following several decades of patchy landscape scale burning in a sub-tropical  
461 mixed species eucalypt forest.

462         The fast growth rates and ingrowth of trees at harvested sites may well have been  
463 hampered by the level of coppicing of stumps particularly in harvested mid-sized trees. With  
464 32% of stumps coppicing following harvesting, resources would have been more limited than  
465 if tree stumps had been killed. Coppicing of stumps from younger trees was less likely, which  
466 was unintuitive as these young eucalypt stems are adept at resprouting from basal buds

467 following fire induced topkill (Fairman et al. 2019). It is possible that many young stumps  
468 produced sprouts that subsequently died as a result of insufficient resources in below ground  
469 storage organs (Smith et al. 2018). Low levels of coppicing in larger, older trees has been  
470 observed across many eucalypt species, and likely arises due to reduced availability of viable  
471 epicormic bud strands, or suppression of bud emergence because of the thicker bark at the  
472 base of large stems (see Burrows 2002).

473         Although the Eden Burning Experiment is ‘long-term’ (~30 years) in the context of  
474 research, the ecological effects of timber harvesting and repeated prescribed burning may  
475 play out over longer time frames. This will be particularly relevant for communities  
476 dominated by tree species that display strong resistance to low severity fires, such as the  
477 resprouting eucalypts examined in our study. The low rates of adult mortality (typically <5  
478 %) experienced during a low severity fire event (Denham et al. 2016, Bennett et al. 2016)  
479 result in subtle changes in population structure. However, if regimes of very frequent low  
480 severity burning are maintained over extended periods (e.g. >50 years), the cumulative  
481 effects of fire related mortality could lead to dramatic demographic changes, unless some  
482 feedback mechanism occurs (e.g. fuel limitation due to reduced plant density). Insights into  
483 these longer-term processes will only be made through continuation of existing ‘long-term’  
484 experiments such as the EBSA.

#### 485 4.1 **Management Implications**

486         The loss of large trees associated with low retention harvesting and short-interval  
487 prescribed burning has led to significant declines in habitat (e.g. hollow availability),  
488 biodiversity and ecosystem function across eucalypt forests (e.g. Roxburgh et al. 2006,  
489 Lindenmayer and Sato 2018). Minimising the impact of these practices on large tree  
490 abundance, via protection of large trees or practices that accelerate their recruitment, will be  
491 critical for sustainable forest management (Lindenmayer et al. 2012a). Insights gained from



492 long-term manipulative experiments, such as the EBSA, will aid in the development of best  
493 practices to achieve this outcome (Lindenmayer et al. 2019).

494         Harvesting intensity is an important determinant of the impact of selective harvesting  
495 systems on large tree abundance, structural complexity and biomass of broadleaf forests (Sist  
496 and Nguyen-Thé 2002, Solarik et al. 2012, Collins et al. 2019). The optimal rate of tree  
497 retention for selective harvesting operations will depend on defined silvicultural and  
498 environmental objectives. Our research, and the work of others (e.g. Tatsumi et al. 2014),  
499 highlights that retention rates need to account for the elevated mortality and collapse of  
500 retained trees, owing to mechanical damage sustained during harvesting operations. In mature  
501 temperate dry eucalypt forest, selective harvesting of 60 -70% of stand basal area ( $\sim 20 \text{ m}^2 \text{ ha}^{-1}$ )  
502 <sup>1</sup>) could be expected to cause substantial damage to the crowns of  $\sim 40\%$  of smaller trees (10  
503 cm - 30 cm DBH) and  $\sim 30\%$  of larger trees (30 cm – 60 cm), with 40% of these damaged  
504 trees experiencing mortality over the coming decades. The propensity toward complete crown  
505 loss in small trees suggests that harvesting damage will not increase the availability of old  
506 growth structure through accelerated hollow formation (Gibbons and Lindenmayer 2002).  
507 Reducing the intensity of selective harvesting would have dual benefits in terms of increasing  
508 the number of retained trees and decreasing the proportion of trees damaged by harvesting  
509 operations. This will be desirable to ensure the replacement of old trees in managed forests,  
510 particularly over successive harvesting cycles.

511         This study has identified that prescribed burning and harvesting interact to influence  
512 some, but not all, demographic processes. Of concern is the loss and high mortality of trees in  
513 larger size classes in response to harvesting and frequent prescribed burning, which can lead  
514 to a long-term loss of these keystone habitat structures in intensively managed forests  
515 (Lindenmayer and Laurance 2017). Practices aimed at protecting large old trees from  
516 mortality and collapse during prescribed burns, such as the mechanical removal of fine and

517 coarse fuels around the base of large trees (Bluff 2016), may be desirable in forests managed  
518 for timber extraction. Release from competition has some advantages for trees left following  
519 harvest or burning, as shown by increases in ingrowth and growth rates, which may  
520 accelerate the rate of habitat development and the fire resilience of young trees. However,  
521 whether attaining a large diameter is the important factor in the value of large trees, or  
522 whether it is the hollows and complexity at the site level that are important needs to be  
523 assessed.

524 Australia's unprecedented 2020 fire season affected more than 6.5 million ha of  
525 temperate broadleaf forest across the southeast of the continent (Boer et al. 2020, Nolan et al.  
526 2020). Considerable social and political debate around forest management and wildfire risk  
527 mitigation has ensued (e.g. Lindenmayer et al. 2020, Adams et al. 2020), which will  
528 undoubtedly influence policy decisions around harvesting and prescribed burning for years to  
529 come (Penman et al. 2011). Decisions around wildfire management need to balance social  
530 and environmental considerations, and should make use of the best available evidence on the  
531 efficacy of prescribed burning and harvesting in this regard (FAO and UNEP 2020, Penman  
532 et al. 2020). The findings of our study indicate that broadscale intensification of harvesting  
533 and burning would likely lead to undesirable environmental outcomes across eucalypt forests.  
534

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542 **6 REFERENCES**

543 Adams, M. A., M. Shadmanroodposhti, and M. Neumann. 2020. Causes and consequences of  
544 Eastern Australia's 2019–20 season of mega-fires: A broader perspective. *Global*  
545 *Change Biology* 26:3756–3758.

546 Alencar, A. A. C., L. A. Solórzano, and D. C. Nepstad. 2004. Modeling forest understory  
547 fires in an Eastern Amazonian landscape. *Ecological Applications* 14:139–149.

