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Tree hollows and forest stand structure in Australian warm temperate *Eucalyptus* forests are adversely affected by logging more than wildfire

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ABSTRACT

Ecologically sustainable forest management aims to maintain biodiversity values within managed forest ecosystems. A key habitat component within Australian forest ecosystems are hollow-bearing trees which are crucially important for fauna species requiring tree hollows for diurnal shelter and nesting. The effect of disturbance regimes, in particular logging and fire, on hollow dynamics is poorly understood. The aim of this study was to determine the relationships between logging intensity and fire frequency on hollow abundance and forest stand structural attributes in two different eastern Australian *Eucalyptus* forest types.

We found that average stand tree diameter at breast height was negatively correlated to logging intensity. Logging intensity was negatively correlated with tree diameter at breast height (DBH), and the density of both hollow-bearing trees and hollows. Losses of hollow-bearing trees and hollows occurred through an interaction between logging intensity and fire frequency, resulting in an absence of recruitment of hollow trees. However in unlogged forest, fire was positively correlated to the density of hollows. Under a regime of frequent fire, in areas that have had some degree of logging activity, a net loss of hollows may occur. We recommend additional hollow recruitment trees be retained on logged sites in the future if no net losses of hollows are to occur in the future, or for wider unlogged buffers to be established adjacent to the cutting area.

1. Introduction

Tree hollows are semi-enclosed cavities that form in a range of tree species (Gibbons and Lindenmayer, 2003; Ranius et al., 2009; Remm and Lohmus, 2011). In the northern hemisphere, they are important for the conservation of a range of vertebrate fauna including woodpeckers (Hartwig et al., 2004; Roberge et al., 2008), flying squirrels (Hanski et al., 2000; Shafique et al., 2009; Pyare et al., 2010), microbats (Lucan et al., 2009) along with large forest owls (Saurola, 2009), and even invertebrate fauna (Jansson et al., 2009), many of which are threatened due to declines in the hollow resource. In Australia, tree hollows are a key habitat component for animals (Goldingay, 2009; Goldingay, 2012). They are required for breeding and shelter by more than 15% of the vertebrate fauna, in particular mammalian taxa (Gibbons and Lindenmayer, 2003). Many forest fauna species, such as forest owls and gliding possums, are obligate hollow users that depend on the presence of old, hollow-bearing trees for their continued occupancy, and these species are sensitive to forestry practices that reduce the availability of this resource (Kavanagh, 2004; Kavanagh et al., 2004; Lindenmayer et al., 2012; Lindenmayer et al., 2014; Eyre, 2007).

In Australian forests hollow formation is slow, with small hollows taking at least 80 years to form (Koch et al. 2008), while larger hollows, suitable for occupation by animals such as forest owls, may take as long as 220 years (Goldingay, 2012; Gibbons and Lindenmayer, 2003). Consequently, the hollow resource needs to be carefully managed within Australian forests. Within the northern hemisphere vertebrate fauna are known to excavate hollows (Bull et al., 1992; Hartwig et al., 2004). By contrast, forest vertebrates in Australian forests do not build hollows. Hollow formation is dependent upon termites gaining access and the subsequent fungal decay of internal heartwood (Mackowski, 1984); processes that may be facilitated by branch shear following wind (Harper et al., 2005) or fire (Inions et al., 1989).

Ecologically Sustainable Forest Management (ESFM) aims to maintain biodiversity in multi-use forests (Kotwal et al., 2008). ESFM relies on the identification of forest indicators including species, habitat attributes and processes that can act as sentinels for

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ecosystem health (Lindenmayer et al., 1999; Lindenmayer et al., 2000a; Lindenmayer et al., 2006). The status of forest habitat elements such as tree hollows are particularly important in this regard (Lindenmayer et al., 2006; Gibbons and Lindenmayer, 2003; Burgman, 1996; Ranius et al., 2009; Remm and Lohmus, 2011). In the fire-prone, *Eucalyptus* dominated forests of Australia, detailed insights into the effects of logging and fire regimes on the dynamics (i.e. losses and gains) of hollows are required in order to conserve vertebrate fauna and meet ESFM guidelines (Eyre, 2005; Goldingay, 2012). Logging preferentially removes large, usually older, rather than small (i.e. younger) trees and therefore reduces the number of trees of a suitable size and age for hollow formation (Lindenmayer et al., 2012; Lindenmayer et al., 2014). Such losses are additional to those that result from the natural collapse of existing hollow trees (Gibbons et al., 2010; Lindenmayer et al., 2012). Current logging practices in Australia require the reservation of hollow-bearing trees (HBT) and future recruitment trees during logging. The specified tree retention densities vary across different management jurisdictions (e.g. 1–10 HBT ha^{-1}; Anon, 1999; Gibbons and Lindenmayer, 2003). Within unlogged eucalypt forests, the density of HBTs generally ranges from 10 to 25 ha^{-1} (Kavanagh and Stanton, 1998; Ross, 1999; Gibbons et al., 2000a). Retention rates are therefore significantly lower than the naturally occurring density of hollow-bearing trees. In some forests up to 20 cutting cycles have occurred over the last 150 years, thus densities are often significantly lower than in unlogged or less frequently harvested forests (MacKowski, 1984, Forests NSW unpublished compartment histories).

