Time-since-fire and inter-fire interval influence hollow availability for fauna in a fire-prone system


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Abstract

Tree hollows are a critical, yet potentially limiting habitat resource for many animal species. Fire influences hollow availability, and the associated indirect effects on fauna can threaten the persistence of hollow-dependent species in fire-prone systems. We investigated the influence of two temporal aspects of fire regimes (time-since-fire, inter-fire interval) on hollow occurrence in a semi-arid, fire-prone region in south-eastern Australia. Empirical data on the characteristics of hollow-bearing eucalypt stems and fire-history attributes were compiled for 581 study sites. Mixed models were used to examine the relative influence of time-since-fire and inter-fire interval on hollow occurrence. Time-since-fire and inter-fire interval both affected the probability of hollow occurrence, but in different ways. Time-since-fire influenced the occurrence of hollows in live and dead stems. As time-since-fire increased, so too did the probability of live and dead stems containing hollows. Live stems did not provide hollows before 40 years post-fire, while the probability of dead stems containing hollows peaked at 50–60 years. Inter-fire interval influenced the availability of hollows in dead stems. Longer inter-fire intervals resulted in an increased density of dead hollow-bearing stems. In this region, hollow-dependent fauna will benefit from increased fire-free periods, both in terms of individual fire events and the intervals between repeated fires. These results highlight the complex way in which fire affects the availability of faunal habitat resources, and the extended time periods over which such influences operate. Understanding the effects of fire regimes on slow-developing habitat resources over long time-frames is imperative for sound ecological fire management.

1. Introduction

Fire affects the occurrence of fauna in fire-prone regions around the world (Hutto, 2008; Lindenmayer et al., 2008). As well as directly affecting animals, via individual mortality or increased predation (Russell et al., 2003), fire also indirectly affects fauna by altering habitat characteristics and resource availability (Fox, 1982). Such indirect effects are particularly important because they influence population abundance and persistence (Friend, 1993), and may operate over long time-frames (Kelly et al., 2011). Furthermore, the indirect effects of fire on fauna are determined not only by single fire events and the ensuing changes to habitat through post-fire succession (Fox, 1982), but also by the cumulative effects of multiple fires, due to the impact of fire intervals on habitat characteristics (Gill and McCarthy, 1998). Understanding how such indirect effects are influenced by temporal aspects of fire regimes is complex and inadequate in many systems (Driscoll et al., 2010). As fire management is often guided by prescriptions relating to time-since-fire and inter-fire interval (Fernandes and Botelho, 2003; Gill and McCarthy, 1998), and both factors can influence the persistence of fauna (Barlow and Peres, 2004; Brown et al., 2009), such knowledge is imperative for the development of ecologically-sound fire plans.

Tree hollows (‘cavities’) provide critical breeding and refuge habitat for many animal species (Goldingay, 2009; Newton, 1994). The value of hollows for fauna is influenced by many factors, including tree species, whether trees are alive or dead, and the size and position of the hollow (Chambers and Mast, 2005; Gibbons and Lindenmayer, 1996; Whitford, 2002). Animal species differ in
terms of their requirements for hollows with these characteristics (Lumsden et al., 2002; Wormington et al., 2003). In many parts of the world, primary hollow-nesters such as woodpeckers excavate hollows in dead trees (‘snags’: Newton, 1994). No such species occur in Australia, and so hollow development relies on natural decay processes initiated by limb loss or fire, and facilitated by invertebrates, fungi or bacteria (Adkins, 2006; Gibbons and Lindenmayer, 1996). Thus, hollow formation is a much slower process: trees may take up to 100–300 years to develop hollows (Koch et al., 2008; Wormington et al., 2003), and even longer to become suitable for some hollow-dependent species (Gibbons and Lindenmayer, 2002). The strong influence of temporal factors on hollow availability, and the potential for hollows to limit faunal occurrence in many systems (Bültler et al., 2004; Lindenmayer and Wood, 2010), makes them an ideal resource by which to examine the potential indirect effects of fire on fauna.

Fire affects hollow availability in a range of ways. In Australia, fire may create hollows for fauna (Inions et al., 1989), but it can also reduce hollow availability (Eyre et al., 2010). Furthermore, the habitat value of burnt hollow-bearing trees is often short-lived because of their reduced lifespan (Lindenmayer and Wood, 2010). Slow rates of natural hollow formation mean it can take many decades before new hollows develop in post-fire habitats (Haslem et al., 2011). Less is known about the effects of the inter-fire interval on hollows and hollow-dependent fauna (but see Mackey et al., 2002). However, some insight is provided by research in harvested forests, where disturbance processes also alter the age structure of vegetation. Short harvesting rotations prevent natural recruitment of hollows and snags, thus jeopardizing the ongoing provision of these resources for fauna (Smith et al., 2008). This topic requires further attention because understanding of the indirect effects of fire on fauna, derived from research into single fire events, may be misleading as results do not account for the possible effects of fire regimes (Bradstock and Cohn, 2002).

