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Wildfire and Climate Impacts Tree Hollow Density in a Temperate Australian Forest

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Abstract: Tree hollows are an important landscape resource used by fauna for shelter, nesting, and predator avoidance. In fire-prone landscapes, wildfire and climate may impact hollow dynamics; however, assessments of their concurrent impacts are rare. We conducted a field survey at 80 sites in the Sydney Basin bioregion (Australia) to understand how fire frequency, fire severity, mean annual temperature, and mean annual precipitation concurrently impacted the site-density of small- (<5 cm entry width), medium- (5–10 cm entry width) and large-size (>10 cm entry width) tree hollows and tree basal scars (which mediate hollow formation via invertebrate access to heartwood), when tree-size and dead/live status were considered. A unimodal relationship occurred between medium- and large-sized hollow densities and fire frequency and severity, respectively, with hollow densities greatest at intermediate frequencies/severities. Increases of 1.82, 1.43, and 1.17 hollows per site were observed between the 1 (reference) and 2, 2 and 3, and 3 and >3 fire frequency categories. Increases of 1.26, 1.75 and 0.75 hollows per site were observed between the low (reference) and moderate, moderate and high, and high and very high fire severity categories. Fire severity was also positively associated with basal scar density, with increases of 2.52, 8.15, and 8.47 trees per site between the low (reference) and moderate, moderate and high, and high and very high categories. A weak positive and stronger negative association was observed between mean annual temperature and small-sized hollow and basal scar density, respectively. Dead and medium-sized tree density was positively associated with medium-sized hollow and basal scar tree density, respectively. Collectively, our results suggest that wildfires, and in some cases climate, have diverse and size-specific impacts on tree hollow and basal scar density. Our results imply that fire regimes that allow for moderately severe wildfire will promote larger-sized tree hollows, which are a limiting resource for many fauna species.

Keywords: climate; fire frequency; fire severity; tree hollow; wildfire; Sydney Basin bioregion; Australia

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1. Introduction

Tree hollows are semi-enclosed cavities within the stems of trees. In American and Eurasian forests, woodpecker birds physically excavate hollows in synergy with or independently from the actions of fungi and invertebrates [1,2]. In Australian forests, however, termites and fungi are the dominant hollow-forming taxa [3]. These species enter the tree heartwood via external bark lesions and scars, and hollows form when decay reaches the outside surface of stems or when stems are broken by exogenous processes (e.g., wind or fire). A high proportion of tree hollows occur in large, old, and often dead or senescing trees where the proportion of heartwood to sapwood (and hence the potential area of hollowing) is high [4]. For example, tree ages > 100 years are required to form hollows in Douglas-fir (*Pseudotsuga menziesii*) trees in western North America [5] and tree ages of 80 to >200 years are often required to form small- and large-sized hollows, respectively, in sclerophyllous forests of eastern Australia [3,6]. Because of the long time-periods required to form hollows, the re-establishment of hollow "stocks" in landscapes impacted by severe disturbance events may take decades or centuries.

Hollows are an important habitat resource used by fauna for shelter, nesting, and predator avoidance. Globally, >350 mammal species [7,8], 9%–18% of bird species [9,10], and up to 30% of all vertebrate species use hollows in some capacity [3,11]. Although hollows are utilised by many species, their usage is both size- and context-dependant [12,13]. For example, species with relatively large bodies may be limited to hollows with wide openings; however, these same species may also require deep hollows for specific purposes, such as nesting. Similarly, smaller-bodied species may temporally exploit both large- and small-sized hollows, but may require narrow entry widths for nesting and predator avoidance. Given this, the availability of suitable hollows is a key factor limiting population density for many fauna [10,14,15], especially in Australian forests where most fauna do not construct their own hollows [3,15,16]. Therefore, knowledge of tree hollow densities and size distributions within forests is required for the targeted conservation of hollow-dwelling fauna.

Wildfires are a common and recurrent disturbance in temperate forests [17,18]. In these fire-prone landscapes, vegetation and tree hollow dynamics have been hypothesised to be concurrently influenced by different aspects of the short- and long-term fire regimes [19,20].