Fires affect hollow dynamics by causing both losses and gains in Australian forests (Adkins, 2006). Substantial losses of hollow-bearing trees (i.e. 15–70%) have been measured across a range of eucalypt forest ecosystems as a direct consequence of fires (Inions et al., 1989; Murphy and Legge, 2007; Parnaby et al., 2010; Lindenmayer et al., 2012). By contrast, Munks et al. (2007), Taylor and Haseler (1993) and Whitford (2002) have each found that trees with fire-induced basal injuries were more likely to contain a hollow than trees without injuries in Tasmanian and Western Australian sclerophyll forests. In *Eucalyptus obliqua* forest in Tasmania, Koch et al. (2008) determined that hollow production in dry forests was faster than in mesic forests, potentially as a result of a regime of more frequent fire.

Research is lacking that considers the interaction between fire and logging regimes in influencing average tree size, basal area and resultant hollow abundance. In particular, differing combinations of fire frequency and intensity may alter the balance between loss of hollow-bearing trees and hollow formation. This balance is further affected by logging. The aim of this study was to determine the effects of fire frequency and logging intensity on forest structural attributes, tree hollows and HBTs in a warm temperate forest landscape in south-eastern Australia. We predicted that:

(1) The percentage of trees with tree basal injury will be positively related to fire frequency. This process is a precursor to tree collapse, and so has the potential to remove existing and potential HBTs.
(2) Average diameter at breast height (DBH) and stand basal area (BA) will be negatively related to logging intensity due to the preferential removal of large trees. This process will be amplified by higher frequencies of fire because fires also remove large trees.

We therefore predicted that the net effect of the processes in (1) and (2) may result in a reduction of hollows via the loss of large trees, as a result of increasing logging intensity and/or fire frequency. In particular, hollow loss under frequent fire may be compounded in the long term by an absence of recruitment due to a lack of suitably sized trees.

2. Method

2.1. Study area

This study was located in the contiguous *Eucalyptus* forests of the Dorrigo, Guy Fawkes and Chaelundi plateaux, New South Wales, Australia, approximately 500 km north of Sydney (Fig. 1). The climate of the study area is warm temperate, with between 1100 and 1950 mm of rainfall per annum with an autumn maximum (Bureau of Meteorology, 2012). The forest is extensive and mostly unfragmented with some losses due to clearing for agriculture situated predominantly along fertile flats of large rivers and streams. Two different forest types were selected for sampling. These were a wet sclerophyll forest (WSF) dominated by New England Blackbutt (*Eucalyptus andrewsii* ssp. *campanulata*), Sydney Blue Gum (*E. saligna*), Tallowwood (*E. microcorys*) and Silvertop Stringybark (*E. laevopinea*), classified as Forest Type 163 (Baur, 1989), and a dry sclerophyll forest (DSF) dominated by Spotted Gum (*E. henryii*), Grey Gum (*E. biturbinata*) and Northern Grey Ironbark (*E. siderophloia*), classified as Forest Type 74 (Baur, 1989).

Approximately 60 years of timber extraction has occurred in the study area; however, in recent decades significant areas have been converted from State Forests to conservation reserves in which logging is excluded. Selective logging, which targets large, straight trees for sawlogs, commenced on the study sites in the 1960s. Logging rotation intervals in the study area are currently between 15 and 30 years with most logged sites previously logged twice (Forestry Corporation NSW unpublished data). Riparian areas within the majority of sites have been logged though this practice ceased recently. Logged areas are usually subjected to a fuel reduction ‘slash’ burn to reduce coarse woody debris and to assist the establishment of *Eucalyptus* regeneration (Forestry Corporation NSW unpublished data).

The fire season is late winter to early summer (August to December). Major, intense fires (>50,000 ha) occurred in 1994 and also in 2000, 2001 and 2002. These were coincident with hot, dry, windy weather. Smaller, less intense fires (<1000 ha) are commonly lit by leaseholders (graziers) in most years but usually under milder weather conditions. Approximately 10% of the study area has remained unburnt since 1980.

