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Environmental and human drivers influencing large old tree abundance in Australian wet forests

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ABSTRACT

Large old trees are keystone structures in numerous ecosystems globally. They play a wide range of critical ecological roles and therefore quantifying the factors influencing their distribution and abundance therefore has significant management implications. Yet, there are few ecosystems worldwide for which quantitative statistical models of the factors affecting large old tree distribution and abundance have been produced. We constructed a suite of such models using cross-sectional data on the occurrence of large old hollow-bearing trees gathered in 2015 on 166 sites, each of 1 ha in size within the montane ash forests of the Central Highlands of Victoria, south-eastern Australia. Our analyses included two broad groups of models, those for: (1) the overall abundance of large old hollow-bearing trees at a site, and (2) the abundance of large old hollow-bearing trees in four different morphological states of decay. These were large old living trees, large old hollow-bearing trees deemed potentially suitable for marsupial gliders, large old hollow-bearing trees deemed potentially suitable for non-gliding marsupial possums, and large old collapsed hollow-bearing trees.

Most of the models we built encompassed a combination of covariates encompassing environmental factors (such as elevation and topographic wetness), human disturbance (e.g. land tenure), and natural disturbance (wildfire). The overall total abundance of large old hollow-bearing trees (irrespective of morphological form) was greatest at unburned sites, within stands of old-growth forest, within reserves, and on wet sites (as reflected by a topographic wetness index). Conversely, sites in young forests and sites subject to moderate or high severity fire supported the highest abundance of collapsed large old hollow-bearing trees.

Our results demonstrate that different sets of environmental factors and attributes reflecting human disturbance, and natural disturbance affect the abundance of different morphological forms of large old hollow-bearing trees. Therefore, different parts of landscapes are most suitable for different kinds of large old hollow-bearing trees. The findings of this study can help direct management toward places where actions to recover populations of large old hollow-bearing trees are needed and/or are most likely to be effective, such as for conserving cavity-dependent animals.

1. Introduction

Large old trees are a critical resource in a wide range of ecosystems globally, ranging from forests, woodlands and deserts to agricultural landscapes and urban environments (Lindenmayer et al., 2014b). They have an array of key ecological roles, including in hydrological regimes and nutrient cycles as well significantly affecting the distribution and abundance of populations of plants and animals (Manning et al., 2006; Lindenmayer et al., 2012b). However, populations of large old trees are declining in a range of ecosystems worldwide (Lindenmayer et al., 2012b) and understanding the natural and human-derived factors affecting the distribution and abundance of these keystone ecological structures (sensu Tews et al., 2004; Manning et al., 2006) has therefore never been more critical. At landscape and local scales, factors like slope, aspect, proximity to watercourses, topographic wetness, soil depth, and the prevalence of herbivores can be important determinants of the occurrence of large old trees (Lindenmayer et al., 1991a; Pederson, 2010; Vanak et al., 2011; Thomas et al., 2013; Ikin et al., 2015). The distribution and abundance of large old trees is

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also driven by natural disturbances, such as droughts (Choat et al., 2012; Rowland et al., 2015) and windstorms (Webb, 1988). For example, recurrent fire also can reduce or eliminate populations of large old trees from particular areas (Barlow et al., 2003; Lindenmayer et al., 2012a) as can widespread insect attack (Kashian et al., 2011; Popkin, 2015) and dieback (Palik et al., 2011). Conversely, floods, high-severity fire or periodic relief from high-intensity ungulate grazing can trigger regeneration cohorts that lead to recruitment pulses of trees (George et al., 2005; Moe et al., 2009; Smith et al., 2013). Human management is also a key driver of the distribution and abundance of large old trees; logging, clearing, prescribed fire and other activities like habitat fragmentation and prolonged livestock grazing strongly influences where large old trees are found (Laurance et al., 2000; Nilsson et al., 2006; Kauppi et al., 2015). There also can be significant cultural factors (beyond those associated with natural resource management and human disturbance) that underpin the occurrence of large old trees. For instance, some very large trees occur in particular places because they have been preserved for religious or other cultural reasons (Blicharska and Mikusinski, 2014). The array of natural factors and attributes of human disturbance that can influence the distribution of large old trees operate at different spatial and temporal scales and this can make it challenging to accurately model their occurrence. Nevertheless, such modelling is essential for improved understanding of where such trees occur, why they occur where they do and, in turn, how to best target management actions (Ikin et al., 2015) such as determining the spatial location of refugia for large old trees (Mackey et al., 2012).

In this paper, we quantify the factors influencing the abundance of large old hollow-bearing trees in the montane ash forests of the Central Highlands of Victoria, south-eastern Australia. Large old trees in these ecosystems, particularly Mountain Ash (*Eucalyptus regnans*) trees are among the tallest flowering plants on earth (Ashton, 1975), provide critical habitat for an array of cavity-dependent species (Lindenmayer et al., 2015), and store large amounts of carbon (Keith et al., 2009). Moreover, earlier work has shown that the fastest-growing Mountain Ash trees are also the largest and oldest individuals, even though these trees are often the most decayed. These largest trees continue to produce very large amounts of biomass up to the time of apical crown collapse (Koch et al., 2015).

