Forest Ecology and Management 430 (2018) 259–264

Contents lists available at ScienceDirect

Forest Ecology and Management

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

The road to oblivion – Quantifying pathways in the decline of large old trees

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ARTICLE INFO

Keywords:
Hollow-bearing tree
Snag
Fire
Ash-type eucalypt forests
Tree fall
Tree mortality

ABSTRACT

Large old hollow-bearing trees have a wide range of key ecological roles in forest and other ecosystems globally. Patterns and rates of mortality and decay of these trees had profound effects on the size and composition of their populations. Using an 18-year empirical study of large old trees in the Mountain Ash (*Eucalyptus regnans*) forests of the Central Highlands of Victoria, we sought to determine if there are particular patterns of decline that are shared by a proportion of the trees in a tree population. We also sought to identify drivers of decline of these trees by quantifying relationships between the condition state of trees (*viz*: tree form) and a range of covariates.

We found that time, stand age and fire can individually and in combination, strongly affect the decay (and eventual collapse) of large old trees. In particular, we found compelling evidence that patterns of tree decline were markedly different in old growth forest (stands dating from ∼1850) relative to three other younger age classes examined. Trees in older forest decayed less rapidly than trees of equivalent tree form in younger forest. Old growth stands also were characterized by trees in an overall much lower (more intact) form category than the other age classes of forest. A key pattern in our study was the rapid deterioration of large old trees in the youngest aged stands (*viz*: those regenerating after fires in 1939 and following disturbance between 1960 and 1990). In these forests, a very high proportion of large old trees were either in the most advanced state of tree decay (form 8) or had collapsed (form 9). This is a major concern given that 98.8% of the Mountain Ash forest ecosystem supports forest belonging to these (or even younger) age cohorts. Our investigation highlights the need for forest management to: (1) increase levels of protection for all existing large old hollow-bearing trees, (2) expand the protection of existing regrowth forest so there is the potential to significantly expand the currently very limited areas of remaining old growth forest.

1. Introduction

Large old trees are keystone structures in many forested, agricultural and urban ecosystems worldwide (Manning et al., 2006; Moga et al., 2016; Lindenmayer and Laurance, 2017). These trees have many ecological roles including habitat provision for wildlife (Fischer and McClelland, 1983; Rose et al., 2001; Lindenmayer and Laurance, 2017), acting as a source of fallen coarse woody debris on the forest floor (Elton, 1966; Maser and Trappe, 1984), and affecting nutrient cycles (including storing large amounts of carbon) (Keith et al., 2009). In common with the populations dynamics of all long-lived organisms, rates and patterns of mortality of adult trees strongly affects the size and long-term dynamics of populations of large old trees (Gibbons et al., 2008). Indeed, high levels of adult mortality is one of the key factors underpinning elevated rates of decline of large old trees in many ecosystems globally (Lindenmayer et al., 2012).

Trees can pass through a range of morphological stages over their lifespan and after they have died. A range of decay classes has been identified for large old trees in several forest types such as the Douglas Fir (*Pseudotsuga menziesii*) forests of north-western North America (e.g. Cline et al., 1980), the wet ash eucalypt forests of south-eastern Australia (Lindenmayer et al., 2016), the boreal forests of Canada (Burton et al., 2003) and oak forests of eastern Europe (Moga et al., 2016). These stages correspond to trees in a sequence of conditional states from intact living trees to dead collapsed trees (Keen, 1955; Cline et al., 1980; Lindenmayer et al., 2016). The progression of trees through these stages is probabilistic with any given tree not necessarily passing through all decay classes; for example, a living intact tree may not undergo any deterioration (such as becoming a dead standing tree), but rather collapse directly to the forest floor. Given such probabilistic changes, two key inter-related questions are:

Are there particular patterns of change in condition that trees follow

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https://doi.org/10.1016/j.foreco.2018.08.013
Received 3 May 2018; Received in revised form 1 August 2018; Accepted 8 August 2018

through the process of decay and collapse? That is, are there particular patterns of change shared by a proportion of the trees in a tree population? If so, are these patterns influenced by the age of forest in which trees are located and/or whether the stands have been affected by disturbances such as fire?

For this investigation, we sought to answer these questions for the iconic Australian tree, Mountain Ash (*Eucalyptus regnans*), which is the tallest flowering plant on earth. Large old trees in these forests are important nesting sites for a wide range of cavity-dependent vertebrates (Lindenmayer et al., 2017) and understanding their patterns of decline is critical for predicting temporal changes in biodiversity, including for a range of threatened species such as the Critically Endangered Leadbeater's possum (*Gymnobelideus leadbeateri*) and the Vulnerable greater glider (*Petauroides volans*) and yellow-bellied glider (*Petaurus australis*) (Lindenmayer et al., 2015). Large old trees also store large amounts of carbon (Keith et al., 2009; Keith et al., 2017) and influence the water cycle in Mountain Ash forests (Vertessy et al., 2001). Quantifying the pathways of decline and the factors influencing the pattern of occurrence of large old trees is therefore important to better inform how to best manage populations of these keystone structures. Moreover, the approach we have employed to model pathways of decline in cohorts of large old trees has potential application in other kinds of forests, particularly those in places like western North America and boreal forest environments where such trees are critical for an array of cavity-using taxa (e.g. see Rose et al., 2001; Franklin et al., 2002; Burton et al., 2003).