2.2. Site selection

Digitised data layers were obtained for vegetation type (CRA vegetation; produced by NSW National Parks and Wildlife Service; NSW NPWS) which was supplemented by examining a forest type layer (Forests NSW; Baur, 1989) prior to field verification. Fire and logging histories were also obtained (Forests NSW for State Forest areas and NSW NPWS for NPWS areas). Logging records included the volume of timber removed and the year of each logging event (Forests NSW unpublished data). Fire history, usually for wildfires only, was reliable from 1980-present, but included only the perimeter of the fire and no data were available for fire severity or patchiness. Fire frequency was categorised for both the wet and dry sclerophyll forests as: (1) a regime of very infrequent fire (i.e. no recorded fire); (2) infrequent fire (1 fire since 1980), (3) frequent fire (2 fires since 1980), and; (4) very frequent fire (3 fires since 1980). The latter category occurred exclusively within the dry sclerophyll forest (Table 1).

Sites were selected so that treatment combinations were spread and inter-mixed. This occurred through ensuring that sites of the same logging intensity and fire frequency were dispersed away

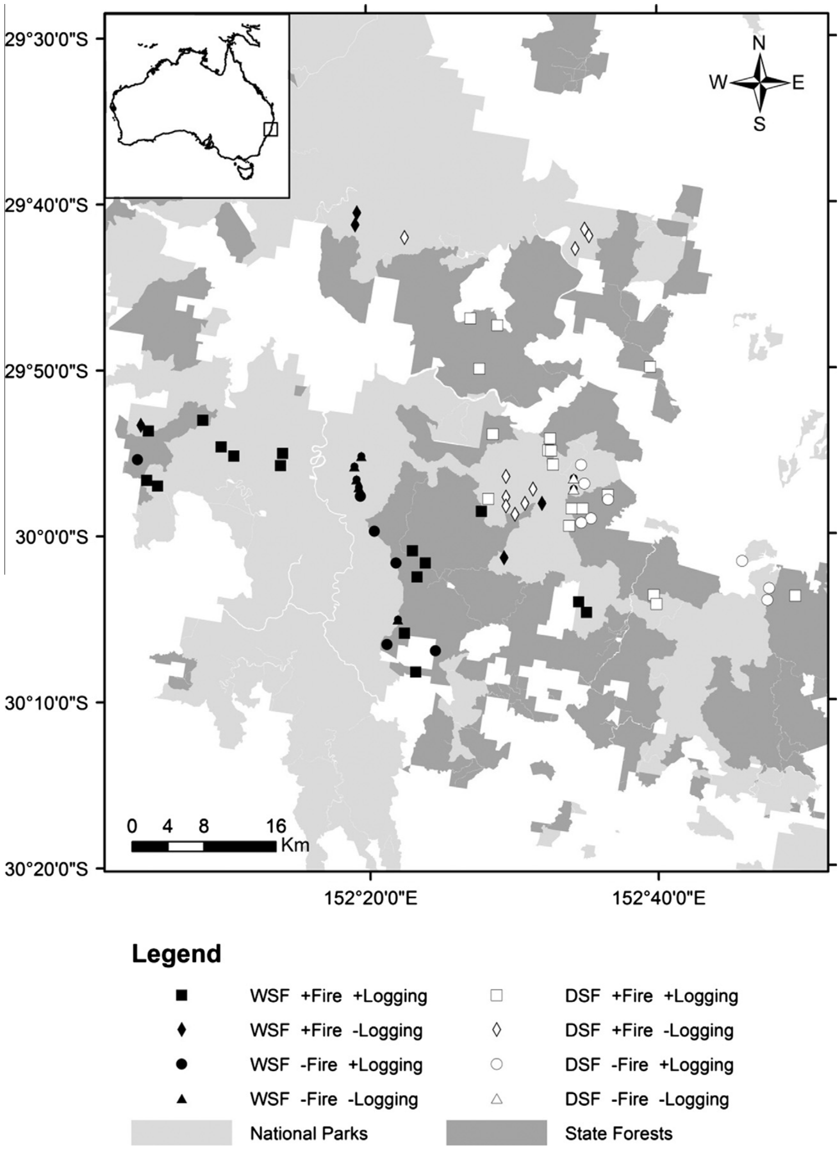

Fig. 1. Location of sites used in this study.

from one another, across the landscape (Fig. 1). The number of replicates within each fire frequency treatment was variable, as some treatments were uncommon and could not be heavily replicated (Table 1). Time since fire was standardised by sampling only areas burnt in 2000–2002 (8–10 years prior to sampling) within treatments that had at least one fire. Within each fire frequency category, logging intensity (i.e. total volume of commercial timber removed per hectare since 1960) was calculated from logging records held by Forests NSW. The logging intensity assessed in this way was relative; it was possible for large volumes of timber to have been removed from a wet sclerophyll forest but the residual volumes (basal area) may have been greater than in some unlogged dry sclerophyll forests. The characteristics of logged sites prior to logging were also unknown, i.e. some logged sites prior to the commencement of logging may have had larger trees, with a higher density of hollows than the unlogged sites.