Fire regimes characterised by frequent and severe fires may increase rates of tree hollow formation and occurrence via multiple direct and indirect pathways. For example, wildfires may impact tree hollows directly via tree damage (i.e., through basal or aerial fire scars) that enables the entry of fungi and invertebrates into the heartwood [21,22], by promoting the decomposition of anti-fungal and invertebrate-deterring chemicals in wood [19,23], by increasing the risk of stem collapse which exposes pre-hollowed sections of the stem [19,24], or may further excavate pre-existing hollows through burning [25]. Frequent severe wildfires may also indirectly facilitate hollow formation by moderating tree death (i.e., many hollows occur in large dead trees; [4]), but may alternatively reduce hollow occurrence by reducing the density of larger live trees where most hollows occur (i.e., by felling trees; [26]). Previous studies have investigated the impacts of different aspects of fire regimes on hollow occurrence, such as fire frequency [27], fire severity [26], time-since-fire, and inter-fire interval [28]. However, few have investigated the concurrent impacts of different aspects of the fire regime on size-specific hollow density, or attempted to formally test indirect effects pathways impacting hollow density.

Along with fire disturbance, climate influences hollow occurrence and hollow-forming processes by affecting rates of tree growth (i.e., trees must reach a certain size before forming hollows), tree and tree hollow decomposition, and/or by selecting for specific vegetation assemblages or vegetation traits that promote hollow formation [8,29,30]. Climate may also indirectly influence hollow density by promoting specific fire regimes, which influence rates of hollow formation (see above).

In temperate forests of eastern Australia, temperature, precipitation, and soil water retention are thought to influence hollow density [29–31]. For example, hollow density follows a unimodal relationship with moisture retention, rainfall, and solar radiation during summer in the Northern Tablelands bioregion of New South Wales, Australia [29], and tree biomass/size (which is an appropriate proxy for hollow density because most hollows form in larger trees) is highest in cool–dry landscapes of south-east Australia which facilitate tree growth but not decomposition [32,33]. Future climate projections for the region suggest increases in mean annual temperature (e.g., 1.9 °C in the Sydney Metropolitan area) and site-specific increases or decreases in mean annual precipitation and water retention by 2070 [34]. Therefore, knowledge of tree hollow responses to climate will be important for the current and future conservation of hollow-dwelling fauna.

Here, we conduct a landscape-scale field survey at 80 biophysically comparable sites in the Sydney Basin bioregion, Australia, to investigate associations between important aspects of the fire regime (fire frequency, severity), climate (mean annual precipitation, temperature), and size-specific hollow density, when tree density and dead/live status is accounted for. We additionally assess associations between wildfire, climate, and basal scarring, which is a key hollow-forming process (i.e., by allowing hollow-forming taxa access to tree heartwood). Our specific hypotheses were that:

(1) Tree hollow density will be highest at intermediate fire frequencies and severities which allow for hollow formation but do not reduce large tree density;
(2) Basal scarring will be greatest at high fire frequencies and severities which promotes tree damage;
(3) Tree hollow density and basal scarring will be greatest in warm, moist climates which facilitate hollow formation via decomposition.

2. Materials and Methods

2.1. Study Area

The study was conducted in dry sclerophyll forests of the Sydney Basin bioregion of New South Wales, Australia (Figure S1). The area is dominated by Hawkesbury and Narrabeen group sandstone plateaux and ridges with sandy soils. The climate is temperate with mean annual temperature ranging from 11.5 to 16.6 °C and mean annual precipitation ranging from 783 to 1410 mm at the study sites [35]. Both vary in latitude and distance from the coast (Figure S1). *Eucalyptus*, *Corymbia*, and *Angophora* trees (*E. piperita*, *C. gummifera*, *E. sparsifolia*, *E. sieberi*, *C. eximia*, and *A. bakeri*) are the dominant overstorey canopy species and a variety of shrubs and herbs from, but not limited to, the Proteaceae, Fabaceae, Casurinaceae, and Myrtaceae families are the dominant understorey species. Wildfires are common within the region and fire-return intervals are usually between 10 and 30 years [36].

2.2. Site Selection

Field surveys were conducted at 80 sites located on flat or gently sloping ridgetops with sandy and shallow soils that fell within Keith's [37] "shrubby" dry sclerophyll forest vegetation sub-formation (distance between sites: mean = 52.58 ± SD 29.29 km, range = 0.10–135.76 km; Figure S1). Overall, 5 to 14 sites (here defined as a 50 m × 20 m quadrat within which all field surveys were conducted) were located within 8 discrete "study regions". The study regions represented near orthogonal combinations of mean annual temperature (mean values for sites within three broadly similar categorical groups: 12.3 °C, 15.0 °C, 16.1 °C) and precipitation (mean values for sites within three broadly similar categorical groups, 858 mm, 1033 mm, and 1325 mm; Figure S1 and Box S1; [35]). All sites were last burnt by wildfire in 2001 or 2002.