Fire is commonly used in the management of fire-prone regions, both to minimize wildfire hazard and for ecological objectives (Fernandes and Botelho, 2003). Time-since-fire is a key indicator used in fire management for hazard reduction, due to often rapid rates of fuel accumulation following fire (Fernandes and Botelho, 2003). Fire management may also include prescriptions relating to the length of time between fires: the inter-fire interval (e.g., Gill, 2009). Such prescriptions are often based on an understanding of the life-history attributes of particular plant species (e.g., ‘vital attributes’ sensu Noble and Slatyer, 1980). Vital attributes, such as time to first seed set and species longevity, are used to identify the minimum and maximum intervals between fire events that systems are likely to have the capacity to withstand (Noble and Slatyer, 1980). However, the validity of assuming that inter-fire intervals derived from the attributes of plants will be appropriate for fauna has been questioned (Clarke, 2008). Whether undertaken for hazard reduction or ecological objectives, the indirect effects of fire management are particularly likely to affect fauna that rely on slow-developing resources such as tree hollows.

This study was undertaken in Australian semi-arid vegetation that is strongly structured by fire (Bradstock and Cohn, 2002). Hollow-dependent fauna in this system include a range of mammals (e.g., insectivorous bats: Lumsden and Bennett, 1995) and birds (e.g., parrots, cockatoos, pardalotes: Woinarski, 1999). Understanding of historical fire regimes is limited to the most recent 40 years; the period for which satellite imagery is available (Avitabile et al., submitted for publication). However, strong relationships between stem diameter and tree age in this system have facilitated age predictions for areas burnt before this time, thus extending knowledge of time-since-fire to over a century (Clarke et al., 2010). Here, we use the approach of Clarke et al. (2010) to estimate the number of years between the two most recent fires, to also provide information on inter-fire interval. Thus we can investigate the influence of both time-since-fire and inter-fire interval on hollow availability over an extended time period. We address three objectives: (1) to determine the influence of tree species and vegetation type on broad patterns of hollow availability; (2) to document rates of hollow development in live stems of different tree species; and (3) to investigate the influence of time-since-fire and inter-fire interval on the occurrence of hollows in live and dead stems.

2. Methods

2.1. Study area

The study area covers ~100 000 km² of the Murray Mallee, a semi-arid region in south-eastern Australia (see Haslem et al., 2011 for map). Undulating dune/swale formations dominate the region and reflect variation in both soil characteristics and moisture availability (Land Conservation Council, 1987). Mean annual rainfall is low (220–330 mm) and temperatures are high in summer and mild in winter (mean daily maxima >32 °C and 16 °C, respectively) (data supplied by the Australian Bureau of Meteorology).

Native vegetation has been extensively cleared for agriculture (cropping and grazing); that which remains occurs mostly within large conservation reserves located in areas of low fertility (Land Conservation Council, 1987). ‘Tree mallee’, the most common vegetation type, is characterized by short (<5 m tall) ‘mallee’ eucalypts above an understory of shrubs and grasses. Mallee eucalypts have a multi-stemmed habit which reflects their primary mechanism for post-fire regeneration; the coppicing of many new stems from an underground lignotuber (Gill, 1981). Three broad associations of tree mallee occur in the region (Haslem et al., 2010). Triodia Mallee typically comprises Eucalyptus dumosa and E. socialis in the canopy and Triodia scariosa in the understory, the latter being a perennial hummock grass known for its flammability and importance in a range of mallee fauna (Bradstock and Cohn, 2002). Chenopod/Shrubby Mallee (hereafter Chenopod Mallee) is dominated by E. oleosa subsp. oleosa and E. gracilis above a diversity of low chenopod shrubs which exhibit relatively reduced flammability (Pausas and Bradstock, 2007). Heathy Mallee is characterized by E. costata subsp. murrayana and Callitris verrucosa and a range of small heathy shrub species. Floristic nomenclature follows Barker et al. (2005) and Ross and Walsh (2003).

Fire is a dominant process in this system: it influences the distribution of plant and animal species (Bradstock and Cohn, 2002); and inappropriate fire regimes may also negatively affect some mallee fauna (Brown et al., 2009; Nimmo et al., in press). Fire has burnt 40% of tree mallee vegetation in the region in the last 40 years (mean annual burn rate: 1.14% of tree mallee vegetation). However, only a small percentage (<3%) has burnt more than once during this period (Avitabile et al., submitted for publication). Large fires (~100 000 ha) are common, typically occurring somewhere in the region every 15–20 years (Avitabile et al., submitted for publication). Fire management involves both the suppression of wildfires and the use of prescribed fire, primarily to reduce wildfire risk (Sandell et al., 2006), and is guided by assessment of fuel loads and information on the vital attributes of key plant species (Department of Sustainability and Environment, 2008).

