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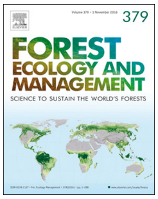

The effects of fire history on hollow-bearing tree abundance in montane and subalpine eucalypt forests in southeastern Australia

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ABSTRACT

Hollow-bearing trees provide critical habitat resources for forest fauna, yet there is evidence of a ubiquitous decline in the large, old trees most likely to provide this resource. Fire can influence the formation and persistence of tree hollows. In this study, we investigated the effects of stand-level fire history and individual tree attributes on tree hollow abundance in two forest types in Namadgi National Park in the Australian Capital Territory: subalpine woodlands dominated by *Eucalyptus pauciflora* Sieber ex Spreng (snow gum); and tall-open *E. delegatensis* R.T.Baker (alpine ash) montane forest. These forests can be differentiated by their distinct response to fire; *E. pauciflora* resprouts following fire and *E. delegatensis* reproduces exclusively via seed. We employed a ground-based approach to measure 1044 trees across 36 sites selected by forest type and fire history as recorded since 1920. For both species, hollow abundance decreased with total fire count at stand level and increased for *E. delegatensis* in response to an extensive wildfire that occurred in the study area in 2003. The probability of a tree containing a hollow increased with tree diameter and if the tree was dead. Our results show that fire frequency and severity have strong implications for tree hollow abundance in montane and subalpine eucalypt forests.

1. Introduction

Many species of fauna rely exclusively on the structural aspects of trees for shelter and nesting (Koch et al., 2008; van der Hoek et al., 2017). Globally, up to 18% of bird species and many mammal and invertebrate species utilise tree hollows (Remm and Lõhmus, 2011). In Australia, at least 15% of all vertebrates, including 42% of all mammals (Ambrose, 1982) and 15% of all birds, use tree hollows in some manner (Gibbons and Lindenmayer, 2002). Many hollow-using species in Australia, and worldwide, are considered rare, threatened or near-threatened (Snape et al., 2015; Rueegger, 2017; McLean et al., 2018), possibly due to the limiting nature of available habitat (Sedgwick and Knopf, 1986). Common uses of tree hollows, or cavities, include nesting, roosting, hunting, obtaining water and thermoregulation (Gibbons et al., 2000; Gibbons and Lindenmayer, 2002; Walker et al., 2005; Koch et al., 2008; Manning et al., 2013). Despite their importance to fauna, suitable tree hollows can take a long time to form (> 100 years) (Parnaby et al., 2010) and are more common in older trees that are less resistant to decay (Rudman, 1965). The imminent shortage of tree hollows predicted for the future has led many Australian states to declare the “loss of hollow-bearing trees” as a threatening process (Parnaby et al., 2010). It is widely acknowledged that fire history influences the availability of hollows, yet the relationship is not well understood.

The global stock of large, old trees, which are more likely than younger trees to be hollow-bearing, is suffering a net decline across many of Earth’s forested regions (Lindenmayer et al., 2014a, 2014b; Case et al., 2017). This may have serious implications for biodiversity and ecosystem function and integrity (Le Roux et al., 2014). Despite the ecosystem services they provide, large old trees are disproportionately vulnerable to decline compared to younger trees (Remm and Lõhmus, 2011; Lindenmayer et al., 2012a, 2014b). Agriculture poses a significant threat as large, old trees are often cleared for grazing, cropping and firewood (Schmiegelow and Mönkkönen, 2002; Maron and Fitzsimons, 2007; Lindenmayer et al., 2012b). These trees are also threatened by logging, wildfire and urban encroachment into rural areas (Lindenmayer et al., 2012b; Le Roux et al., 2014). Changes in climate and fire patterns are posited as further factors behind the rapid change in ecosystem structure that makes large trees so vulnerable (Gill, 1975; Cary et al., 2012).

Wildfires have played a key role in the structure and composition of vegetated ecosystems worldwide (Vivian et al., 2008; Bowman et al.,

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2009). The eucalypt forests of Australia support many species with life history strategies adapted to co-exist with fire (Noble and Slatyer, 1980; Cary et al., 2012; Haslem et al., 2012). Both wildfire and prescribed fire can influence the formation of tree hollows and the collapse of hollow-bearing trees (Gibbons and Lindenmayer, 2002). Through direct or indirect pathways, fire is a catalyst for cavity formation in eucalypts and other trees, yet hollow-bearing trees are particularly vulnerable to collapse following fire events (Eyre et al., 2010; Banks et al., 2011). Global climate change may lead to a shift in fire regimes (Cary et al., 2012) which have the potential to change floral distribution at the ecosystem level (Walther et al., 2002). Coupled with changes in land management and the shifting priorities of prescribed burning, there is a need to understand how these changes will affect hollow-bearing tree abundance.