Within each study region, sites were stratified between four fire frequencies (1, 2, 3, or >3 fires (4 fires: 12 sites; 5 fires: 1 site) between 1972 and 2016) and severity (see below) categories (Table 1). Orthogonal replication of sites across the climate and fire regime combinations was not always possible due to a lack of fire frequency and severity categories in some regions; however, replication was still broadly similar across the climate and fire combinations. The climate data was obtained from BIOCLIM surfaces interpolated from local weather station data (0.86 km × 0.86 km resolution; [35]) and a comprehensive fire history of the study area was provided by the New South Wales Department of Planning, Industry and Environment.

The severity of the 2001 and 2002 wildfires was mapped by Hammill and Bradstock [38] using Landsat7 images (30 m resolution) taken before and after (first cloud free day) fires and the Normalised Difference Vegetation Index. The Normalised Difference Vegetation Index measures the 'greenness' of vegetation, and the comparison of images before and after fires measures the loss of greenness as fire severity. Using these maps, we assessed fire severity at our sites as either low (surface fire, tall shrubs and the tree canopy unburnt), moderate (low shrub fire, tall shrubs scorched but the tree canopy unburnt), high (shrub fire, all shrubs burnt, and the tree canopy scorched), or very high (tall shrub fire, sub-canopy consumed, and the tree canopy burnt).

Table 1. Site replication within four fire frequencies (1, 2, 3 or >3 wildfires between 1972 and 2016) and fire severity (low, moderate, high, or very high during the 2001/2002 wildfires) categories stratified between three mean annual precipitation (mean within-group values: 858 mm, 1033 mm, and 1325 mm) and mean annual temperature (mean within-group values: 12.3 °C, 15.0 °C, and 16.1 °C) categories.

Climate Variable	Fire Frequency					Fire Severity				
	1	2	3	>3	Total	Low	Moderate	High	Very High	Total
Mean annual precipitation										
858 mm	0	13	9	4	26	14	8	2	2	26
1033 mm	4	17	9	8	38	5	12	14	7	38
1325 mm	5	4	6	1	16	1	2	4	9	16
Total	9	34	24	13	80	20	22	20	18	80
Mean annual temperature										
12.3 °C	5	12	8	4	29	4	4	9	12	29
15.0 °C	2	11	8	4	25	10	6	3	6	25
16.1 °C	2	11	8	5	26	6	12	8	0	26
Total	9	34	24	13	80	20	22	20	18	80

2.3. Sampling Protocol

At each site, the number of small- (2–5 cm minimum entry width), medium- (5–10 cm minimum entry width) and large-sized (> 10 cm minimum entry width) tree hollows was counted within a 50 m × 20 m quadrat via active searches [3,4,12]. Only trees with a DBH > 20 cm were considered because hollows were rarely seen in trees with a DBH < 20 cm. Tree hollows were defined as any tree cavity > 2 m from the ground with a minimum depth of 5 cm. The size of all hollows was assessed visually by the same experienced observer (CEG; up to 30 min per survey) [12]. We initially preferred the double-sampling approach suggested by Harper [29]; however, logistical constraints on the field surveyed negated its use here. Although ground-based surveys can misidentify or fail to detect some tree hollows, they are a reliable method for assessing relative hollow density across sites within similar landscape types [6]. The small-, medium-, and large-sized hollows were counted at each site and expressed as a density per 0.1 ha.

Hollow density was positively correlated with hollow bearing tree density across sites, and, therefore, the variable of small- (R = 0.92), medium- (R = 0.96), large- (R = 0.93) sized hollows were interchangeable.

At each site, all standing live and dead trees with a diameter over-bark at 130 cm height (henceforth DBH) > 20 cm were counted within the 50 m × 20 m quadrat and the presence of basal scars was noted from live trees. Only standing dead trees > 3 m height above the ground were included, and ground-lying logs and coarse woody debris were not assessed. A basal scar injury was defined as any basal bark lesion extending through the sapwood greater than 1 cm in width within 10 cm from the ground. If trees had more than one stem originating from the same sub-surface lignotuber, DBH measures were taken from the largest stem and these trees were considered as individuals. The number of live trees with a DBH between 20 and 50 cm (medium trees) and > 50 cm (large trees), dead trees with a DBH > 10 cm, and trees with basal scars (basal scars) were counted at each site and expressed as a density per 0.1 ha.

