Forest Ecology and Management 391 (2017) 221–229

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Relationships between tree size and occupancy by cavity-dependent arboreal marsupials

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ARTICLE INFO

Article history:
Received 16 December 2016
Accepted 7 February 2017
Available online 21 February 2017

Keywords:
Hollow-bearing trees
Cavity trees
Snags
Forest management
Leadbeater's Possum
Mountain Ash forests
Possums and gliders
Large old trees
South-eastern Australia

ABSTRACT

Hollow-bearing trees are keystone structures in many ecosystems worldwide and they play critical habitat roles for a vast array of fauna through providing denning and/or nesting sites. We quantified empirical relationships between the diameter of hollow-bearing trees and probability of occupancy of these trees by cavity-dependent arboreal marsupials in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, south-eastern Australia. We also quantified the effects of other variables such as stand age and elevation on tree occupancy. Finally, we compared the diameter of occupied and unoccupied hollow-bearing trees with non-hollow-bearing trees in 77-year old forest that regenerated after fires in 1939 and which form the dominant age cohort of trees in our study region.

Hollow-bearing trees occupied by arboreal marsupials had a larger diameter than unoccupied hollow-bearing trees. The mean diameter of both occupied and unoccupied hollow-bearing trees was almost three times that of 1939-aged trees that did not contain hollows. Our analyses contained evidence of inter-specific differences in the diameter of hollow-bearing trees occupied by different species of arboreal marsupials. Beyond the influence on occupancy of tree-level factors such as diameter, we also found that the probability of occupancy of a hollow-bearing tree was affected by the age of the surrounding forest and landscape attributes such as elevation. The probability of occupancy of an individual hollow-bearing tree was highest when that tree was located in regrowth forest, most likely because of the scarcity of these critical nesting and denning resources in such stands.

Populations of large hollow-bearing trees, including those typically selected for occupancy by arboreal marsupials, are in rapid decline in Mountain Ash forests. This decline, coupled with the prolonged period until current cohorts of existing younger trees eventually reach an age (and therefore diameter) that are suitable for occupancy by arboreal marsupials, underscores the critical need to protect all existing hollow-bearing trees from practices that can otherwise destroy them, including industrial clearfelling operations. Better protection is important not only in the small remaining areas of old growth Mountain Ash forest but also in regrowth forest where such trees are scarce and have high marginal value as nesting sites, as reflected by high rates of per tree occupancy rates in stands of this age.

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1. Introduction

Large old trees are a critical structural feature of many ecosystems worldwide and they have several key characteristics not found in small young trees or small old trees (Lindenmayer and Laurance, 2016). One of these characteristics is the presence of cavities that provide nesting and denning sites for a wide range of fauna globally (Fischer and McClelland, 1983; Rose et al., 2001; Gibbons and Lindenmayer, 2002; Remm and Lohmus, 2011). Australia lacks primary cavity-excavating vertebrates such as woodpeckers, and trees on the continent develop cavities in several ways, for example through the activities of organisms such as fungi and termites (Perry et al., 1985; Remm and Lohmus, 2011), disturbances such as fires (Inions et al., 1989), and age-related changes in tree physiology such as incomplete occlusion of wound tissue following damage such as stem wounding and/or branch breakage

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http://dx.doi.org/10.1016/j.foreco.2017.02.014
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(Gibbons and Lindenmayer, 2002). The effects of these processes can be both time and tree-size mediated, meaning that hollow-bearing trees should be the largest and longest-living individuals in most ecosystems. Those trees with large cavities suitable for occupancy by cavity-dependent species should be larger than unoccupied trees. We tested these simple premises in an investigation from the wet Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, south-eastern Australia.

Hollow-bearing trees in wet ash-type eucalypt forests can be recruited over prolonged periods of ontological development meaning that such trees are typically most abundant in old growth forests (Lindenmayer et al., 2000a). Hollow-bearing trees also may develop in pulses or cohorts as a result of major disturbance events such as wildfires (Gibbons and Lindenmayer, 2002). For example, large numbers of hollow-bearing trees in Mountain Ash forests were created when old growth trees and stands were burned in high-severity, stand-replacing wildfires in 1939 (Lindenmayer et al., 1991b). In contrast, stands subject to clearfell logging commonly retain few or no live or dead large old trees, and new hollow-bearing trees will typically take over 120 years to form (Ambrose, 1982). Importantly, hollow-bearing trees in Mountain Ash forests are critical nesting and denning sites for an array of species of cavity-dependent vertebrates including eight species of arboreal marsupials such as the Critically Endangered Leadbeater's Possum (*Gymnobelideus leadbeateri*) (Lindenmayer et al., 2015) and the nationally vulnerable Greater Glider (*Petauroides volans*) and regionally vulnerable Yellow-bellied Glider (*Petaurus australis*). Specifically, we posed four key questions in this study:

Q1: ***Are there relationships between tree occupancy by arboreal marsupials and the diameter of such trees?*** We predicted there would be strong positive relationships between the diameter of trees and the probability of them being occupied by arboreal marsupials. That is, occupied hollow-bearing trees would also be large diameter trees. This is because larger trees develop more and larger cavities (Mackowski, 1987; Lindenmayer et al., 1993, 2000b) that are more likely to be suitable for occupancy by comparatively large cavity-dependent vertebrates such as arboreal marsupials.