A major indicator of how a forest will respond to fire relates to the reproductive strategy of the dominant species. This response can impact hollow formation (Noble and Slatyer, 1980). Eucalypts can be classified by their response to fire on a spectrum between ‘obligate seeders’, those that regenerate exclusively through seed, and ‘resprouters’, those that regenerate through epicormic buds stored under bark and lignotubers (Jacobs, 1955; Noble and Slatyer, 1980; Adkins, 2006; Vivian et al., 2008; Keith, 2012). Facultative resprouters are those species with the ability to respond to fire through both mechanisms. Increasing inter-fire-interval (IFI) and a reduction in total fires benefits hollow-using fauna in basal resprouting eucalypts in the Murray Mallee region of western Victoria (Haslem et al., 2012). Trees that respond to fire through resprouting may support multiple cavities as the initial growth points of epicormic buds may expose the heartwood (Jacobs, 1955; Adkins, 2006). Forests dominated by obligate seeders like *E. delegatensis* (alpine ash) are expected to feature a different pattern of hollow-bearing tree abundance in relation to fire history. These species often die under full canopy scorch and resort to large-scale seeding to recruit for the next generation (Vivian et al., 2008). The typical stand of obligate seeder ash-type eucalypts, such as *E. delegatensis* and *E. regnans* (mountain ash), requires a minimum of 120 years before trees reach sufficient size for useable hollows for fauna to develop (Fox et al., 2009). However, fire events can have more immediate effects on hollow abundance in such forests, as they can lead to the collapse of hollow-bearing trees as well as the development of hollows from damage to mature trees (Gibbons et al., 2000; Adkins, 2006; Parnaby et al., 2010; Banks et al., 2011).

In this study, we aimed to investigate the factors influencing the abundance of hollow-bearing trees in the montane and subalpine forests of Namadgi National Park, in the north-eastern Australian Alps bioregion (Australian Capital Territory). Our specific focus was on how wild and prescribed fire and individual tree traits (height and diameter) influence the abundance of hollow-bearing trees. This large national park is on the urban interface with the city of Canberra, where hazard reduction burns are implemented regularly and where a large, intense wildfire occurred in 2003. However, little research has been undertaken to understand how fire influences the abundance of hollow-bearing trees. We contrasted forests dominated by two types of eucalypts: a facultative resprouter (snow gum, *E. pauciflora*) and an obligate seeder (alpine ash, *E. delegatensis*). We measured hollow abundance and tree attributes in replicated transects in forest stands with different fire histories to identify how the past 98 years of recorded fire history have influenced hollow abundance. In addition, we quantified relationships between hollows and tree attributes for the two tree species. The study provides insight into the ecology of hollow-bearing trees that can be used in environmental management.

2. Methods

2.1. Study area

Namadgi National Park (35°37′ S 148°52′ E) covers just over 100,000 ha, or 46% of the Australian Capital Territory (ACT), south-eastern Australia (Fig. 1). Set amongst a series of montane to alpine peaks, it occupies the western part of the ACT in the north-eastern Australian Alps region. The park varies from low elevation grassy valleys in frost hollows (900–1100 m) to subalpine and alpine peaks over 1900 m (ACT Government, 2010) including the Brindabella and Scabby Ranges. Sections of Namadgi National Park are snow-covered throughout the winter.

There is evidence of Indigenous occupation in Namadgi National Park for at least 20,000 years (Zylstra, 2006; ACT Government, 2010). Until heavy European settlement in the first half of the nineteenth century, fires in the region were far less frequent than today (Banks, 1982; Carey et al., 2003). Fire frequency increased dramatically during the period of 1850–1950 as a result of agricultural activity (Carey et al., 2003). Land use changed from the 1950s when the value of the water supply was identified and the Park was established in 1984 (ACT Government, 2010). Large fires of natural origin occurred in the park in 1920, 1926 and 1939, as well as more recent large severe fires, such as the 2003 conflagration.

Namadgi National Park has a variety of vegetation communities including grasslands, wetlands, shrublands, woodlands and forests (Hope, 2002). Of particular interest to this research are the montane and subalpine woodlands dominated by *E. pauciflora* subsp. *pauciflora* and *E. pauciflora* subsp. *niphophila,* respectively, and montane tall forest dominated by *E. delegatensis* (ACT Government, 2010). *E. pauciflora* represents an example of a facultative resprouter, having the ability to regenerate following fire from seed or sprouts. Observations of regeneration following the 2003 fires suggest *E. pauciflora* favours lignotubers as the dominant regenerative mechanism, with epicormic shooting as secondary (Carey et al., 2003). Regeneration from lignotubers following fire leads to the multi-stemmed habit often seen in fire-affected stands. Many of the main stems have been observed to die following high severity burns. In contrast, *E. delegatensis* is an obligate seeder (Ashton, 1981; Carey et al., 2003) and is typically killed under full canopy scorch leaving the dense regeneration of seedlings to compete for resources.

2.2. Site selection

The data used in the survey design were provided by the ACT Government Environment, Planning and Sustainable Development Directorate. Maps of the fire history in Namadgi National Park spanning 1920–2015, fire type (wildfire or prescribed), vegetation class (Keith, 2004), and severity of the 2003 wildfire as derived from Barrett (2006) were used in generating site selection. Fire severity has only been recorded since 2003 and a map of fire severity for the 2003 fire was used in this study.

We stratified the sites by fire history and vegetation type, by generating polygons in ESRI ArcGIS (ArcGIS, 2012) where the dominant species in the vegetation class was *E. pauciflora* or *E. delegatensis* intersected with the targeted fire history. We stratified sites by grouping the total number of fires since 1920 into three classes: 0 fires, 1–3 fires and > 3 fires (Fig. 2). Only eight of the total sites selected were subject to a prescribed burn, therefore both natural and prescribed fires were included in the total fire count and prescribed fires were not used as a separate variable in modelling. We used ArcGIS to select eight random sites within each vegetation type and fire history category. Although 48 sites were targeted, some vegetation type by fire history strata did not exist (e.g., long-unburnt *E. delegatensis*). We recorded measurements from a total of 36 sites in Namadgi National Park; 13 *E. delegatensis* forest sites and 23 *E. pauciflora* woodland sites. Thus, our study design is representative of the common fire histories in forest stands in the region, however we acknowledge that these fire histories span a narrow range for this species. A full list of sites is available in Appendix A.