2.4. Statistical Analysis

Separate generalised linear models were used to understand how the site-density of small-sized, medium-sized, and large-sized tree hollows and basal scars (dependant variables) varied with fire frequency, fire severity, mean annual precipitation, mean annual temperature, medium-sized tree density, large-sized tree density, and dead tree density (predictor variables). A negative binomial distribution was used for all models. Fire frequency and severity were treated as ordinal factors and all other variables were treated as continuous. All continuous variables were standardised (mean 0 ± 1 SD) prior to analysis and correlations between all predictor variables were identified as <0.5. The standardised model coefficient estimates and *p*-values (alpha = 0.05) were used for model inference. Pseudo r^2 values were used to assess model fit. Biologically relevant interactions were originally considered in candidate models, however, were shown to be non-significant, and therefore not considered (Box S1).

Spatial autocorrelation was not present within the residuals of the generalised linear models (Figure S2).

Analyses were conducted in the statistical program R (version 4.0.3); Pseudo r^2 values were calculated using the "ncf" package [39].

3. Results

On average, 2.71 (±SD 2.55) small-, 2.81 (±SD 3.19) medium-, and 1.50 (±SD 1.97) large-sized tree hollows were observed at sites. Across all sites, 82.55% and 17.44% of hollows occurred in live and dead trees, respectively. On average, 8.88 (±SD 7.85) live trees with basal scars were detected per site. On average, 18.37 (±SD 7.09) medium- and 2.27 (±SD 2.09) large-sized live trees and 0.92 (±SD 1.21) dead trees were observed at sites.

A significant positive association was observed between small-sized hollow density and mean annual temperature and medium-sized hollow density and dead tree density (Table 2, Figure 1a,c). Significant unimodal associations were also observed between medium-sized hollow density and fire frequency and large-sized hollow density and fire severity (Table 2, Figure 1b,d), with densities greatest at intermediate frequencies/severities. On average, medium-sized hollow density increased by 1.82, 1.43, and 1.17 hollows per site between the 1 fire frequency category when compared with the 2, 3, and > 3 categories, and large-sized hollow density increased by 1.26, 1.75, and 0.72 hollows per site between the low fire severity category when compared with the moderate, high, and very high categories.

Table 2. Coefficient estimates (C.E. mean ± SE) and *p* values from generalized linear models testing relationships between (a) small-, (b) medium-, and (c) large-sized tree hollow density and (d) basal scar density and fire frequency, fire severity, mean annual precipitation, mean annual temperature, medium-sized tree density, large-sized tree density, and dead tree density. * shows significant effects where alpha < 0.05. For the categorical variables fire frequency and severity, C.E. are shown as comparisons between a reference group (1 fire frequency, low fire severity) and the other groups (e.g., 2, 3, and 4 fire frequency categories).

Variable	(a) Small-Sized Hollow		(b) Medium-Sized Hollow		(c) Large-Sized Hollow		(d) Basal Scar	
	C.E.	*p*	C.E.	*p*	C.E.	*p*	C.E.	*p*
Fire frequency: 1–2	0.230 ± 0.309	0.457	0.048 ± 0.334	0.885	−0.493 ± 0.325	0.130	0.104 ± 0.147	0.478
1–3	−0.112 ± 0.269	0.678	−0.564 ± 0.285	0.048 *	0.101 ± 0.292	0.727	−0.077 ± 0.134	0.561
1 ≥ 3	−0.003 ± 0.196	0.987	0.065 ± 0.202	0.745	0.079 ± 0.234	0.733	−0.078 ± 0.099	0.429
Fire severity: L-M	−0.065 ± 0.269	0.809	0.229 ± 0.273	0.403	0.900 ± 0.347	0.009 *	0.286 ± 0.140	0.041 *
L-H	0.114 ± 0.239	0.632	−0.126 ± 0.241	0.601	−0.703 ± 0.287	0.014 *	−0.058 ± 0.124	0.639
L-VH	−0.168 ± 0.210	0.423	0.064 ± 0.214	0.762	0.088 ± 0.227	0.698	−0.116 ± 0.105	0.272
Mean annual precipitation	0.118 ± 0.139	0.396	−0.171 ± 0.147	0.245	−0.147 ± 0.168	0.381	0.049 ± 0.063	0.433
Mean annual temperature	0.409 ± 0.170	0.016 *	0.205 ± 0.173	0.237	0.287 ± 0.180	0.111	−0.337 ± 0.081	<0.001 *
Medium-sized tree density	0.169 ± 0.142	0.235	−0.155 ± 0.148	0.293	0.155 ± 0.160	0.333	0.384 ± 0.072	<0.001 *
Large-sized tree density	0.192 ± 0.134	0.153	0.047 ± 0.136	0.727	0.288 ± 0.152	0.057	0.0567 ± 0.065	0.387
Dead tree density	0.132 ± 0.110	0.230	0.266 ± 0.106	0.012 *	0.209 ± 0.120	0.081	−0.019 ± 0.068	0.775