Animals require not only access to denning and sheltering sites, but also areas in which to forage. The suitability of foraging substrates may be influenced by the structure of the forest surrounding nesting sites that can vary in response to factors such as stand age. Our second key question was therefore:

Q2: Is the occupancy of hollow-bearing trees by arboreal marsupials influenced the age of the surrounding forest? At the outset of this study, we were agnostic about the kinds of relationships that might occur between tree occupancy and the age of the surrounding forest. Potentially, the proportion of hollow trees used per animal may vary with hollow tree availability (for instance, due to changes in resource sharing (Banks et al., 2011), or due to resources other than the availability of hollow trees limiting animal occurrence (Banks et al., 2013)). For example, the probability of occupancy of individual hollow-bearing trees may be reduced in old growth forests where animals have access to many alternative trees; that is, the marginal value of a given tree will be lower where there are already many hollow-bearing trees (Fischer et al., 2010). Conversely, the probability of occupancy of trees in old growth forest may be greater because of the suitability of surrounding areas as a food source for particular species (Lindenmayer et al., 1990b). In addition to test for the effects of stand age, we also sought to determine tree occupancy was influenced by factors such as the elevation of the site in which trees were located.

Q3. *Are there inter-specific differences in the diameter of trees selected by different species of arboreal marsupials?* Many species of animals select cavities in trees that are large enough to permit entry but with an entrance that precludes larger-bodied species that may be predators or competitors (Gibbons and Lindenmayer, 2002). Given relationships between tree size and cavity size (Mackowski, 1987; Lindenmayer et al., 1993), we postulated there would be positive relationships between the body size of particular species of arboreal marsupials and the diameter of trees they occupied.

The selection of trees for analyses of relationships between occupancy and diameter was based on those trees supporting obvious cavities (as determined using a pair of binoculars; see Section 2.2). However, it was important to determine if trees occupied by arboreal marsupials differed in diameter relative to other (non-hollow-bearing) trees in the remainder of the stand. We therefore posed a fourth question:

Q4: Are there differences in the diameter of hollow-bearing trees occupied by arboreal marsupials and the diameter of non-hollow-bearing trees? For this analysis, we focused on stands of trees that regenerated following the 1939 wildfires. We targeted this age class because it is the dominant age cohort in Mountain Ash forests and given the current lack of old growth forest in this ecosystem (<1.16% of the estate (Lindenmayer et al., 2012a)), trees in these stands will be the next ones to develop into old growth if they are able to reach ecological maturity (Lindenmayer et al., 2015). Cavities in 77-year-old trees are very rare and typically lack the depth required for use by arboreal marsupials. As cavities typically develop in older and therefore larger Mountain Ash trees (Lindenmayer and Laurance, 2016), we postulated that hollow trees would be significantly larger than other Mountain Ash trees that lacked cavities in the surrounding stand.

Populations of large old hollow-bearing trees are declining in many (although not all) ecosystems globally (Lindenmayer et al., 2012b; Lindenmayer and Laurance, 2016). Such declines characterise Mountain Ash forests in the Central Highlands of Victoria (Burns et al., 2015). The loss of these trees will likely have corresponding negative conservation outcomes for an array of cavity-dependent species, including arboreal marsupials. Therefore, better understanding of the patterns of occupancy of trees of different sizes and contexts (i.e. relative to surrounding stand conditions) will have important implications for how to best manage ecosystems where hollow-bearing trees are keystone structures (sensu Tews et al., 2004).

2. Methods

2.1. Study area

We completed this study in the Mountain Ash forests of the Central Highlands of Victoria, south-eastern Australia (Fig. 1). We established 119 long-term ecological research sites in the study region (Lindenmayer et al., 2003). Each of these sites measured 1 ha in size and were well distributed throughout the study region, covering a wide range of variation in environmental conditions. Our sites varied in slope (inclination: 2–38°), elevation (220–1040 m), topographic position (gully, midslope, ridge) and aspect (assigned to one of the following categories: north, east, south, west). At the outset of this investigation (1997), we assigned our 119 field sites to one of four stand age classes: old growth (stands where the dominant age class of the overstorey had established pre-1900), stands that regenerated after the major wildfires in 1939, stands that regenerated after logging conducted between 1960 and 1990, and stands of overstorey trees of mixed age.

We completed three kinds of repeated surveys on our 119 field sites: (**1**) surveys of arboreal marsupials, (**2**) measurements of hollow-bearing trees, and (**3**) measurements of vegetation structure, primarily stand age. We briefly describe these surveys and

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