548 Bailey, J. D., and J. C. Tappeiner. 1998. Effects of thinning on structural development in 40-  
549 to 100-year-old Douglas-fir stands in western Oregon. *Forest Ecology and Management*  
550 108:99–113.

551 Balfour, D. A., and J. J. Midgely. 2006. Fire induced stem death in an African acacia is not  
552 caused by canopy scorching. *Austral Ecology* 31:892–896.

553 Bellingham, P. J., and A. D. Sparrow. 2000. Resprouting as a life history strategy in woody  
554 plant communities. *Oikos* 89:409–416.

555 Bennett, L. T., C. Aponte, K. G. Tolhurst, M. Löw, and T. G. Baker. 2013. Decreases in  
556 standing tree-based carbon stocks associated with repeated prescribed fires in a  
557 temperate mixed-species eucalypt forest. *Forest Ecology and Management* 306:243–255.

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

561 Binns, D. L., and R. G. Bridges. 2003. Ecological impacts and sustainability of timber  
562 harvesting and burning in coastal forests of the Eden area: establishment and progress of  
563 the Eden Burning Study. Page State Forests of NSW.

- 564 Bluff, L. 2016. Reducing the effect of planned burns on hollow-bearing trees Fire and  
565 adaptive management report no. 95. Melbourne.
- 566 Boer, M. M., V. Resco de Dios, and R. A. Bradstock. 2020, March 1. Unprecedented burn  
567 area of Australian mega forest fires. Nature Research.
- 568 Bonan, G. B. 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate  
569 Benefits of Forests. Science 320.
- 570 Bowman, D. M. J. S. 2008. The impact of Aboriginal landscape burning on the Australian  
571 biota. New Phytologist 140:385–410.
- 572 Bowman, D. M. J. S., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C.  
573 M. D’Antonio, R. S. Defries, J. C. Doyle, S. P. Harrison, F. H. Johnston, J. E. Keeley,  
574 M. A. Krawchuk, C. A. Kull, J. B. Marston, M. A. Moritz, I. C. Prentice, C. I. Roos, A.  
575 C. Scott, T. W. Swetnam, G. R. van der Werf, and S. J. Pyne. 2009. Fire in the Earth  
576 system. Science (New York, N.Y.) 324:481–4.
- 577 Bowman, D. M., B. P. Murphy, M. M. Boer, R. A. Bradstock, G. J. Cary, M. A. Cochrane, R.  
578 J. Fensham, M. A. Krawchuk, O. F. Price, and R. J. Williams. 2013. Forest fire  
579 management, climate change, and the risk of catastrophic carbon losses. Frontiers in  
580 Ecology and the Environment 11:66–67.
- 581 Bradstock, R. A. 2008. Effects of large fires on biodiversity in south-eastern Australia:  
582 disaster or template for diversity? International Journal of Wildland Fire 17:809.
- 583 Bradstock, R. A. 2010. A biogeographic model of fire regimes in Australia: current and  
584 future implications. Global Ecology and Biogeography 19:145–158.
- 585 Bridges, R. G. 2009. Effects of logging and burning regimes on overstorey species of dry  
586 sclerophyll forest in south eastern NSW: initial results (1986-2001) from Eden Burning  
587 Study Area.
- 588 Bureau of Meterology. 2016. Climate Statistics for Merimbula Airport AWS.

- 589 [http://www.bom.gov.au/climate/averages/tables/cw\\_069147.shtml](http://www.bom.gov.au/climate/averages/tables/cw_069147.shtml).
- 590 Burrows, G. E. 2002. Epicormic strand structure in Angophora, Eucalyptus and Lophostemon  
591 (Myrtaceae) - implications for fire resistance and recovery. *New Phytologist* 153:111–  
592 131.
- 593 Catry, F. X., J. G. Pausas, F. Moreira, P. M. Fernandes, and F. Rego. 2013. Post-fire response  
594 variability in Mediterranean Basin tree species in Portugal. *International Journal of*  
595 *Wildland Fire* 22:919.
- 596 Charles-Dominique, T., H. Beckett, G. F. Midgley, and W. J. Bond. 2015. Bud protection: a  
597 key trait for species sorting in a forest-savanna mosaic. *New Phytologist* 207:1052–  
598 1060.
- 599 Clarke, P. J., M. J. Lawes, J. J. Midgley, B. B. Lamont, F. Ojeda, G. E. Burrows, N. J.  
600 Enright, and K. J. E. Knox. 2013. Resprouting as a key functional trait: how buds,  
601 protection and resources drive persistence after fire. *New Phytologist* 197:19–35.
- 602 Collins, L. 2020. Eucalypt forests dominated by epicormic resprouters are resilient to  
603 repeated canopy fires. *Journal of Ecology* 108:310–324.
- 604 Collins, L., R. Bradstock, F. Ximenes, B. Horsey, R. Sawyer, and T. Penman. 2019.  
605 Aboveground forest carbon shows different responses to fire frequency in harvested and  
606 unharvested forests. *Ecological Applications* 29:e01815.
- 607 Collins, L., P. Griffioen, G. Newell, and A. Mellor. 2018. The utility of Random Forests for  
608 wildfire severity mapping. *Remote Sensing of Environment* 216:374–384.
- 609 Collins, L., T. Penman, F. de A. Ximenes, D. Binns, A. York, and R. Bradstock. 2014.  
610 Impacts of frequent burning on live tree carbon biomass and demography in post-harvest  
611 regrowth forest. *Forests* 5:802–821.
- 612 Coomes, D. A., R. P. Duncan, R. B. Allen, and J. Truscott. 2003. Disturbances prevent stem  
613 size-density distributions in natural forests from following scaling relationships. *Ecology*