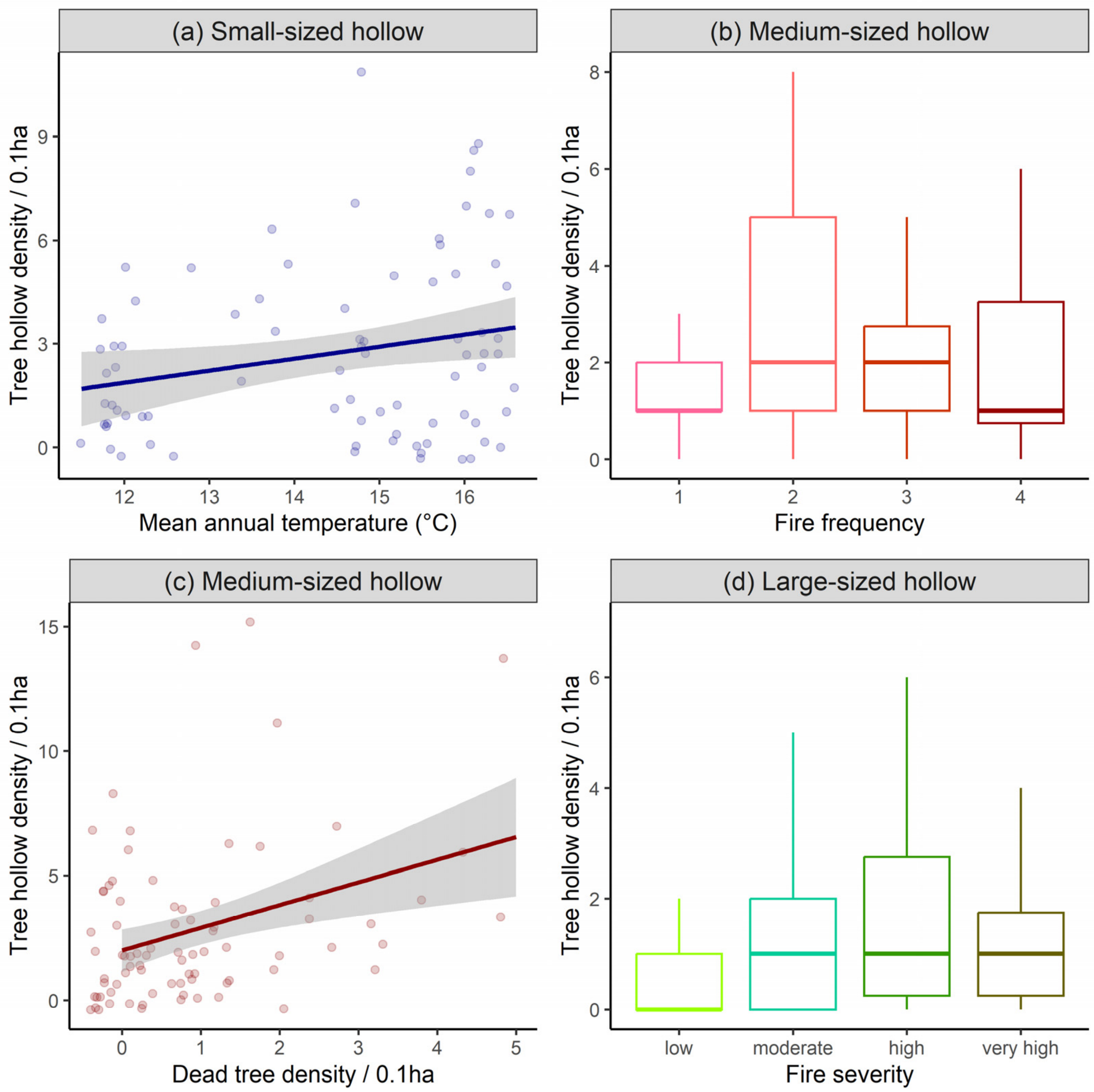

Figure 1. Associations between (**a**) small-sized tree hollow density (per 0.1 ha) and mean annual temperature, (**b**) medium-sized hollow density (per 0.1 ha) and fire frequency, (**c**) medium-sized hollow density (per 0.1 ha) and dead tree density, and (**d**) large-sized hollow density (per 0.1 ha) and fire severity. Line plots show mean trend lines ± 1 SE using raw data values. Box plots show the distribution of raw data values: median values (thick horizontal line), the range of the 25th and 75th percentiles (extent of box), the range of the 5th and 95th percentiles (extent of vertical lines). Outliers have been excluded from boxplots. Only "significant" effects from Table 2 are shown.

Significant negative and positive associations were observed between basal scar density and mean annual temperature and medium-sized tree