Montane ash forests are sensitive to the effects of fire, particularly high-severity stand-replacing conflagrations (Taylor et al., 2014) which can kill trees or damage them, leaving significant fire scars (McCarthy and Lindenmayer, 1998). Such fires also usually trigger germination (Smith et al., 2013) of a new cohort of the eucalypts. If the mature overstory trees survive the fire, the result can be stands with multiple age cohorts of trees comprising both young post-fire regenerating trees. Large old trees in these disturbed stands are the living and/or dead biological legacies (sensu Franklin et al., 2000) of the pre-disturbance stand. Thus, these biological legacies can be of a markedly different age to the surrounding regenerating stand, although this may not necessarily be the case in pure stands of old-growth forest when the majority of overstory trees will be of similar age (Lindenmayer et al., 2000).

Past work in montane ash forests has documented the rate of collapse of large old hollow-bearing trees (e.g. Lindenmayer et al., 1997, 2012a). However, spatial patterns of overall abundance of large old hollow-bearing trees as well as the factors affecting such patterns remain poorly understood. Moreover, in common with other kinds of forest worldwide (e.g. see Cline et al., 1980), large old trees in montane ash forests exist as a range of morphologically different forms that correspond to trees in different stages of decay (Fig. 1). These morphological forms of trees are important for different elements of the biota (Lindenmayer et al., 1991b) and also contrast markedly in the amount of carbon that they store (Keith et al., 2009). However, it is not known whether the abundance of these different kinds of trees varies across landscapes and in response to different sets of predictor variables. In particular, the effects on morphological forms of large old hollow-bearing trees of wildfire, which is a major form of natural disturbance in these ecosystems, (Ashton, 1975; Lindenmayer et al., 2011) has not previously been documented. Yet, such information on large old hollow-bearing trees is critical for planning management zones that attempt to integrate wildlife conservation and wood production in montane ash forests (Lindenmayer et al., 2014a), including the Critically Endangered Leadbeater's Possum (*Gymnobelideus leadbeateri*). We therefore sought to quantify the environmental and human-derived factors influencing the abundance of large old hollow-bearing trees in the montane ash forests of the Central Highlands of Victoria. Specifically, we sought to answer two key questions:

Q1. What environmental and human factors influence the abundance of large old hollow-bearing trees? To address this question, we quantified relationships between the numbers of large old hollow-bearing trees at 166 sites distributed widely across our study region and an array of potential explanatory variables including topography (measures of slope, aspect, elevation), topographic wetness, the age of the stand in which these trees are located, the severity of past fire, and land tenure.

Q2. Do different factors or combinations of factors influence the abundance of different morphological forms of large old hollow-bearing trees? We sought to quantify the impacts of potential explanatory variables on the abundance at a site of four broad kinds of large old hollow-bearing trees. These four morphological categories of large old trees encompass critical stages in large tree development, decay and loss in montane ash forests. We quantified the fraction of the total number of large old hollow-bearing trees that were in each category (decay stage). Trees in different stages of decay vary in their suitability as potential nesting and denning habitat for different species of cavity-dependent vertebrates such as arboreal marsupials in montane ash forests. The four categories of trees were: (1) Living trees (forms 1–2 in Fig. 1). (2) Collapsed trees (form 9 in Fig. 1). (3) Trees in forms 2–4 inclusive. These are trees are ones which previous studies of arboreal marsupials have indicated will be those most suitable for marsupial gliders such as the Greater Glider (*Petauroides volans*) and the Yellow-bellied Glider (*Petaurus australis*) (Lindenmayer et al., 1991b). And, (4) Trees in forms 5–8 inclusive which are trees typically most likely to be occupied by non-gliding possums such as the Critically Endangered Leadbeater's Possum as well as other species like the Mountain Brushtail Possum (*Trichosurus cunninghamii*) (Lindenmayer et al., 1991b). Notably, we made no assumption that these kinds of trees would be occupied, merely that they would be potentially suitable for occupancy by marsupial gliders or possums. We postulated that different sets of environmental, disturbance and other factors would influence the abundance of the different morphological kinds of trees (shown in Fig. 1). We made this prediction for a range of reasons but particularly because, for example, fire may have greater impacts on large old dead trees than large old living trees given the potential for a conflagration to consume decayed wood (Banks et al., 2011). Thus, there will be substantial differences in the likely persistence of different morphological types of trees on sites subject to wildfire.

2. Methods

2.1. Study area and surveys of large old trees

We completed this study in the montane ash forests of the Central Highlands of Victoria, south-eastern Australia (Fig. 2).