- 614 Letters 6:980–989.
- 615 Crowther, T. W., H. B. Glick, K. R. Covey, C. Bettigole, D. S. Maynard, S. M. Thomas, J. R.  
616 Smith, G. Hintler, M. C. Duguid, G. Amatulli, M.-N. Tuanmu, W. Jetz, C. Salas, C.  
617 Stam, D. Piotto, R. Tavani, S. Green, G. Bruce, S. J. Williams, S. K. Wiser, M. O.  
618 Huber, G. M. Hengeveld, G.-J. Nabuurs, E. Tikhonova, P. Borchardt, C.-F. Li, L. W.  
619 Powrie, M. Fischer, A. Hemp, J. Homeier, P. Cho, A. C. Vibrans, P. M. Umunay, S. L.  
620 Piao, C. W. Rowe, M. S. Ashton, P. R. Crane, and M. A. Bradford. 2015. Mapping tree  
621 density at a global scale. *Nature* 525:201–205.
- 622 Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J.  
623 Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J.  
624 Stocks, and B. M. Watton. 2001. Climate change and forest disturbances. *BioScience*  
625 51:723–734.
- 626 Denham, A. J., B. E. Vincent, P. J. Clarke, and T. D. Auld. 2016. Responses of tree species to  
627 a severe fire indicate major structural change to Eucalyptus–Callitris forests. *Plant*  
628 *Ecology* 217:617–629.
- 629 Enright, N. J., J. B. Fontaine, B. B. Lamont, B. P. Miller, and V. C. Westcott. 2014.  
630 Resistance and resilience to changing climate and fire regime depend on plant functional  
631 traits. *Journal of Ecology* 102:1572–1581.
- 632 Fairman, T. A., L. T. Bennett, and C. R. Nitschke. 2019. Short-interval wildfires increase  
633 likelihood of resprouting failure in fire-tolerant trees. *Journal of Environmental*  
634 *Management* 231:59–65.
- 635 FAO, and UNEP. 2020. *The State of the World’s Forests: Forests, Biodiversity and People*.  
636 Rome.
- 637 Fedrigo, M., S. Kasel, L. T. Bennett, S. H. Roxburgh, and C. R. Nitschke. 2014. Carbon  
638 stocks in temperate forests of south-eastern Australia reflect large tree distribution and

- 639 edaphic conditions. *Forest Ecology and Management* 334:129–143.
- 640 Fernandes, P. M., and H. S. Botelho. 2003. A review of prescribed burning effectiveness in  
641 fire hazard reduction. *International Journal of Wildland Fire* 12:117–128.
- 642 Gibbons, P., R. B. Cunningham, and D. B. Lindenmayer. 2008. What factors influence the  
643 collapse of trees retained on logged sites?. A case-control study. *Forest Ecology and*  
644 *Management* 255:62–67.
- 645 Gibbons, P., and D. Lindenmayer. 2002. *Tree hollows and wildlife conservation in Australia*.  
646 CSIRO Publishing, Collingwood, VIC.
- 647 Gibbons, P., D. B. Lindenmayer, S. C. Barry, and M. T. Tanton. 2000. The effects of slash  
648 burning on the mortality and collapse of trees retained on logged sites in south-eastern  
649 Australia. *Forest Ecology and Management* 139:51–61.
- 650 Gordon, C. E., E. R. Bendall, M. G. Stares, L. Collins, and R. A. Bradstock. 2018.  
651 Aboveground carbon sequestration in dry temperate forests varies with climate not fire  
652 regime. *Global Change Biology* 24:4280–4292.
- 653 Guinto, D. F., A. P. . House, Z. H. Xu, and P. G. Saffigna. 1999. Impacts of repeated fuel  
654 reduction burning on tree growth, mortality and recruitment in mixed species eucalypt  
655 forests of southeast Queensland, Australia. *Forest Ecology and Management* 115:13–27.
- 656 He, T., B. B. Lamont, and J. G. Pausas. 2019. Fire as a key driver of Earth’s biodiversity.  
657 *Biol. Rev* 94:1983–2010.
- 658 Hood, S. M., J. M. Varner, P. van Mantgem, and C. A. Cansler. 2018. Fire and tree death:  
659 understanding and improving modeling of fire-induced tree mortality. *Environmental*  
660 *Research Letters* 13.
- 661 Hurteau, M. D., S. Liang, K. L. Martin, M. P. North, G. W. Koch, and B. A. Hungate. 2016.  
662 Restoring forest structure and process stabilizes forest carbon in wildfire-prone  
663 southwestern ponderosa pine forests. *Ecological Applications* 26:382–391.

- 664 Keith, D. A., and M. Bedward. 1999. Native vegetation of the South East Forests region,  
665 Eden, New South Wales. *Cunninghamia* 6:1–60.
- 666 Kotwal, P. C., M. D. Omprakash, S. Gairola, and D. Dugaya. 2008. Ecological indicators:  
667 Imperative to sustainable forest management. *Ecological Indicators* 8:104–107.
- 668 Lawes, M. J., D. A. Keith, and R. A. Bradstock. 2016. Advances in understanding the  
669 influence of fire on the ecology and evolution of plants: a tribute to Peter J. Clarke. *Plant*  
670 *Ecology* 217:597–605.
- 671 Lawes, M. J., A. Richards, J. Dathe, and J. J. Midgley. 2011. Bark thickness determines fire  
672 resistance of selected tree species from fire-prone tropical savanna in north Australia.  
673 *Plant Ecology* 212:2057–2069.
- 674 Lindenmayer, D. B., R. M. Kooyman, C. Taylor, M. Ward, and J. E. M. Watson. 2020, July  
675 1. Recent Australian wildfires made worse by logging and associated forest  
676 management. *Nature Research*.
- 677 Lindenmayer, D. B., and W. F. Laurance. 2017. The ecology, distribution, conservation and  
678 management of large old trees. *Biological Reviews* 92:1434–1458.
- 679 Lindenmayer, D. B., W. F. Laurance, and J. F. Franklin. 2012a. Global decline in large old  
680 trees. *Science* 338:1305–1306.
- 681 Lindenmayer, D. B., W. F. Laurance, and J. F. Franklin. 2012b. Global decline in large old  
682 trees. *Science* 338:1305–1306.
- 683 Lindenmayer, D. B., and C. Sato. 2018. Hidden collapse is driven by fire and logging in a  
684 socioecological forest ecosystem. *Proceedings of the National Academy of Sciences of*  
685 *the United States of America* 115:5181–5186.
- 686 Lindenmayer, D., D. Blair, and L. McBurney. 2019, December 1. Variable retention  
687 harvesting in Victoria’s Mountain Ash (*Eucalyptus regnans*) forests (southeastern  
688 Australia). Springer Verlag.