density, respectively (Table 2, Figure 2b,c). A significant positive association was also observed between basal scar tree density and fire severity (Table 2, Figure 2a). On average, basal scar tree density increased by 2.52, 8.15, and 8.47 trees per site between the low fire severity category when compared with the moderate, high, and very high categories.

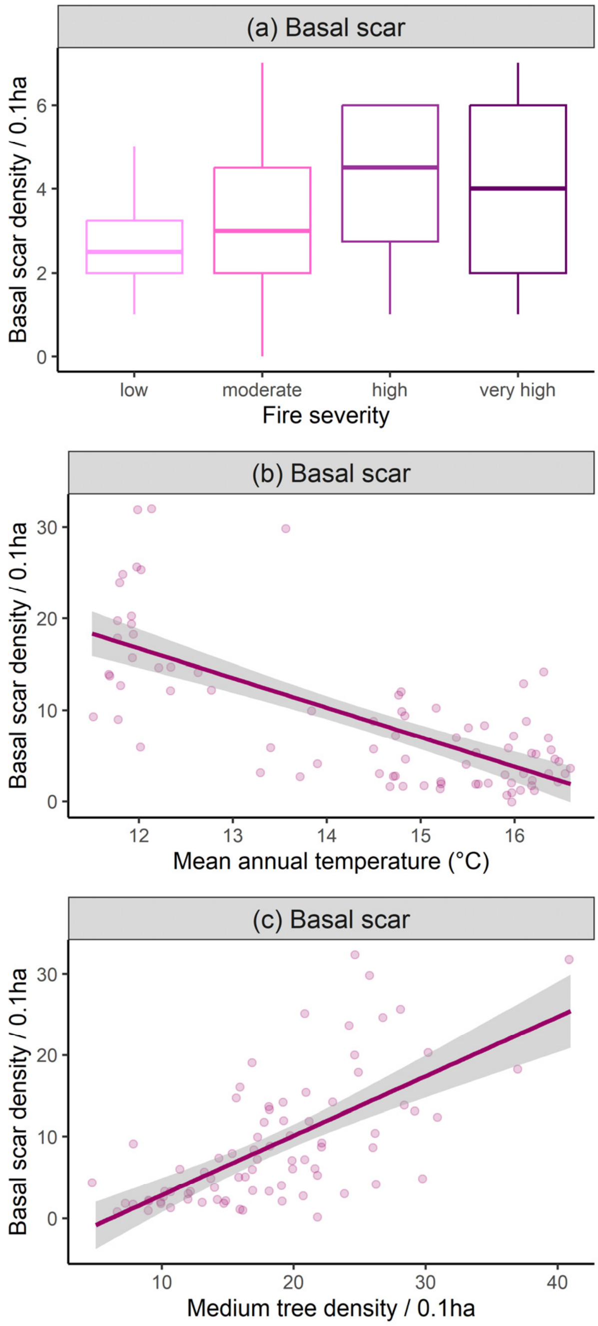

Figure 2. Associations between basal scar density (per 0.1 ha) and (**a**) fire severity, (**b**) mean annual temperature, and (**c**) medium-sized tree density (per 0.1 ha). Box plots show the distribution of raw data values: median values (thick horizontal line), the range of the 25th and 75th percentiles (extent of box), the range of the 5th and 95th percentiles (extent of vertical lines). Outliers have been excluded from boxplots. Only "significant" effects from Table 2 are shown.