2.2. Study design and data collection

All 581 study sites were located in tree mallee vegetation and were clustered in circular landscape units (4 km diameter; 12.56 km²) spread across the region. On average, there were 21 sites per landscape unit (range: 7–30 sites) and they were selected...
to encompass a range of variation in post-fire age and topographic and soil characteristics. Sites within the same landscape unit were positioned an average of 1.5 km apart (range: 72 m–3.9 km), and landscapes were separated by a mean distance of 130 km (range: 6.3–217.7 km). All sites were located within conservation reserves.

Characteristics of eucalypt trees (i.e., individual lignotubers with varying numbers of stems) were recorded within a 50 × 4 m transect at each site. The following data were collected for each tree: (1) tree species (including 'unidentified eucalypt' when identification to species level was not possible); (2) number of stems; (3) stem status (alive/dead) and diameter (cm; measured ~30 cm above ground); and (4) hollow type, with each stem being classified as (a) not containing a hollow, (b) containing only basal hollows (hollows <1 m above ground), (c) containing only canopy hollows (hollows >1 m above ground) or (d) containing both basal and canopy hollows. Hollows were defined as any cavity or spout (i.e., hollow located in the end of a broken branch) with an entrance ≥2 cm diameter. Data were collected for the first 10 trees encountered on each transect, and stem measurements were not recorded for stems <1 cm diameter. When transects contained trees belonging to multiple age cohorts (i.e., trees with stems differing by >2 cm diameter), data were collected for the first 10 trees in each cohort. On average, data were collected for 86% of trees located on transects (range 20–100%). Sites were surveyed between June and August, 2007. A range of other data were also compiled for each site: (1) vegetation type (Triodia Mallee, Chenopod Mallee, Heathy Mallee: see Haslem et al., 2010); (2) estimated mean annual rainfall (data supplied by the Australian Bureau of Meteorology); (3) the number of years since the most recent fire ('time-since-fire'); and (4) the number of years between the two most recent fires ('inter-fire interval').

2.3. Time-since-fire

Comprehensive fire-history mapping for the region, based on Landsat satellite imagery for 15 individual years between 1972 and 2007 (Avitabile et al., submitted for publication), was used to identify the year of the most recent fire for sites burnt since 1972. For sites burnt before 1972, an alternative approach was required. Regression models were used to quantify the relationship between the mean diameter of live stems and tree age (identified by fire-year) at sites of known fire-age (i.e., those burnt >1972), for the six most common eucalypt species (Clarke et al., 2010). When fitted to data on live stem diameter collected from sites burnt prior to 1972, these models allowed prediction of fire-year (based on tree-age estimates, averaged across species). Model validation using independent data revealed a highly significant correlation between actual and predicted tree ages (r = 0.71, P < 0.001, n = 88), thus confirming the reliability of this approach (Clarke et al., 2010). Time-since-fire was calculated as the number of years between 2007 (when field data were collected) and the actual/predicted year of the most recent fire.

2.4. Inter-fire interval

For sites burnt twice since 1972, fire-history mapping identified the number of years between the two most recent fires. As with time-since-fire, insufficient fire-history records necessitated an alternative approach when determining inter-fire interval for sites burnt only once since 1972. Clarke et al. (2010) demonstrated that the strong relationship between the diameter of live stems and tree age in this region provides a reliable estimate of fire-year. As fire in tree mallee vegetation kills (or consumes) live stems, the diameter of dead stems is an indicator of their age when killed by fire (i.e., their age at the most recent fire). Therefore, dead stems can be used to infer the number of years between the two most recent fires.

Two key assumptions underpinning such an approach are that all dead stems at a site resulted from the most recent fire, and that the diameter of dead stems is not influenced by time-since-fire. Several factors may cause these assumptions to be violated: (1) stems die from causes other than fire, thus dead stems at sites will comprise those killed by fire (suitable for inferring inter-fire interval) and those resulting from other causes (e.g., natural senescence: unsuitable for such inference); (2) the diameter of live stems may influence their likelihood of remaining standing after fire as dead stems; (3) the diameter of dead stems may influence their post-fire longevity; and (4) some already-dead stems may remain standing after fire, thus 'surviving' two fires.