- 689 Lindenmayer, D., and M. A. McCarthy. 2002. Congruence between natural and human forest  
690 disturbance: a case study from Australian montane ash forests. *Forest Ecology and*  
691 *Management* 155:319–335.
- 692 McCarthy, G., K. Moon, and L. Smith. 2017. Mapping fire severity and fire extent in forest in  
693 Victoria for ecological and fuel outcomes. *Ecological Management and Restoration*  
694 18:54–65.
- 695 McKemey, M. B., M. (Lesley) Patterson, B. Rangers, E. J. Ens, N. C. H. Reid, J. T. Hunter,  
696 O. Costello, M. Ridges, and C. Miller. 2019. Cross-Cultural Monitoring of a Cultural  
697 Keystone Species Informs Revival of Indigenous Burning of Country in South-Eastern  
698 Australia. *Human Ecology* 47:893–904.
- 699 Morrison, D. A., G. J. Cary, S. M. Pengelly, D. G. Ross, B. J. Mullins, C. R. Thomas, and T.  
700 S. Anderson. 1995. Effects of fire frequency on plant species composition of sandstone  
701 communities in the Sydney region: Inter-fire interval and time-since-fire. *Australian*  
702 *Journal of Ecology* 20:239–247.
- 703 Murphy, B. P., R. A. Bradstock, M. M. Boer, J. Carter, G. J. Cary, M. A. Cochrane, R. J.  
704 Fensham, J. Russell-Smith, G. J. Williamson, and D. M. J. S. Bowman. 2013. Fire  
705 regimes of Australia: A pyrogeographic model system. *Journal of Biogeography*  
706 40:1048–1058.
- 707 Murphy, B. P., J. Russell-Smith, and L. D. Prior. 2010. Frequent fires reduce tree growth in  
708 northern Australian savannas: Implications for tree demography and carbon  
709 sequestration. *Global Change Biology* 16:331–343.
- 710 Nolan, R. H., M. M. Boer, L. Collins, V. Resco de Dios, H. Clarke, M. Jenkins, B. Kenny,  
711 and R. A. Bradstock. 2020. Causes and consequences of eastern Australia’s 2019–20  
712 season of mega-fires. *Global Change Biology* 26:1039–1041.
- 713 Nolan, R. H., P. N. J. Lane, R. G. Benyon, R. A. Bradstock, and P. J. Mitchell. 2015. Trends

- 714 in evapotranspiration and streamflow following wildfire in resprouting eucalypt forests.  
715 *Journal of Hydrology* 524:614–624.
- 716 Ooi, M. K. J. 2012. Seed bank persistence and climate change. *Seed Science Research*  
717 22:S53–S60.
- 718 Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A.  
719 Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D.  
720 McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A Large and Persistent  
721 Carbon Sink in the World’s Forests. *Science* 333:988–993.
- 722 Pausas, J. G., and J. E. Keeley. 2017. Epicormic Resprouting in Fire-Prone Ecosystems.  
723 *Trends in Plant Science* 22:1008–1015.
- 724 Pausas, J. G., R. B. Pratt, J. E. Keeley, A. L. Jacobsen, A. R. Ramirez, A. Vilagrosa, S. Paula,  
725 I. N. Kaneakua-Pia, and S. D. Davis. 2016. Towards understanding resprouting at the  
726 global scale. *New Phytologist* 209:945–954.
- 727 van Pelt, R. 2007. Identifying mature and old forests in western Washington. Olympia, WA.
- 728 Peña-Claros, M., T. S. Fredericksen, A. Alarcón, G. M. Blate, U. Choque, C. Leño, J. C.  
729 Licona, B. Mostacedo, W. Pariona, Z. Villegas, and F. E. Putz. 2008. Beyond reduced-  
730 impact logging: Silvicultural treatments to increase growth rates of tropical trees. *Forest*  
731 *Ecology and Management* 256:1458–1467.
- 732 Penman, T. D., D. L. Binns, R. J. Shiels, R. M. Allen, and R. P. Kavanagh. 2008. Changes in  
733 understorey plant species richness following logging and prescribed burning in shrubby  
734 dry sclerophyll forests of south-eastern Australia. *Austral Ecology* 33:197–210.
- 735 Penman, T. D., F. J. Christie, A. N. Andersen, R. A. Bradstock, G. J. Cary, M. K. Henderson,  
736 O. Price, C. Tran, G. M. Wardle, R. J. Williams, and A. York. 2011. Prescribed burning:  
737 how can it work to conserve the things we value? *International Journal of Wildland Fire*  
738 20:721–733.

- 739 Penman, T. D., L. Collins, T. D. Duff, O. F. Price, and G. J. Cary. 2020. Scientific evidence  
740 regarding the effectiveness of prescribed burning. Pages 99–111 in A. Leavesley, M.  
741 Wouters, and R. Thornton, editors. Prescribed burning in Australasia: The science,  
742 practice and politics of burning the bush. Australasian Fire and Emergency Service  
743 Authorities Council., East Melbourne.
- 744 Penman, T. D., R. P. Kavanagh, D. L. Binns, and D. R. Melick. 2007. Patchiness of  
745 prescribed burns in dry sclerophyll eucalypt forests in South-eastern Australia. *Forest  
746 Ecology and Management* 252:24–32.
- 747 Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: Fire frequency effects  
748 on stand structure and dynamics. *Ecological Applications* 11:914–927.
- 749 Remm, J., and A. Lõhmus. 2011. Tree cavities in forests - The broad distribution pattern of a  
750 keystone structure for biodiversity. *Forest Ecology and Management* 262:579–585.
- 751 Roxburgh, S. H., S. W. Wood, B. G. Mackey, G. Woldendorp, and P. Gibbons. 2006.  
752 Assessing the carbon sequestration potential of managed forests: A case study from  
753 temperate Australia. *Journal of Applied Ecology* 43:1149–1159.
- 754 Schall, P., M. M. Gossner, S. Heinrichs, M. Fischer, S. Boch, D. Prati, K. Jung, V.  
755 Baumgartner, S. Blaser, S. Böhm, F. Buscot, R. Daniel, K. Goldmann, K. Kaiser, T.  
756 Kahl, M. Lange, J. Müller, J. Overmann, S. C. Renner, E. D. Schulze, J. Sikorski, M.  
757 Tschapka, M. Türke, W. W. Weisser, B. Wemheuer, T. Wubet, and C. Ammer. 2018.  
758 The impact of even-aged and uneven-aged forest management on regional biodiversity  
759 of multiple taxa in European beech forests. *Journal of Applied Ecology* 55:267–278.
- 760 Sebbenn, A. M., B. Degen, V. C. R. Azevedo, M. B. Silva, A. E. B. de Lacerda, A. Y.  
761 Ciampi, M. Kanashiro, F. da S. Carneiro, I. Thompson, and M. D. Loveless. 2008.  
762 Modelling the long-term impacts of selective logging on genetic diversity and  
763 demographic structure of four tropical tree species in the Amazon forest. *Forest Ecology*