4. Discussion

Our results lend support to the hypothesis that wildfire disturbance and climate have diverse and size-specific impacts on tree hollows and basal scarring. Our statistical models suggested that fire frequency and severity were significant predictors of medium- and large-sized tree hollow density, respectively, and mean annual temperature was a significant, but weak, predictor of small-sized hollow density. Fire severity and mean annual temperature were supported as important drivers of basal scarring, which is a key hollow-forming process. The size-dependent responses of tree hollows and basal scars reported here will aid in the conservation of hollow-dwelling fauna because they imply that the density of larger-sized hollows, which are a limiting resource for threatened fauna, are promoted at intermediate fire frequencies and severities.

4.1. Fire Effects

The density of medium- and large-sized tree hollows was greatest at intermediate fire frequencies and severities, respectively. Previous studies in south-east Australian forests have shown negative associations between long-term fire frequency and hollow density in montane subalpine forests [40], and negative effects of a one-off severe wildfire event on hollow density in cool temperate forests, which was mediated through tree collapse and reduced rates of hollow recruitment [26]. However, positive associations have also been observed between long-term fire frequency and hollow density in warm temperate forests [27], presumably due to increased rates of productivity. Given that our study was conducted in dry forests with nutrient poor soils and low productivity, it is likely that the lower hollow densities observed at higher fire frequencies and severities here were due (at least in part) to fire-mediated tree felling.

Previous studies have also shown positive associations between fire severity and hollow density with some increases in rates of hollow formation at higher fire frequencies [25] and higher rates of hollow production in dry (where fire is relatively common) than wet (where fire is relatively rare) forests [6]. Collectively, these studies suggest that the unimodal relationships observed here between fire frequency/severity and medium- and large-sized hollow densities represented a compromise between high rates of tree felling at higher frequencies/severities and low incidence of hollow-forming processes (e.g., branch breaking, physical excavation) at lower frequencies and severities.

In support of this hypothesis, we observed positive associations between the density of trees with basal scars and fire severity in our study, which presumably occurred because of increased fire intensities at tree bases during high rather than low severity wildfire. Fire scars are thought to facilitate hollow formation by allowing hollow-forming taxa access to tree heartwood [19]. Given this, and the caveat that our study utilized a correlative dataset, our data provide some support for the prediction that fire severity promotes hollow density via basal scarring; however, the density of large-sized tree hollows in our study was highest at intermediate fire severities where levels of basal scarring were moderate. As suggested above, this implies that the indirect benefits that fire may provide for hollow formation (via basal scaring) may be outweighed by tree losses caused by exposure to high severity and frequent fires.

Interestingly, our results suggest that fire frequency and severity had different impacts on medium- and large-sized hollow densities; e.g., fire frequency was associated with medium-sized hollows only, and fire severity was associated with large-sized tree hollows only. These trends, while seemingly contradictory, may reflect an interaction between fire frequency, fire severity, and tree hollow formation through canopy branch breaking and landscape exposure.

High severity fire may facilitate the formation of both medium- and large-sized hollows by breaking tree branches and exposing pre-hollowed stems [4]. Landscape exposure (e.g., related to prevailing wind or extreme weather) may similarly facilitate hollow formation; however, the probability of branch breakage may be higher for medium- than large-sized hollows because larger branches may be more difficult to break than medium-sized ones. If so, we could expect a weaker association between medium-sized hollow density and fire severity because it is strongly impacted by both severity and exposure-mediated branch breakage, whereas we could expect a stronger association between larger-sized hollow density and fire severity because it is strongly impacted by severity-mediated branch breakage only. This hypothesis could also explain why fire severity and frequency did not impact small-sized hollow density in our study, i.e., because small-sized hollow density may have been primarily moderated by exposure-mediated branch breakage.

In the case of fire frequency, over longer timeframes, more frequent fire should facilitate the formation of medium- and large-sized hollows by allowing hollow-forming taxa access to tree heartwood through basal scars [4,19]. However, in this situation, larger hollows may take longer to form than medium-sized ones because a larger volume of wood decomposition is required. If so, medium-sized hollow density should be more strongly associated with fire frequency than large-sized hollow density, which is what we observed in our study. These hypotheses are complex and speculative, and therefore, further research is required to test them.