The potential for these factors to affect the diameter of dead stems at sites was examined using three methods. First, histograms of dead stem diameter in different time-since-fire intervals were used to identify the minimum size of stems likely to withstand, rather than be consumed by fire. Second, plots of mean dead stem diameter per tree (for each species), and mean number of stems per tree (in different size classes), against time-since-fire were assessed to determine whether the diameter of dead stems influenced their post-fire standing life. Third, to investigate the likelihood of dead stems surviving two fires, the range of diameter measurements recorded for dead stems at sites was examined for each species. This graphical exploration indicated that dead stems <2 cm diameter might violate the assumptions of this approach because they are more likely to be consumed by fire, and exhibited strong variation in number across the time-since-fire gradient; increasing at ~15–20 years post-fire (as post-fire coppice senesced) and declining thereafter (as these stems fell over). Dead stems <2 cm diameter were therefore considered unrepresentative of tree age when killed by fire, and so were excluded from calculations of inter-fire interval.

The species-specific models relating live stem diameter to tree age (Clarke et al., 2010) were then applied to data on mean diameter of dead stems to estimate tree age at the time of last fire. For a small number of sites with fewer than five trees (n = 59), data collected from a larger 50 × 50 m transect were used. Age predictions were then averaged across models for all eucalypt species recorded at the site. The resultant prediction of tree age at time of stem death provided an estimate of the number of years between the two most recent fires: the inter-fire interval.

To assess the accuracy of this approach, the correlation between actual (based on fire-history mapping) and estimated (based on dead stem diameter/tree-age relationships) inter-fire intervals for sites burnt twice since 1972 was examined. There was a highly significant Spearman rank correlation between actual and estimated inter-fire intervals (r = 0.61, P < 0.001, n = 57).

Our approach involved a space-for-time substitution to investigate the effect of time-since-fire and inter-fire interval on hollow occurrence, with sites representing a chronosequence in both fire-history attributes. Fire generally removes both canopy and understory vegetation in tree mallee vegetation (Caughley, 1985), typically resetting the successional clock to year zero. To ensure this was the case, we only examined sites considered to have been completely burnt in the most recent fire (based on occurrence of a single age-cohort of eucalypt trees).

2.5. Data analyses

To account for variation in the number of trees measured at sites, the proportion of stems containing a hollow, out of the overall number of stems recorded, was calculated for each site. These data were further grouped by additional factors, including: eucalypt species, vegetation type, stem status (alive/dead), and hollow...
type (basal hollow/canopy hollow). For example, the proportion of E. gracilis stems containing a hollow at sites, or the proportion of dead stems containing basal hollows at sites.

Two different modelling approaches were employed to investigate variation in the proportion of stems containing a hollow at sites. Linear mixed models provided the simplest approach to identifying differences in the proportional occurrence of hollows between vegetation types and eucalypt species (i.e., categorical predictor variables). Preliminary data exploration and a priori understanding indicated a linear approach would not be appropriate when examining relationships between hollow occurrence and stem diameter, time-since-fire and inter-fire interval (i.e., continuous predictor variables). Therefore, these data were modelled using generalized additive mixed models (GAMMs: Zuur et al., 2009), which use smoothing functions to fit nonlinear relationships (Wood, 2006). In both approaches, the clustering of sites in landscape units necessitated the inclusion of a random term to account for any associated correlation structure in the data: thus, all models were fitted with ‘landscape’ as a random effect (Zuur et al., 2009). More details about each approach are given below.

In the linear mixed models, the response variable was the proportion of stems per site that contained a hollow of any type and was modelled with a Gaussian error distribution. The predictor variables, examined in separate models, were vegetation type (Triodia Mallee, Chenopod Mallee, Heathy Mallee) and eucalypt species (E. costata subsp. murrayana, E. dumosa, E. gracilis, E. leptophylla, E. oleosa subsp. oleosa, E. socialis). In addition, a term for time-since-fire was also included in both models. Tree age affects hollow occurrence (Gibbons et al., 2000) and so the inclusion of time-since-fire (a proxy for tree age) removed any confounding effect associated with the varying distribution of site-ages across vegetation types or eucalypt species. Lastly, each model included a variance structure (to accommodate unequal variances between vegetation types or eucalypt species. Lastly, each model included a variance structure (to accommodate unequal variances between time-since-fire and the proportion of hollow-bearing stems at sites (Table 1).

3. Results

3.1. Broad patterns in the occurrence of hollows

The proportional occurrence of tree stems with hollows differed significantly between vegetation types (Table 1). Chenopod Mallee (the reference category) contained the greatest proportion of eucalypt stems with hollows (as indicated by the negative parameter estimates for Heathy Mallee and Triodia Mallee) while, proportionally, stems in Heathy Mallee had the fewest hollows. Eucalyptus gracilis stems provided significantly more hollows, proportionally, than other common eucalypts in the region (Table 1). Both models showed significant, positive relationships between time-since-fire and the proportion of hollow-bearing stems at sites (Table 1).