- 764 and Management 254:335–349.
- 765 Silvério, D. V., P. M. Brando, M. M. C. Bustamante, F. E. Putz, D. M. Marra, S. R. Levick,  
766 and S. E. Trumbore. 2019. Fire, fragmentation, and windstorms: A recipe for tropical  
767 forest degradation. *Journal of Ecology* 107:656–667.
- 768 Sist, P., and N. Nguyen-Thé. 2002. Logging damage and the subsequent dynamics of a  
769 dipterocarp forest in East Kalimantan (1990-1996). *Forest Ecology and Management*  
770 165:85–103.
- 771 Smith, M. G., S. K. Arndt, R. E. Miller, S. Kasel, and L. T. Bennett. 2018. Trees use more  
772 non-structural carbohydrate reserves during epicormic than basal resprouting. *Tree*  
773 *Physiology* 38:1779–1791.
- 774 Solarik, K. A., W. J. A. Volney, V. J. Lieffers, J. R. Spence, and A. Hamann. 2012. Factors  
775 affecting white spruce and aspen survival after partial harvest. *Journal of Applied*  
776 *Ecology* 49:145–154.
- 777 Strasser, M. J., J. G. Pausas, and I. R. Noble. 1996. Modelling the response of eucalypts to  
778 fire, Brindabella Ranges, ACT. *Austral Ecology* 21:341–344.
- 779 Tatsumi, S., T. Owari, H. Kasahara, and Y. Nakagawa. 2014. Individual-level analysis of  
780 damage to residual trees after single-tree selection harvesting in northern Japanese  
781 mixedwood stands. *Journal of Forest Research* 19:369–378.
- 782 Whitford, K. R., and M. R. Williams. 2001. Survival of jarrah (*Eucalyptus marginata* Sm.)  
783 and marri (*Corymbia calophylla* Lindl.) Habitat trees retained after logging. *Forest*  
784 *Ecology and Management* 146:181–197.
- 785 Wood, S., and F. Scheipl. 2017. Package “*gamm4*.”
- 786 Yamada, T., T. Hosaka, T. Okuda, and A. R. Kassim. 2013. Effects of 50 years of selective  
787 logging on demography of trees in a Malaysian lowland forest. *Forest Ecology and*  
788 *Management* 310:531–538.

789 Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects  
790 models and extensions in ecology with R. Springer Science+Business Media LLC, New  
791 York.

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794 **7 FIGURES**

795 **Figure 1** Location of the study area in southern Australia. The treatment blocks are depicted  
 796 by the shaded polygons. Treatment codes are as follows: Unharvested, no fire (UN);  
 797 Unharvested, routine burning (UR); Unharvested, frequent burning (UF); Harvested, no fire  
 798 (HN); Harvested, routine burning (HR); and Harvested, frequent burning (HF).

799 **Figure 2** Histograms showing the number of trees ha<sup>-1</sup> recorded across (a) unharvested and  
 800 (b) harvested sites. The white histograms show the number of trees before harvesting while  
 801 the grey histograms in panel (b) show the number of trees following timber harvesting.  
 802 Numbers above the bars in panel (b) show the % of trees removed by harvesting in each DBH  
 803 size class.

804 **Figure 3** The effect of diameter at breast height (DBH) on the likelihood of coppicing from  
 805 the stumps of trees that were harvested. The DBH was measured prior to harvesting. *P*-values  
 806 are for the GAMM smooth terms. Solid lines show the fitted mean and polygons show the  
 807 95% confidence intervals.

808 **Figure 4** The effect of diameter at breast height (DBH) on the likelihood of tree mortality on  
 809 sites that were: a) unharvested and unburnt (UN); b) harvested and unburnt (HN); c)  
 810 unharvested and burnt (UB); d) and harvested and burnt (HB). Trees considered in the  
 811 analysis were those greater than 10 cm DBH prior to the implementation of the burning  
 812 treatments. *P*-values are for the GAMM smooth terms. Solid lines show the fitted mean and  
 813 polygons show the 95% confidence intervals. Predictions were made for 'stringybark' bark  
 814 type.

815 **Figure 5** Heat map showing the effect of stem diameter (DBH) and the number of fires on  
 816 the likelihood of tree mortality at harvested sites for a) trees damaged by harvesting and b)

817 trees not damaged by harvesting. Trees considered in the analysis were those greater than 10  
818 cm DBH prior to the implementation of the burning treatments, but post harvesting.

819 Predictions were made for 'stringybark' bark type.

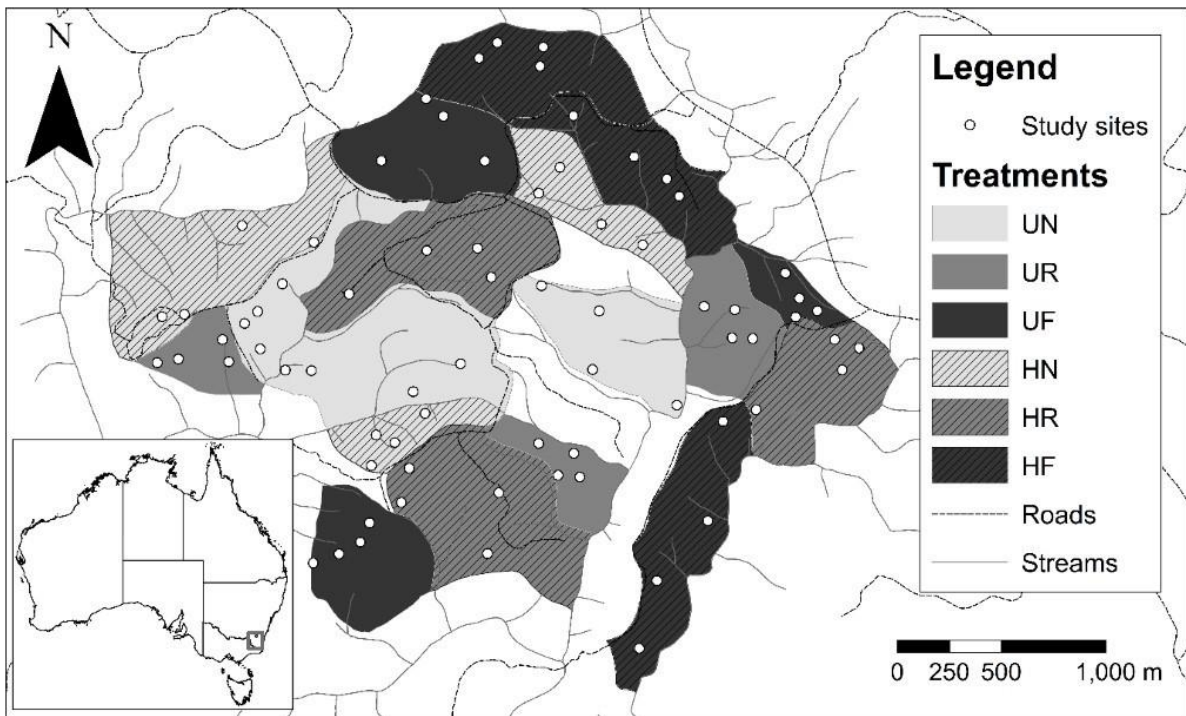
820 **Figure 6** The effect of (a) diameter at breast height (DBH) and (b) basal area of trees  
821 removed on the likelihood that a tree sustained harvesting damage. Trees considered in the  
822 analysis were those greater than 10 cm DBH prior to the implementation of the burning  
823 treatments. *P*-values are for the GAMM smooth terms. Solid lines show the fitted mean and  
824 polygons show the 95% confidence intervals. The mean value of basal area of timber  
825 removed ( $17 \text{ m}^2 \text{ ha}^{-1}$ ) was used to make predictions in (a).