2.3. Forest structure and hollow abundance sampling

Each site (a 500 m $\times$ 100 m quadrat) was located across a vehicular trail, at least 100 m from the nearest fire frequency boundary. The quadrat was divided longitudinally down the centre by the trail and at the 0, 100, 200, 300 and 400 m points on the trail a 50 m transect was established perpendicular to and on both sides of the trail. The overstorey vegetation was sampled within five metres on each side of the five transects, providing an overall sampling area of 0.5 ha per site. Average DBH, BA and stem density for trees larger than 15 cm DBH was calculated along all transects, with DBH being estimated to the nearest cm with a DBH tape measure. The presence of tree basal injury was determined by examining the base of each tree. A basal injury is a scar on the base of the tree where the bark has been removed and the internal timber of the tree has become damaged. The density per ha of hollows (at a height >2 m) and HBTs was calculated by examining all sides of every tree with binoculars. Observed cavities of depth $\geqslant$2 cm and widt $\geqslant$2 cm and having the potential to be used by small insectivorous bats as a roost were scored as hollows.

2.4. Data analysis

Analysis of variance (ANOVA) was used to examine the effects of fire frequency and logging intensity and their interactions using five measures of stand structure (basal injury, average DBH, basal area all trees DBH >15 cm, basal area all trees DBH >50 cm, stem

Table 1
The number of sites sampled in relation to differing disturbance regime combinations in warm temperate eucalypt forest landscapes (wet and dry sclerophyll forest; WSF and DSF). categories of logging intensity represent differing volumes of timber removal ($m^3\ ha^{-1}$) since 1960 (i.e. unlogged, 0; low logging, 1–40; high logging, >40). Categories of fire frequency are represented by the number of fires recorded since 1980. Time of last fire was standardised for all burnt sites (i.e. last burnt in 2001–2002).

Number of fires in previous 30 years	Unlogged		Low logging intensity		High logging intensity		
	DSF	WSF	DSF	WSF	DSF	WSF	TOTAL
0	2	5	5	4	0	4	20
1	5	1	6	3	0	4	19
2	3	4	6	5	0	2	20
3	6	0	4	0	0	0	10
TOTAL:	16	10	21	12	0	10	69

Table 2
Results of two factor analyses of variance (ANOVA) for relationship of fire frequency ([FF]; 0, 1, 2 and 3 fires since 1980; where last fire burnt in 2001/2) and logging intensity ([LI]; high [H]; low [L]; none [N]; representing volumes of recent removal of timber) on forest stand attributes (% trees with basal injuries; diameter at breast height [DBH]; stem density; total basal area of trees; basal area of large trees [>50 cm]) and hollow abundance (density of hollow-bearing trees [HBT]; density of hollows) in Wet Sclerophyll [WSF] and Dry Sclerophyll [DSF] forest. Significant results for main effects, interactions and post hoc comparisons of means (Tukey's Test) are indicated ($^*p < 0.05$; $^{**}p < 0.001$; $^{***}p < 0.0001$). For Tukey's test letters and numbers on separate lines indicate significant differences between variables.

Variable	Forest type	F ratio	FF	LI	FF*LI	Tukey's FF	Tukey's LI
Basal injury	DSF	[7,29] = 5.31	***	–	–	0 fire 123 fires	–
	WSF	[8,23] = 4.47	***	–	–	0 fire 123 fires	–
DBH	DSF	[6,62] = 17.4	–	**	–	–	N L
	WSF	[4,27] = 8.23	*	**	–	0 fire 1 fire	N L,H
Stem Density	DSF		–	–	–	–	–
	WSF	[8,23] = 2.49	–	**	–	–	N L H
Basal area all stems	DSF	[7,29] = 3.81	–	***	*	–	N L
	WSF	[6,22] = 4.06	–	**	–	–	N,L H
Basal area stems DBH > 0.5 m	DSF	[7,29] = 4.96	–	***	*	–	N L
	WSF	[8,22] = 3.12	–	**	–	–	N H
HBT density	DSF	[7,29] = 3.98	–	**	*		N L
	WSF	[6,23] = 4.27	–	**	–		N H
Hollow density	DSF	[7,29] = 5.67	–	***	*	–	N L
	WSF	[8,23] = 4.17	*	**	–	1 fire 2 fire	N L H

density) and two measures of hollow availability (hollow-bearing trees and total hollows). Fire frequency was represented by four categories (no fire, 1 fire, 2 fires, 3 fires; Table 1) and logging intensity was divided into three categories (unlogged, low intensity logging, high intensity logging; Table 1). Separate two-factor ANOVAs were performed for each forest type (i.e. wet and dry sclerophyll), with a more constrained range of fire frequency and logging intensity present for dry sclerophyll (Table 1). The Shapiro–Wilks test was used to examine the normality of response variables prior to analysis. This test indicated that all variables were normally distributed. Analyses were therefore performed on untransformed data in all cases. Post-hoc Tukey tests were used to examine differences among mean responses in appropriate treatment groups.