3.2. Hollow development in live tree stems

The probability of live stems containing a hollow showed a significant positive relationship with mean stem diameter in all eucalypt species (Table 2; Fig. 1). Large stems had a higher probability of containing a hollow than small stems: no species were predicted to provide hollows before stems reached around 7–10 cm diameter (Fig. 1). The live stem diameter/tree-age models of Clarke et al. (2010) estimate stems of this size to be around 50–60 years old (see Fig. 1). Differences in rates of hollow development were identified only for two species, and only for stems >11 cm diameter: live E. gracilis stems had a significantly higher probability of containing a hollow than live E. oleosa subsp. oleosa stems of the same size (non-overlapping confidence intervals of predictions: not shown). However, when looking at hollow development in relation to tree age (using predictions of Clarke et al. (2010)), there were no differences between species (confidence intervals of all predictions overlapped: not shown). Mean annual rainfall affected the probability of live stems containing a hollow only for E. dumosa and E. oleosa subsp. oleosa: both relationships were positive (Table 2). Overall, these models explained between 28% and 51% of variation in the probability of live stems containing hollows (Table 2).

### Table 1

Results of linear mixed models investigating the effect of vegetation type and eucalypt species on the proportion of tree stems containing hollows. Reference categories were Chenopod Mallee (vegetation type) and Eucalyptus gracilis (eucalypt species).

<table>
<thead>
<tr>
<th>Model</th>
<th>Term</th>
<th>Parameter estimate</th>
<th>Std. error</th>
<th>df</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation type (n = 581 sites)</td>
<td>Intercept</td>
<td>0.031</td>
<td>0.015</td>
<td>550</td>
<td>3.62</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Heathy Mallee</td>
<td>−0.088</td>
<td>0.022</td>
<td>550</td>
<td>4.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Triodia Mallee</td>
<td>−0.031</td>
<td>0.011</td>
<td>550</td>
<td>2.78</td>
<td>&lt;0.006</td>
</tr>
<tr>
<td></td>
<td>Time-since-fire</td>
<td>0.002</td>
<td>&lt;0.001</td>
<td>550</td>
<td>8.90</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Eucalypt species (n = 563 sites)</td>
<td>Intercept</td>
<td>0.063</td>
<td>0.020</td>
<td>1149</td>
<td>3.16</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>E. costata subsp. murrayana</td>
<td>−0.069</td>
<td>0.022</td>
<td>1149</td>
<td>−3.14</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>E. dumosa</td>
<td>−0.047</td>
<td>0.019</td>
<td>1149</td>
<td>−2.51</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>E. leptophylla</td>
<td>−0.044</td>
<td>0.021</td>
<td>1149</td>
<td>−2.05</td>
<td>0.041</td>
</tr>
<tr>
<td></td>
<td>E. oleosa subsp. oleosa</td>
<td>−0.063</td>
<td>0.020</td>
<td>1149</td>
<td>−3.17</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>E. socialis</td>
<td>−0.057</td>
<td>0.019</td>
<td>1149</td>
<td>−3.06</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Time-since-fire</td>
<td>0.002</td>
<td>&lt;0.001</td>
<td>1149</td>
<td>9.66</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 2
Results of generalized additive mixed models quantifying the effect of mean diameter of live stems (cm) and mean annual rainfall (mm) on the probability of live stems containing a hollow for six species of mallee eucalypts. The percentage of deviance explained by each model is shown, as is the number of sites included in each.