826 **Figure 7** The effect of timber harvesting on relative growth rate (RGR) of living trees. The  
827 effect of the harvesting treatments are shown in panel (a). Bars show the fitted mean and  
828 whiskers show the 95% confidence interval. The effect of the percent of the original basal  
829 area that was felled is shown in panel (b). Solid lines show the fitted mean and polygons  
830 show the 95% confidence interval. Trees considered in the analysis were those greater than  
831 10 cm DBH prior to the implementation of the burning treatments. Predictions were made for  
832 *E. agglomerata*.

833 **Figure 8** The effect of timber harvesting on ingrowth i.e. the number of newly recorded trees  
834 >10cm DBH per 5 m radius plot. The effect of the harvesting treatments are shown in panel  
835 (a). Bars show the fitted mean and whiskers show the 95% confidence interval. The effect of  
836 the basal area (%) of the stand that was felled is shown in panel (b). Solid lines show the  
837 fitted mean and polygons show the 95% confidence interval.

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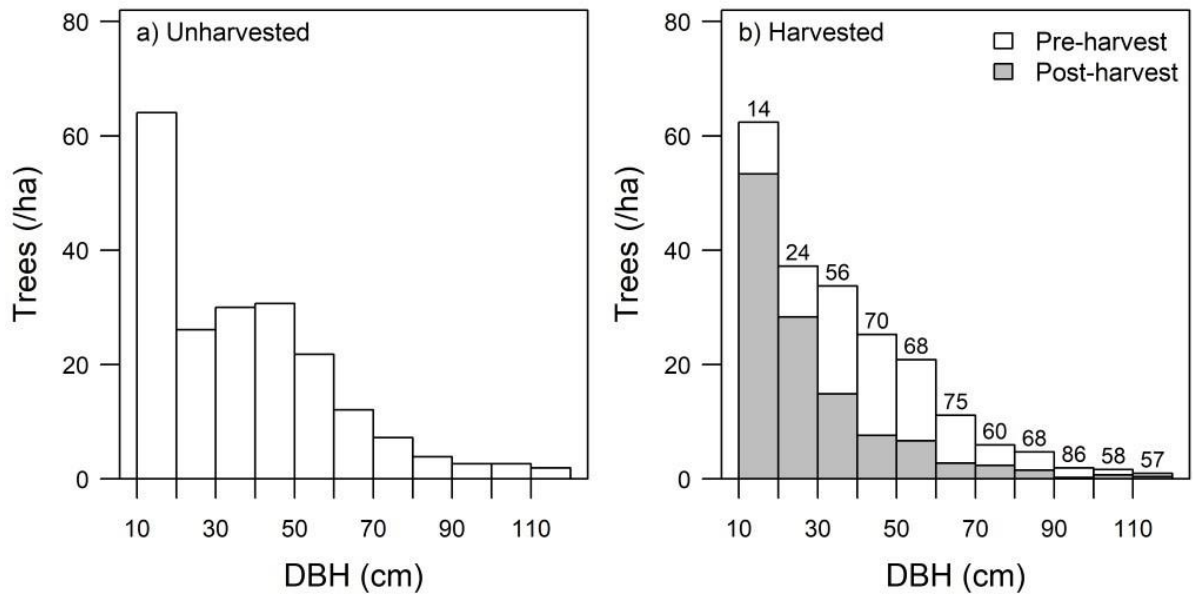
839 Figure 1



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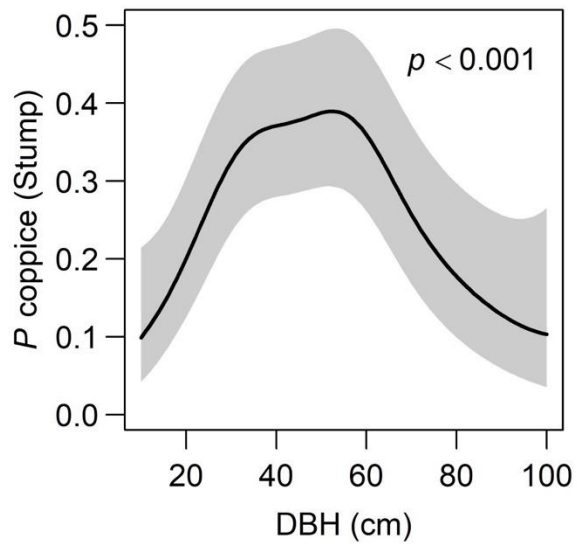


