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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

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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 (Bütler 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 km^2 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 $\geqslant$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 understorey 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 understorey, the latter being a perennial hummock grass known for its flammability and importance to 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 km^2) spread across the region. On average, there were 21 sites per landscape unit (range: 7–30 sites) and they were selected