<table>
<thead>
<tr>
<th>Eucalypt species</th>
<th>Sites (#)</th>
<th>Deviance explained (%)</th>
<th>Predictor variable</th>
<th>edf*</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. costata</em> subsp. <em>murrayana</em></td>
<td>130</td>
<td>38.4</td>
<td>Mean live stem diameter</td>
<td>2.96</td>
<td>16.19</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean annual rainfall</td>
<td>1.37</td>
<td>0.27</td>
<td>0.679</td>
</tr>
<tr>
<td><em>E. dumosa</em>&lt;sup&gt;b&lt;/sup&gt;</td>
<td>270</td>
<td>40.1</td>
<td>Mean live stem diameter</td>
<td>2.64</td>
<td>20.57</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean annual rainfall</td>
<td>1.00</td>
<td>13.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><em>E. gracilis</em>&lt;sup&gt;c&lt;/sup&gt;</td>
<td>131</td>
<td>40.5</td>
<td>Mean live stem diameter</td>
<td>1.00</td>
<td>61.38</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean annual rainfall</td>
<td>1.00</td>
<td>0.04</td>
<td>0.837</td>
</tr>
<tr>
<td><em>E. leptophylla</em></td>
<td>137</td>
<td>51.1</td>
<td>Mean live stem diameter</td>
<td>3.39</td>
<td>14.90</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean annual rainfall</td>
<td>1.00</td>
<td>0.58</td>
<td>0.449</td>
</tr>
<tr>
<td><em>E. oleosa</em> subsp. <em>oleosa</em>&lt;sup&gt;b&lt;/sup&gt;</td>
<td>146</td>
<td>28.4</td>
<td>Mean live stem diameter</td>
<td>1.00</td>
<td>41.34</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean annual rainfall</td>
<td>1.00</td>
<td>6.10</td>
<td>0.015</td>
</tr>
<tr>
<td><em>E. socialis</em></td>
<td>251</td>
<td>33.1</td>
<td>Mean live stem diameter</td>
<td>2.16</td>
<td>30.40</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean annual rainfall</td>
<td>1.00</td>
<td>2.66</td>
<td>0.104</td>
</tr>
</tbody>
</table>

<sup>a</sup> Estimated degrees of freedom (edf = 1.00 represents a linear relationship).
<sup>b</sup> One outlier removed.
<sup>c</sup> Three outliers removed.

Fig. 1. Predicted relationships between mean diameter of live stems (cm) and the probability of live stems containing hollows (per site) for six eucalypt species. Dashed lines show the 95% confidence intervals of predictions; circles show observed values (in the form of proportions). The upper x-axis shows predicted years-since-fire based on mean live stem diameter (Clarke et al., 2010).
3.3. Influence of fire-history attributes on hollow occurrence in live and dead stems

Both time-since-fire and inter-fire interval influenced the probability of stems containing a hollow (Table 3). For live stems, time-since-fire had the strongest effect on hollow occurrence. While inter-fire interval had a statistically significant influence on the probability of live stems containing basal hollows \((P = 0.04; \text{ Table } 3)\), predictions representing this relationship displayed minimal variation with inter-fire interval (not shown). Therefore, inter-fire interval is not considered a strong driver of hollow occurrence in live stems. In contrast, the probability of dead stems containing a hollow was strongly influenced by both time-since-fire and inter-fire interval. Models quantifying these relationships explained just over one-third of the variation in hollow occurrence in live and dead stems (Table 3).

Time-since-fire had a similar effect on the occurrence of basal and canopy hollows in live stems (Fig. 2a). Live stems were not predicted to contain either type of hollow before around 40 years post-fire, and the probability of stems containing either type of hollow, particularly canopy hollows, increased thereafter. These trends corroborate patterns illustrated in Fig. 1.

In contrast, the effect of time-since-fire and inter-fire interval on the probability of dead stems containing a hollow differed between hollow types (Fig. 2b and c). The probability of dead stems containing a basal hollow increased steadily as inter-fire intervals lengthened and peaked at 50–60 years-since-fire (Fig. 2b and c). The probability of dead stems providing canopy hollows varied little over the time-since-fire gradient; however, predicted probabilities increased with inter-fire interval after a lag time of around 40 years. This latter trend is similar to patterns of canopy hollow occurrence in live stems in relation to time-since-fire (Fig. 3a).

Comparison of the mean density (#/ha) of live and dead hollow-bearing stems in relation to time-since-fire, inter-fire interval and stem size reveals further insights (Fig. 3). Dead stems are the primary source of hollows in the first 40–50 years post-fire, a pattern observed irrespective of inter-fire interval or hollow type. Furthermore, these dead hollow-bearing stems are denser and, on average, larger after longer inter-fire intervals (>45 years: lower right plots cf. upper right plots, Fig. 3). Increasing the length of time between fires increases the size of dead hollow-bearing stems even at sites older than 50 years post-fire. Nonetheless, Fig. 3 highlights the crucial role of live stems in providing larger hollow-bearing stems in these older sites, irrespective of hollow type and inter-fire interval.