842 Figure 2



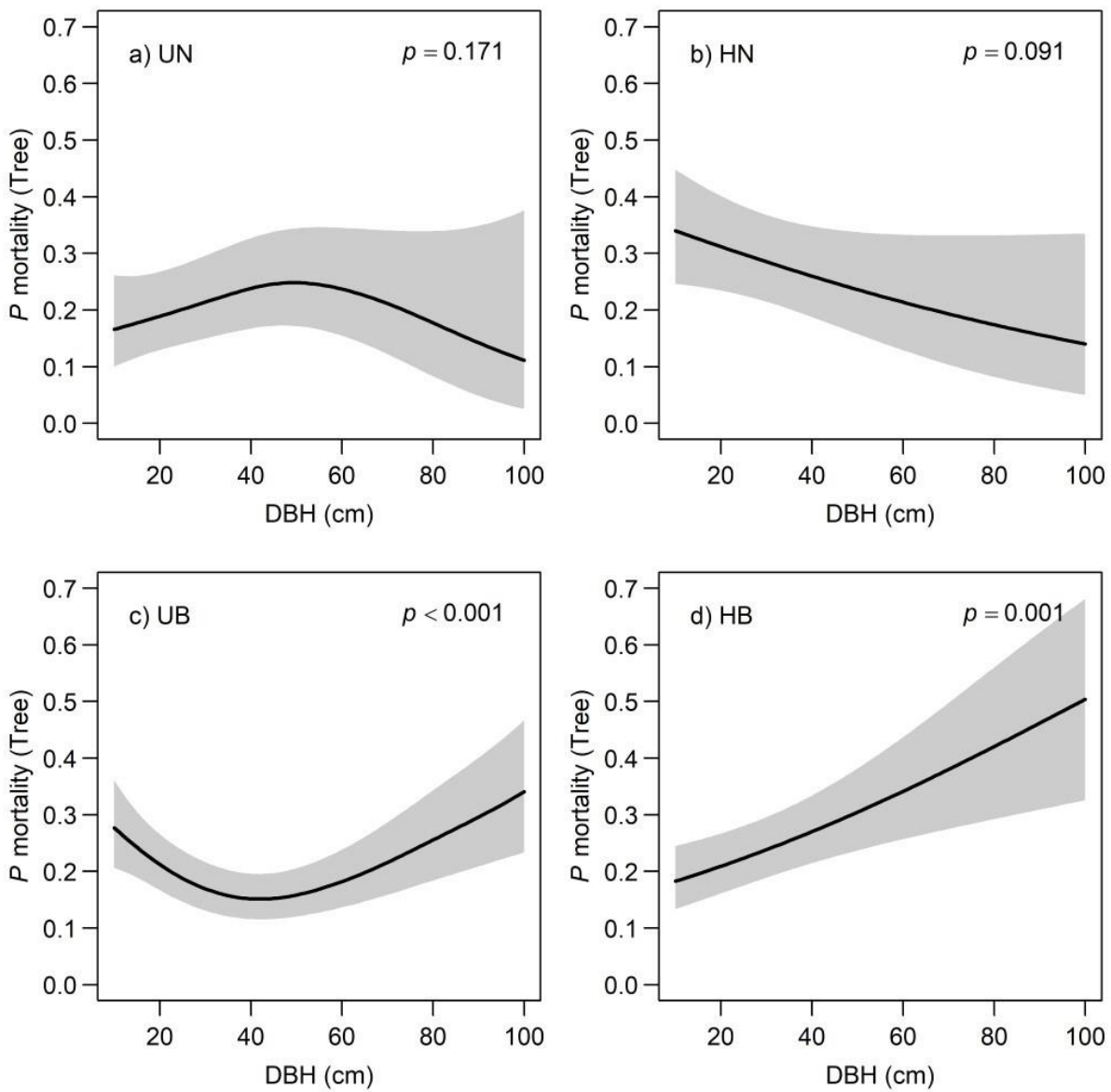
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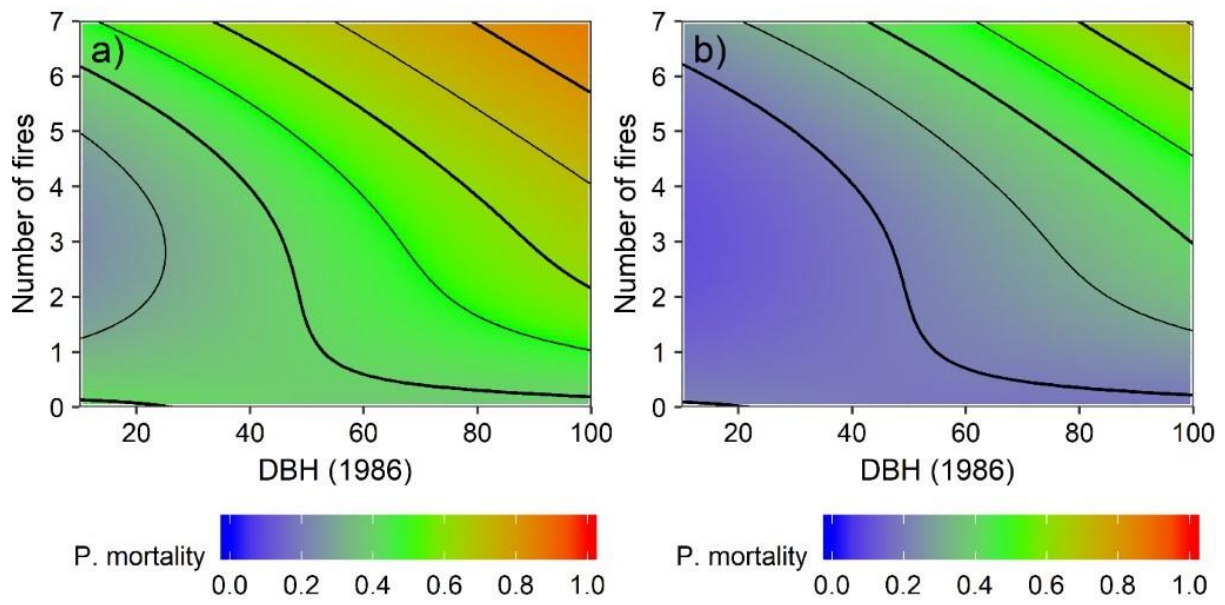
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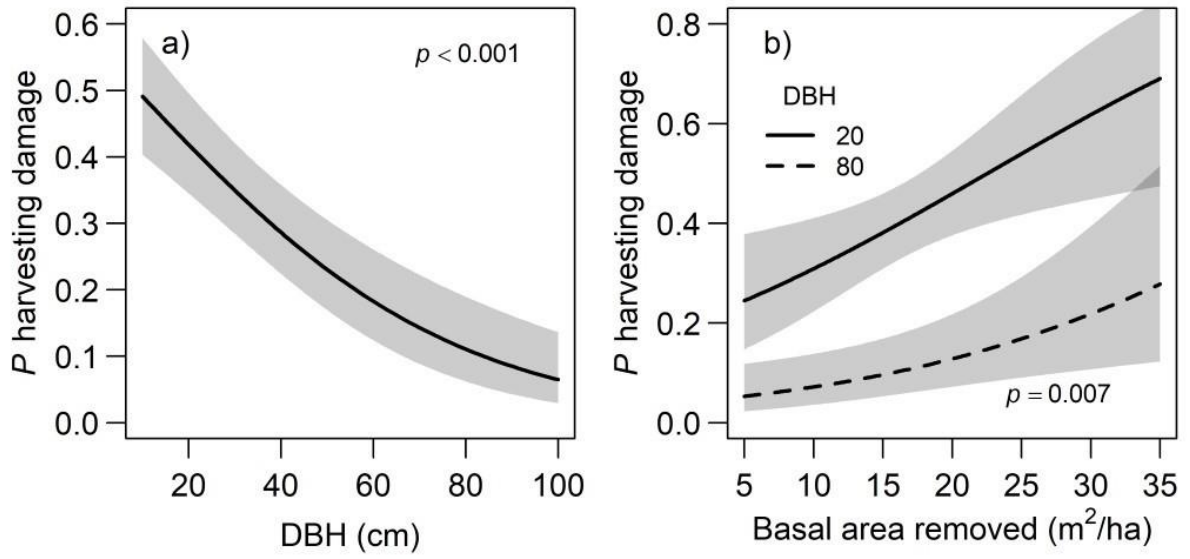
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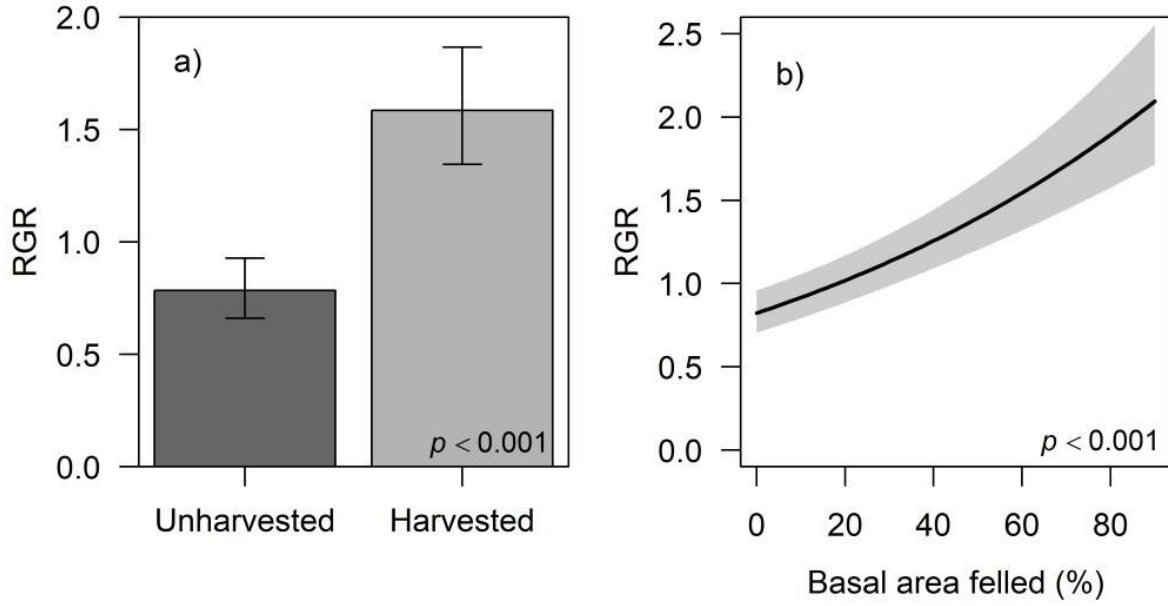