3. Results

3.1. Stand structural characteristics

The percentage of trees with basal injury was significantly affected by fire frequency in both forest types (Table 2). In DSF higher levels of injured trees were found in burned sites, irrespective of fire frequency prior to 2001/2, compared with unburned sites (Fig. 2, Table 2). Similarly, basal injury was positively related to fire frequency in WSF (Fig. 2, Table 2). DBH was significantly affected by logging intensity (Table 2). Unlogged sites had significantly larger mean DBH than most logged sites, for both forest types (Fig. 2, Table 2). Stem density was not significantly affected by either fire frequency or logging intensity in DSF but was significantly affected by logging intensity in WSF (Table 2). Sites with low levels of logging had significantly higher densities of tree stems than either unlogged sites or most sites logged at high intensity (Fig. 2).

Overall BA and BA of large trees (DBH >50 cm) were significantly influenced by the interactions between fire frequency and logging intensity in DSF (Fig. 3, Table 2). Sites unburned and unlogged had significantly higher mean BA than other sites irrespective of fire frequency and logging (Fig. 3, Table 2). A similar trend was found for BA of large trees in DSF (Fig. 2, Table 2). By contrast in WSF, BA and BA of large trees was significantly related to logging intensity only (Fig. 3, Table 2), with higher values

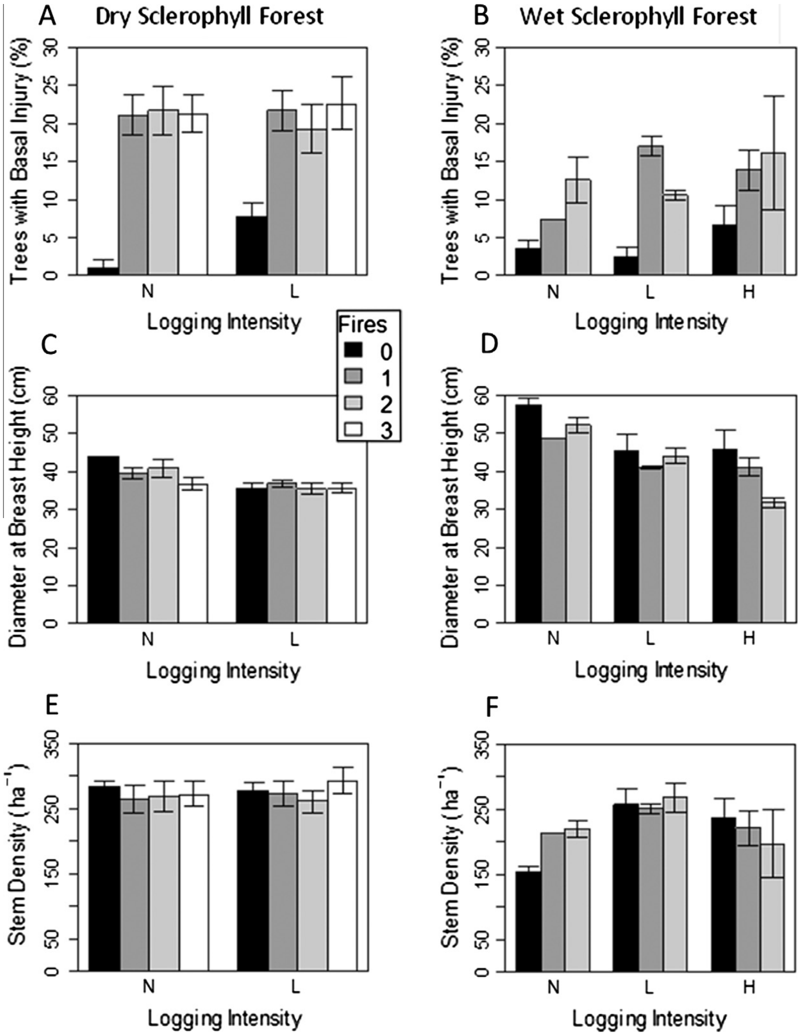

Fig. 2. Recorded forest stand attributes of eucalypt forest stands in relation to logging intensity and fire frequency. A; % trees with injuries in dry sclerophyll forest (DSF) and B; wet sclerophyll forest (WSF). C; diameter at breast height in DSF and D; WSF. E; stem density in DSF and F; WSF. Categories of logging intensity represent total volume of timber removed since 1960 (i.e. Unlogged, zero; Low logging, 1–40; High logging, >40 m^3 $ha^{-1}$of timber removed). Categories of fire frequency are represented by the number of fires recorded since 1980. Graphs show means and standard errors.