Table 3

Results of generalized additive mixed models examining the effect of time-since-fire and inter-fire interval on the probability of live and dead stems containing a hollow at sites. Results are presented separately for stems with basal and canopy hollows. The percentage of deviance explained by each model, and the number of sites included in each, are also shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>Sites (#)</th>
<th>Deviance explained (%)</th>
<th>Fire-history attribute</th>
<th>Hollow type</th>
<th>edf</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live stems</td>
<td>487</td>
<td>38.0</td>
<td>Time-since-fire</td>
<td>Basal</td>
<td>4.13</td>
<td>17.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Canopy</td>
<td>2.38</td>
<td>26.27</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Basal</td>
<td>1.00</td>
<td>4.10</td>
<td>0.043</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Canopy</td>
<td>1.80</td>
<td>1.37</td>
<td>0.255</td>
</tr>
<tr>
<td>Dead stems</td>
<td>540</td>
<td>35.8</td>
<td>Time-since-fire</td>
<td>Basal</td>
<td>3.34</td>
<td>33.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Canopy</td>
<td>4.78</td>
<td>5.60</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Basal</td>
<td>4.71</td>
<td>10.28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Canopy</td>
<td>1.45</td>
<td>40.71</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

* Estimated degrees of freedom (edf = 1.00 represents a linear relationship).

Live stems also provide notably more canopy hollows than dead stems after 40–50 years post-fire.

4. Discussion

4.1. Broad patterns in the occurrence of hollows

Different types of tree mallee vegetation differed in their provision of hollows, as did different eucalypt species. These results are related; proportionally more *E. gracilis* stems contained hollows than other eucalypts and this species is characteristic of Chenopod Mallee, the vegetation type providing most hollows. Hollow prevalence in other systems also varies on the basis of vegetation type and tree species (Bennett et al., 1994; Lehmkuhl et al., 2003). Chenopod Mallee is noted for its reduced flammability (Pausas and Bradstock, 2007), and has experienced a lower incidence of fire
than Triodia Mallee over the last 40 years (Avitabile et al., submitted for publication). Almost half of all Triodia Mallee has burnt at least once since 1972, whereas only 20% of Chenopod Mallee has experienced fire over this same period. The combination of an increased occurrence of hollows, and reduced frequency of fire, make Chenopod Mallee a critical habitat type for hollow-dependent mallee fauna (see also Watson et al., 2012).

4.2. Hollow development in live tree stems

As with previous work (e.g., Gibbons et al., 2000; Lindenmayer et al., 2000), our results showed a clear positive relationship between live stem diameter and hollow occurrence. Larger eucalypt stems are more likely to contain hollows than small stems, a trend consistent with the positive association between stem size and age.
Larger, older stems have been exposed to hollow-forming processes (e.g., wood decay, branch shedding) for longer periods than young stems (Bennett et al., 1994). In addition, the susceptibility of stems to such processes increases with age, further enhancing the likelihood that large stems will develop hollows (Adkins, 2006). However, unlike other systems (e.g., Bennett et al., 1994; Worthington et al., 2003), the rate of hollow development in this region did not differ strongly between eucalypt species.

When combined with tree-age predictions (Clarke et al., 2010), these results provide insights into the length of time taken for mallee eucalypt to develop hollows. Few live stems younger than 50–60 years old have hollows and, even after a century, the predicted probability of live stems containing a hollow was above 0.2 for only two eucalypt species (*E. gracilis* and *E. oleosa* subsp. *oleosa*). While we do not have data on specific hollow characteristics (e.g., size, depth), the value of such old stems is likely to be enhanced by their capacity to provide a greater range of hollow sizes, particularly large hollows, than young stems (Gibbons et al., 2000; Whitford, 2002), as well as different types of hollows (e.g., crevices, spouts on dead branches) which meet the requirements of different animal species (Gibbons and Lindenmayer, 2002). Similarly, large snags provide greatest habitat value for hollow-nesters in USA (Chambers and Mast, 2005).

### 4.3. Influence of fire-history attributes on the occurrence of hollows

The positive relationship between time-since-fire and hollows in live stems is consistent with previous work in other systems also (e.g., Gibbons et al., 2000). The effect of time-since-fire on hollow occurrence in dead stems provides insight into the role of fire in creating hollows. While the occurrence of canopy hollows in dead stems varied little with time-since-fire, the probability of dead stems containing basal hollows increased, reaching a maximum at 50–60 years post-fire (Fig. 2b). This suggests that the process of hollow formation as a result of fire occurs over many decades in this system (see also Inions et al., 1989), in contrast to parts of the USA where fire has a more immediate effect on the creation of snags for primary hollow-nesters (Chambers and Mast, 2005).

Our results documenting the influence of inter-fire interval on hollows in dead stems are particularly novel. While understood to be important, there is often limited scope to empirically investigate the temporal effects of multiple fires (Gill and McCarthy, 1998) and so these findings provide new insight into understanding the indirect effects of fire on fauna. As structures that have survived fire, dead stems with hollows constitute biological legacies (sensu Franklin et al., 2000) and in this system are crucial for the persistence of hollow-dependent fauna for at least the first 50 years following fire, until hollows begin to develop in live stems (see also Lindenmayer and Wood, 2010). However, our results show that the retention of these biological legacies depends on the inter-fire interval. Recurrent fires within a short time-frame (<45 years) result in low densities of dead hollow-bearing stems during this critical period when compared with areas experiencing longer inter-fire intervals (Fig. 3). Furthermore, dead hollow-bearing stems are larger if fires occur more than 45 years apart, indicating that inter-fire interval influences the habitat value, as well as the retention, of biological legacies in this system.