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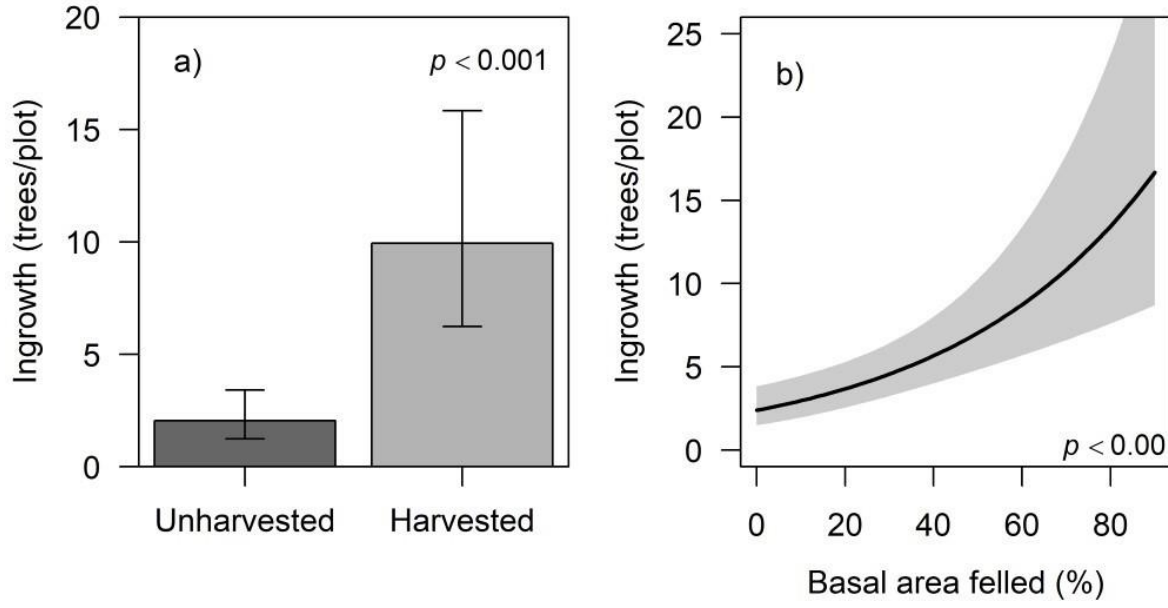
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860 Figure 7



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864 Figure 8



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