evident in the absence of logging (BA and BA of large trees) or under low intensity logging (BA large trees) compared with highest level of logging intensity (Fig. 3, Table 2).

3.2. Hollow-bearing trees and hollows

Both the density of HBTs and the density of hollows were significantly affected by fire frequency and logging intensity but the nature of these effects varied among forest types (Table 2). In DSF these measures of hollow density were significantly affected by the interactions between fire frequency and logging intensity (Table 2). Unlogged sites burnt at the highest frequency (i.e. 3 fires prior to 2001/2) had significantly higher densities of HBTs than logged sites, irrespective of fire frequency (Fig. 4, Table 2). Therefore in unlogged plots there was a positive trend in HBTs with increasing fire frequency while for logged sites the trend was negative. A similar trend was evident for hollow density in DSF (Fig. 4, Table 2). For WSF, the density of HBTs was inversely related to logging intensity, with highest levels of logging intensity containing significantly lower densities of HBTs compared with unlogged sites or sites logged at low intensity (Fig. 4, Table 2). The density of hollows in WSF also showed a significant inverse relationship with logging intensity, while fire frequency had a significant positive effect on hollow density, with sites burnt twice having significantly higher hollow density than sites burnt once or unburnt (Fig. 4, Table 2).

4. Discussion

Forest stand structure and hollow abundance were found to be significantly affected by the frequency of fire and the intensity of logging, in accordance with our hypotheses (Figs. 2–4). There were, however, differences in the patterns of response between the two forest types (WSF and DSF). Generally, increased intensity of logging decreased hollow and hollow-bearing tree densities in the manner we predicted (Fig. 4). Fire frequency however increased hollow and HBT densities in unlogged DSF contrary to predictions. A similar though smaller trend toward increased hollow density with increasing fire frequency was also evident in WSF (Fig. 4).

The stand structural characteristics that underpinned these trends in hollows also exhibited trends in relation to fire frequency and logging intensity that were consistent with predictions. Thus increasing intensity of logging was found to diminish the mean BA and mean Tree DBH, however contrasting effects of fire occurred for basal injury between the two forest types. In DSF

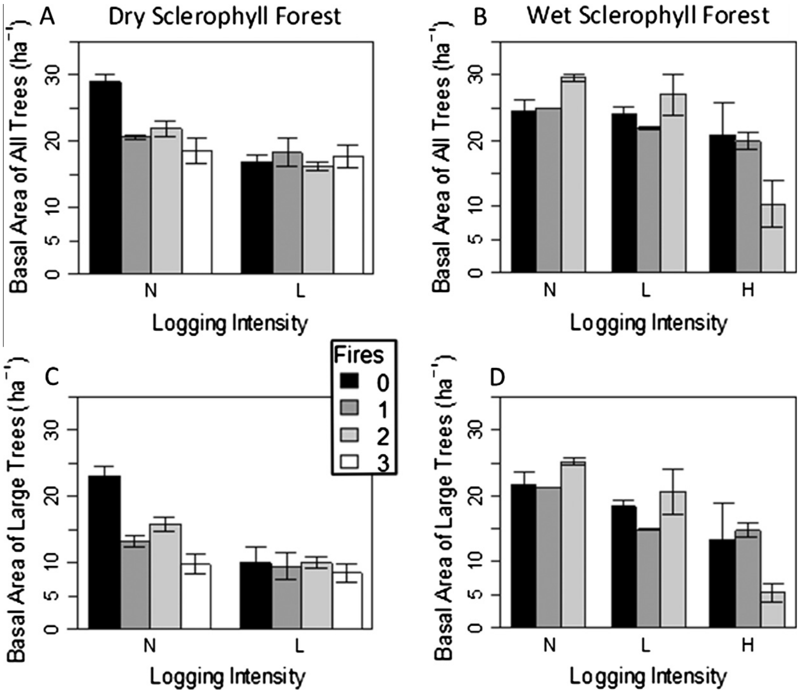

Fig. 3. Recorded basal area (BA) at various sites in relation to logging intensity and fire frequency. A; BA of all trees DBH > 15 cm in dry sclerophyll forest (DSF) and B; basal area of all trees DBH > 15 cm in wet sclerophyll forest (WSF). C; basal area of large trees (i.e. DBH > 50 cm) in DSF and D; WSF.