2. Methods

2.1. Study area and surveys of large old trees

We completed this study in the Central Highlands of Victoria, south-eastern Australia where there is approximately 157 000 ha of Mountain Ash (Keith et al., 2017). The primary form of natural disturbance in this forest is high-severity, stand-replacing or partial stand-replacing wildfire; the last major conflagration was in 2009 when 78 300 ha of Mountain Ash burned (Berry et al., 2015). In addition, approximately 80% of the Mountain Ash forest estate in the Central Highlands is located in areas broadly designated for wood production and the predominant silvicultural system is clearcutting in which cutblocks of 15–40 ha are harvested (Flint and Fagg, 2007).

We established 96 long-term ecological research sites in Mountain Ash forest. Each site was 1 ha in size, on which we completed repeated measurements of the number and condition of large old hollow-bearing trees over an 18-year period between 1997 and 2015. We mapped and marked all 534 large old hollow-bearing trees with permanent metal tags and unique identifying numbers to facilitate re-measurement.

We used maps of past disturbances, together with on-ground reconnaissance of field sites (where tree diameter is strongly correlated to tree age; see Lindenmayer et al., 2017) to assign each of our 96 sites to one of four distinct age classes. These were: (1) stands that regenerated after a wildfire in approximately 1850, (2) stands that regenerated after a major wildfire in 1939, (3) stands that regenerated after fire or logging between 1960 and 1990, and (4) mixed-aged stands that comprised trees from 1730 to 1850 and a younger-aged cohort (typically regeneration from the 1939 fire).

None of our long-term sites was subject to logging over the duration of this study (*viz*: 1997 to 2015). However, parts of the surrounding area of approximately half our sites were subject to timber harvesting between 1950 and 2015, with an average of 16.9% of the adjacent area logged up until 2015.

2.2. Classification of trees into different states of decay

For the purposes of this study, we defined a large old hollow-bearing tree as any tree (live or dead) measuring > 0.5 m dbh and containing an obvious cavity as determined from careful visual inspection using a pair of binoculars. We classified all large old hollow-bearing trees on our long-term sites into one of nine forms based on the condition and level of decay (Fig. 1). Notably, all large old hollow-bearing trees were standing living or dead at the outset of our study in 1997.

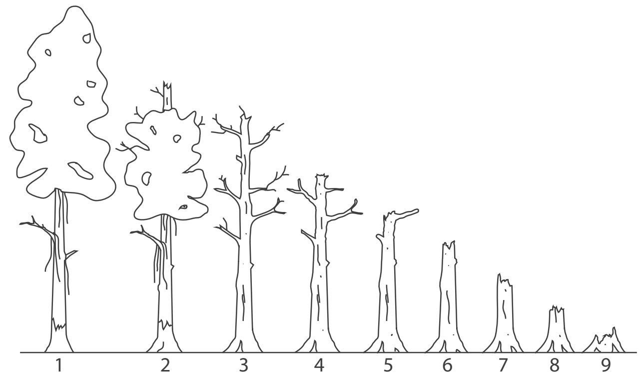

Fig. 1. Nine forms of decayed trees in the Mountain Ash forests of the Central Highlands of Victoria. Form 1: Ecologically mature, living tree with apical dominance; Form 2: Mature living trees with a dead or broken top; Form 3: Dead tree with most branches still intact; Form 4: Dead tree with 0–25% of the top broken off; branches remaining as stubs only; Form 5: Dead tree with top 25–50% broken away; Form 6: Dead tree with top 50–75% broken away; Form 7: Solid dead tree with 75% of the top broken away; Form 8: Hollow stump. Form 9: Collapsed tree.

2.3. Covariates used in statistical analysis

We fitted five potential explanatory variables to our models. These were: (1) year, (2) the age of the stand in which a given site was located, (3) whether a site had been burned in the 2009 fire, (4) the amount of forest burned in 2009 in a 2 km radius circle around the centroid of each site (weighted by the distance from the site centroid), and (5) the amount of forest logged between 1950 and 2015 in a 2 km radius circle around the centroid of each site (weighted by the distance from the site centroid).

3. Statistical analysis

We fit a Bayesian multi-level model to tree form, with two random effects: site and tree. The site level random effect allowed for correlation among trees at a given site and the tree random effect allowed for temporal correlation. We assumed a Gaussian distribution for tree form. However, due to the ordinal nature of this response variable, we explored the sensitivity of the results of model fitting to the assignment of scores in Fig. 1. Specifically, we used normal and log-normal (the inverse to reflect the left-skewed nature of the distribution of forms) ridit scores (Agresti, 2010) to assign scores to the nine forms. We chose this method of analysis over ordinal logistic regression due to the sparsity of forms at certain time periods during the study.

Due to the timing of the 2009 fire (it occurred before our 2009 field assessments of large old trees), we could not fit a straightforward interaction of survey year and burn status at the site level. Our design for these two aspects is given by the following equation:

$$\mu_{ijt} = \beta_0 + \beta_1 D2005_{ijt} + \beta_2 D2009_{ijt} + \beta_3 D2012_{ijt} + \beta_4 D2015_{ijt} + \beta_5 F_{ijt} x D2009_{ijt} + \beta_6 F_{ijt} x D2012_{ijt} + \beta_7 F_{ijt} x D2015_{ijt} + site_i + tree_{ij}$$

where μ_{ijt} is the mean for tree j on site i at time point t; $D2005_{ijt}$ is a dummy variable, which is 1 for year 2005 and 0 otherwise; F_{ijt} is 1 if the site experienced the 2009 wildfire and 0 otherwise; and $site_i$ and $tree_{ij}$ are random effects for the site and tree respectively. This model