4.2. Climate Effects

Unlike larger-sized hollows, small-sized hollow density was not affected by fire frequency and severity. Instead, we found a positive effect of mean annual temperature on small-sized hollow density. It is possible that this association was driven by increased rates of hollow decomposition (and hence hollow formation) in areas experiencing higher than average temperatures [8,29]. It is also possible that such a decomposition effect only manifested for smaller rather than larger hollows in our study because there was less area for hollow-forming taxa to excavate, e.g., smaller hollows may form relatively quickly (when compared to larger hollows) because there is a smaller volume of tree heartwood to decompose.

Although we observed a significant association between mean annual temperature and small-sized hollow density, climate effects were generally weak (i.e., non-significant, low pseudo r^2 values). It is possible that our study would have shown stronger climate effects if we assessed other variables, such as climate seasonality [29] or precipitation maxima. However, the Sydney Basin bioregion is dominated by a temperate climate with relatively weak rainfall seasonality (although rainfall totals are typically greater in summer than winter; [41]) and our climatic variables were strongly correlated with measures of rainfall maxima (e.g., mean annual precipitation was positively correlated with mean precipitation in the wettest (R = 0.97) and driest (R = 0.80) quarters (data extracted from BIOCLIM surfaces; [42]). Further, tree biomass varied strongly across the range of mean annual temperatures reported here [32]. Collectively, this suggests that other climate measures were not key drivers of hollow density in our study region (at least at the scales assessed here) and the range of each climate variable should have been enough to produce significant effects. Therefore, the results of our study imply that fire regime was a stronger overall driver of hollow density than climate.

In contrast to tree hollows, a strong negative association was observed between basal scarring and mean annual temperature. Some physical process, such as fire, is usually required to form tree scars [19]. Therefore, it is possible that climate indirectly impacted basal scarring by selecting for trees with specific life-history traits that facilitate or have a high resistance to basal scarring, i.e., mean annual temperature is a proxy for differences in tree species composition. Bark type is a key life history trait impacting rates of basal scarring, with scarring more likely on trees with loosely held bark (e.g., fibrous, stringy barks), than those with more densely held bark types (e.g., smooth barks; [43–45]). Therefore, bark type may have been an important life history trait influencing incidence of basal scarring [46], and climate may have indirectly influenced basal scarring in our study by moderating the spatial distribution of bark types. This hypothesis requires further investigation by accounting for bark type and tree species variation in future studies.

5. Conclusions

Tree hollow density can limit the abundance of fauna species requiring hollows of specific sizes for nesting, shelter, and predator avoidance [16,47–49]. This is particularly so for larger species because the larger-sized hollows they require occur at relatively low densities (as shown here and in [12]).

Here, we show previously obscure size-dependent relationships between size-specific tree hollow density, basal scar density, and wildfires. Medium- and large-sized hollow densities were greatest at intermediate fire frequencies and severities, respectively, and a positive association was observed between basal scar density and fire severity. Collectively, these results lend support to the hypothesis that the density of larger-sized tree hollows represents a compromise between high rates of hollow formation at lower frequencies/severities and high rates of tree felling at higher frequencies/severities. Therefore, fire regimes characterized by intermediate frequency (e.g., 7–30 years; [50,51]) and moderate severity wildfires may optimize larger-sized tree hollow "stocks" in dry sclerophyll forests.

We also show that climate, namely mean annual temperature, was positively associated with small-sized hollow density, presumably due to increased rates of hollow decomposition (and hence formation). This result has potentially important implications for hollow conservation given anthropogenic climate change. However, given the weak and variable responses observed here, more research is required to clarify this effect and the underlying mechanism governing this trend. For a broader understanding of how fire regimes and climate impact hollow dynamics across landscapes, future research should also focus on similar assessments to those made here across a broad range of sympatric forest types (e.g., wet sclerophyll forests, rainforests).

Threatened hollow-dwelling fauna within the study region requiring large hollows, such as the powerful owl (*Ninox strenua*; [52]) and the yellow-bellied glider (*Petaurus australis*; [53]), are particularly susceptible to anthropogenic disturbances because they often occur at low population densities and/or have wide home-ranges. Collectively, our results will be of importance for the conservation of these species because they can be used to identify areas of suitable habitat (both now and given climate change) and/or implement "best practices" for the targeted management of fire regimes for hollow-dwelling fauna.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14071372/s1, Figure S1: Map of the study region; Figure S2: Spline correlogram testing for spatial autocorrelation in model residuals; Box S1: Considerations of interactions in statistical models.

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