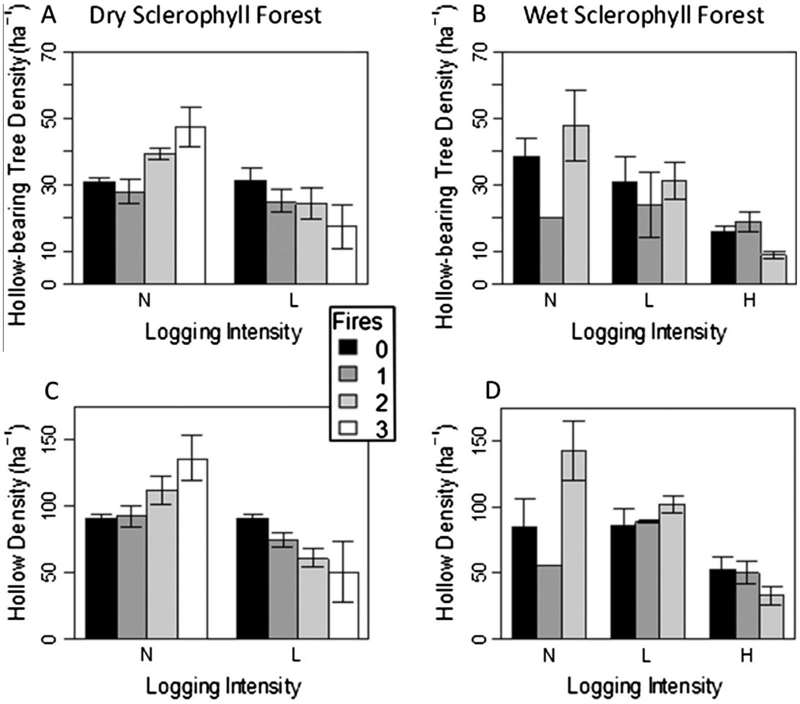

Fig. 4. Recorded hollow-bearing tree density (HBTs) and hollow density in relation to fire frequency and logging intensity in dry sclerophyll forest (DSF); A: HBT density in dry sclerophyll (DSF) and B; wet sclerophyll forest (WSF); C; hollow abundance in DSF and D; WSF. Bars without error bars are either based on a single sample or two samples with very similar values (<0.5% difference).

any occurrence of fire increased the proportion of trees that contained basal injury, with similar levels of injury occurring at sites subjected to one or more fires, whereas increasing fire frequency tended to result in higher levels of basal injury in WSF (Fig. 2). The latter result may have been due to the collapse and loss of injured trees in WSF. The net outcome of these processes was a general tendency for highest abundance of hollows (i.e. density of HBTs and hollows) in unlogged, frequently burnt sites (Fig. 4).

The trends in hollow abundance within the frequently burnt sites, as a function of logging intensity (Fig. 4) were consistent with the hypothesis that logging removed large HBTs and smaller trees that may have been prone to injury. The net effect of these disturbances on the balance between gains and losses of hollows was, however, variable. Thus logged but frequently burnt DSF sites had the lowest levels of HBT and hollow density, whereas unlogged but similarly burnt sites had the highest abundance of hollows (Fig. 4). As a result, DSF sites showed a pronounced divergence in hollow abundance in response to logging and fire (i.e. significant interactions between logging intensity and fire frequency Table 2, Fig. 4) indicating that logging intensity and fire frequency have roughly equal but opposite effects on hollow abundance (Fig. 4). By contrast, in WSF the negative effect of increasing logging intensity on hollow abundance outweighed the positive effect of increasing fire frequency (Fig. 4). The contrast in relative strength of the fire frequency effect between DSF and WSF may, in part, reflect the consequences of higher fire frequencies in DSF compared with WSF sites, and also the greater intensity of logging per logging event that usually occurred in WSF.

The mix of tree species in DSF or other factors may predispose hollow abundance to be more sensitive to the effects of fire frequency. For example, in DSF there were higher proportions of *C. henryii*, *E. biturbinata* and *E. acmenoides* than in WSF. These species may have rough bark characteristics that make them more prone to be predisposed to fire-related injury. Another possibility is that growth rates may be slower in the drier and warmer sites occupied by DSF compared with WSF, as has been shown in studies elsewhere (Wormington and Lamb, 1999). This could slow the transition of smaller trees to the larger size classes. If so, this would have the effect on the one hand of increasing the susceptibility of smaller trees to basal injury from fire, but on the other hand render such trees vulnerable to collapse from repeated fires, prior to hollow development. Slower growth rates may also predispose injured trees to removal by logging before hollows become fully developed. These hypotheses require further testing with appropriate observations or experiments. Currently studies that measure rates of tree collapse as a result of fire in Australian eucalypt forest are lacking and are mainly confined to dry forest types (e.g. Inions et al., 1989; Parnaby et al., 2010; Whitford and Williams, 2001). Further examination of this critical process in a wide range of forest types is required.