These results are a consequence of the nature of fire in this region. Unlike many forested systems, most mallee fires are stand-replacing (i.e., remove both canopy and understory vegetation), effectively resetting the successional clock to year zero. In most cases, the stems retained in post-fire habitats will be those that were alive before the fire, and these will be of similar size and hollow-bearing potential. Existing dead stems will commonly be consumed or collapse during the fire, and few hollows form as a result of the fire itself. Thus, hollow occurrence in dead stems shows clear temporal trends as it is strongly affected by successional processes occurring both before and after individual fire events. Except in cases of severe fire (see Banks et al., 2011), documenting the influence of fire-history attributes on hollow occurrence will be more complex in systems where fewer fires are stand-replacing, as a greater diversity of hollow-bearing trees and snags may survive multiple fires. The relatively limited retention of tree stems after fire in tree mallee vegetation, however, means inter-fire interval plays a particularly important role in ensuring hollows are available in early post-fire years. Management practices aiming to provide sufficient resources for hollow-dependent fauna in this region should consider inter-fire interval as well as time-since-fire. In this system, our data show that the size of dead eucalypt stems provides an indication of the length of time between the two most recent fires when exact information is lacking.

### 4.4. Conservation implications

The implications of these results for fauna require an understanding of which species use hollows for breeding or shelter, and the characteristics of the hollows they select. Such information is negligible for tree mallee vegetation. In the most detailed study available on faunal use of tree hollows in mallee systems, Lumsden et al. (2008) recorded the use of hollows for roosting by the extremely rare South-eastern Long-eared Bat (*Nyctophilus corbenti*). All roost hollows were located in dead stems and most were canopy hollows; however, individuals were found to roost in the most common type of tree/hollow available (Lumsden et al., 2008). In addition, the hollow-bearing stems selected as roost sites were found in areas with abundant hollows, known to have remained unburnt for at least 70 years, possibly over a century or more. Lumsden et al. (2008) concluded that this extended fire-free period was a key factor in providing suitable habitat for the South-eastern Long-eared Bat. Our results provide additional insights, by indicating that long inter-fire intervals (e.g., >50 years) were also influential due to the retention of many dead stems with canopy hollows. Furthermore, individual bats used multiple roost hollows located considerable distances apart (mean 1.9 km: Lumsden et al., 2008), highlighting the need to also consider the wider spatial availability of hollows when managing for hollow-dependent fauna (see Gibbons and Lindenmayer, 1996).

Our results provide insights for fire management employing inter-fire interval prescriptions. The minimum and maximum tolerable fire intervals identified for Triodia Mallee, the dominant type of tree mallee vegetation in the region, are 25 and 90 years respectively (Department of Sustainability and Environment, 2008). These figures are based on the vital attributes of key plant species. However, our findings show that prescriptions within much of this range (e.g., intervals of 30–60 years) are unlikely to maintain sufficient resources for hollow-dependent fauna in the short or long-term. For example, the probability of live stems in the eucalypts characteristic of Triodia Mallee, *E. dumosa* and *E. socialis*, containing hollows was less than 0.1 after 60 years, and these stems were relatively small (7–9 cm diameter). Further, fires occurring every 40–50 years (or less) are likely to eliminate hollows from mallee vegetation, as very few live stems develop hollows within 50 years. Thus, fire management guidelines employing inter-fire intervals based solely on floristic attributes will be inappropriate for providing essential habitat resources for all fauna, particularly species that rely on slow-developing resources such as hollows (see Clarke, 2008). Appreciation of the full length of time taken for such resources to become available after fire is imperative for ecological management.
5. Conclusion

Our results confirm that the temporal characteristics of fire regimes have potentially strong, and complex, indirect effects on hollow-dependent fauna in this system. Time-since-fire and inter-fire interval both affect hollow occurrence over extended time-frames, but their influence differed between live and dead stems. Hollows in live stems were affected only by time-since-fire whereas inter-fire interval had important effects on the probability of dead stems containing hollows. The inter-fire interval is a key determinant of whether post-burn habitats provide hollows during the decades required for them to develop in live stems, and thus is a critical influence on the ongoing persistence of hollow-dependent fauna in this region. Managing fire in a way that maintains habitat resources for hollow-dependent mallee fauna requires long fire-free intervals, in terms of both the length of time since the most recent fire, and between successive fires.

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