Overall, the results suggest that increasing fire frequency does not limit hollow abundance and the possible availability of habitat for arboreal animals in these forests. However, the suitability for occupation of the fire produced hollows requires further investigation. While fire frequency undoubtedly removes trees with existing hollows or candidate trees which possess pre-existing injuries, such losses appear to be outweighed by the overall creation of injuries. Provided that these trees remain (i.e. they are not removed through logging, and they do not fall over) then hollow abundance was positively related to fire frequency (Fig. 4). Thus trends in availability of hollows in relation to fire shown in this study may therefore be only broadly indicative of the availability of habitat for arboreal animals.

The results indicate the importance of understanding and documenting the net outcome of these complex processes across cycles of multiple fires. Existing studies have largely concentrated on only one or two aspects of the processes governing hollow loss or gain (i.e. injury) in response to single fires (e.g. Inions et al., 1989; Gibbons et al., 2000b; Whitford and Williams, 2001; Parnaby et al., 2010). While such insights are valuable, they need to be understood in the context of a complete demography of hollows, over time in response to multiple fires. This study provides some initial insights into the problem.

These results are consistent with other studies that show that logging is likely to cause a net decline in hollow abundance (e.g. Gibbons et al., 2000b; Eyre et al., 2010). Overall, increasing logging intensity may match or outweigh the positive effect of fire frequency on hollow abundance in both forest types (Fig. 4). The effects of logging intensity on BA and DBH are consistent with the assumption that logging removes both large tress (i.e. likely to be hollow-bearing) and smaller hollow-tree recruits (Figs. 2 and 3). Crucially our results suggest the changes to the frequency of fire cannot overcome the deleterious effect of logging on hollow abundance. This has important implications for management. Further analyses based on hollow size classes, in relation to different disturbance regimes is required, as the losses or gains of hollows may have varying effects on different fauna groups.

This study has focussed on habitat availability (i.e. hollow abundance) for arboreal mammals in relation to disturbance regimes. Arboreal marsupials occurring in these forests include the Greater Glider *Petauroides volans*; Kavanagh et al., 1995; Eyre, 2006) which is a major prey species for threatened forest owl species (Kavanagh, 1988) and the threatened Spotted-tailed Quoll *Dasyurus maculatus*; Glen and Dickman, 2006), as well as threatened arboreal marsupial species such as the Yellow-bellied Glider *Petaurus australis*; Kavanagh et al., 1995). While habitat availability, including tree hollows, is crucial for these animals (Goldingay, 2012), disturbance regimes will also have direct effects on these species through processes which affect animal mortality and the capacity for animals to reproduce successfully. Other habitat effects, such as changes to vegetation composition and structure as a result of differing disturbance regimes (Tasker and Bradstock, 2006; Penman et al. 2008, 2011) may also influence populations of these animals. Such effects need to be understood if sustainable management strategies are to be developed. This study did not differentiate between size classes of hollows. Hollow size has been shown to be important for a number of species (Gibbons and Lindenmayer, 2003; Goldingay, 2012), thus further studies are required to determine these effects on different species of hollow-dependent fauna.

This study did not consider the influence of fire severity on losses and gains to the hollow resource. Variation in fire severity may influence the rate of basal injury (contributing to tree collapse), branch destruction (hollow destruction) and/ or fire induced branch/ trunk injury (hollow production). In particular, high intensity fires may increase rates of these processes, though Parnaby et al. (2010) measured substantial losses of hollow-bearing eucalypts in a low intensity prescribed fire. Most fires that affected our study sites were unplanned fires, though in many instances these stem from prescribed fires set by local graziers (Binns, 1995). The intensity of these fires is likely to be highly variable, as with most unplanned fires in *Eucalyptus* forests (Bradstock, 2008; Bradstock, 2010) in response to variation in weather, terrain and fuel variations, though it is likely that a subset of the fires affecting the study sites were of high intensity. Thus the results may not reflect what would happen if fires were either of consistently low or high intensity. Further work is required to elucidate effects of fire intensity in conjunction with fire frequency to provide a more complete understanding of the consequences of differing fire regimes for hollow abundance. The scope for active use of fire to maintain an appropriate regime for hollow formation may be constrained by this lack of understanding.

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