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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.

Keywords: Cavity trees, snags, stags, old-growth forests, regrowth forests, fire, logging, montane ash forests, tree distribution

1.1 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 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; Lindenmayer et al., 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 (Figure 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 Figure 1). (2) Collapsed trees (form 9 in Figure 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 Figure 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.

1.2 Methods

1.2.1 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 (Figure 2). These forests are dominated by largely monotypic stands of Mountain Ash and Alpine Ash (*Eucalyptus delegatensis*) or mixed species stands with Mountain Ash and Shining Gum (*E. nitens*), Messmate (*E. obliqua*), Mountain Grey Gum (*E. cypellocarpa)*, and Manna Gum (*E. viminalis*).

Within the montane ash forests of our study region, we have established 166 long-term ecological research sites (Lindenmayer et al., 2003), each measuring 1 ha and on which we have completed repeated measurements of the number and condition of large old hollow-bearing trees over a 19-year period. We defined a hollow-bearing tree as any stem (live or dead) measuring > 0.5 m in dbh and containing an obvious cavity as determined from careful visual inspection using a pair of binoculars.

All hollow-bearing trees on each site were first measured in 1997 and marked with permanent metal tags with unique identifying numbers. During surveys, we classified all hollow-bearing trees on all long-term sites into one of nine forms based on the condition and level of decay (Figure 1). The trees marked in 1997 were all standing trees in forms 1-8 in 1997, such that there were no trees in form 9 (collapsed) at the commencement of the study. For the study we report here, we completed a cross-sectional analysis of the site-level abundance of large old hollow-bearing trees in 2015 only.

1.2.2 Covariates for each site

Our 166 long-term ecological research sites varied substantially in a wide range of attributes. We measured or calculated values for the following eight covariates for each site for use in constructing statistical models.

Stand age with four levels: 1=old-growth dominated by trees that germinated before 1900, 2=1939 regrowth (dominated by trees that regenerated as a result of the 1939 wildfires), 3=1960-1990s regrowth (i.e. trees that regenerated between 1960 and 1990), and 4=mixed-aged forest (in which there were two or more distinct age cohorts of trees in the stand). Our age class classification was based on the dominant age cohort of living trees in a stand. However, we note that the vast majority of the mixed-aged stands supported an old-growth component with a number of individual large old living hollow-bearing trees.

Land Tenure with two levels: state forests managed by the Department of Environment, Land, Water and Planning for wood production, and formally gazetted large ecological reserves managed by Parks Victoria.

Forest type with three levels: 1=Mountain Ash, 2=Alpine Ash, and 3=Mixed species.

Elevation calculated in meters above sea level with the location based on the centroid of each site.

Topographic Wetness Index (TWI) (Moore and Hutchinson, 1991) which is a measure of relative position in the landscape and thus potential water distribution. Calculation of TWI requires a Digital Elevation Model (DEM) that has hydrological integrity, and we used the ANUDEM algorithm (Hutchinson, 2011) to generate a DEM of our study region at a grid resolution of 20 m. For each cell, the size of the catchment that flows to it was divided by its width, adjusted geometrically by the aspect of inflow direction. This 'specific catchment' was then divided by the cell's local slope. Lower values indicate ridges and upper slopes that have no, or small, contributing catchment, with values increasing for lower slopes, valley bottoms, and drainage lines.

Following Hutchinson (1998), we generated the variables **P** and **Q**, which represent the eastern and northern components of the unit normal vector to the smoothed DEM surface. The variables **P** and **Q** are continuous functions of position, with largest magnitude on steepest slopes, and reducing to zero on flat areas in valley bottoms and on flat ridgetops. **P** can be viewed as an aspect adjusted slope in the east-west direction (negative values correspond to westward facing slopes, values near zero correspond to valley bottoms and ridges and positive values correspond to eastward facing slopes). **Q** can be viewed as the aspect adjusted slope in the north-south direction (negative values correspond to southward facing slopes, values near zero correspond to valley bottoms and ridges and positive values correspond to northward facing slopes). The form of **P** and **Q** used in the current study broadly reflect topographically varying patterns of solar radiation (Hutchinson, 1998).

Fire severity. In 2009, a large proportion of the Central Highlands region was burned in the Black Saturday wildfires (Cruz et al., 2012). A total of 76 of our 166 long-term sites were burned in these fires. In the two months immediately following these fires, we assessed the site-level fire severity and assigned a score of 1 (no fire), 2 (moderate severity fire, where overstory crowns generally remain green), and 3 (high fire severity in which the crowns of the overstory trees had been totally scorched or consumed by the fire). Of the sites burned, 46 experienced a moderate severity fire, and the remaining 30 experienced a high severity fire.

Table 1 contains summary data on the values for a subset of the potential explanatory variables used in our statistical modelling. We tested for collinearity among potential explanatory variables and found no evidence for strong effects (the highest values for correlation among variables was 0.12).

1.3 Statistical analyses

We modeled the abundance of hollow-bearing trees on a site using six different distributional assumptions for the response variable. Specifically, we investigated whether or not the number of large old hollow-bearing trees was best fit by the following distributions which allow for varying amounts of over-dispersion and excess zeros relative to the Poisson: (1) Poisson, (2) hurdle Poisson, (3) zero-inflated Poisson, (4) negative Binomial, (5) hurdle negative Binomial and (6) zero-inflated Negative Binomial. We assessed which distribution best described the variation in the number of large old hollow-bearing trees using the WAIC=Widely Applicable Information Criteria (Watanabe, 2010; Gelman et al., 2014; Vehtari et al., 2015) with all covariates included. Note that for the hurdle and zero-inflated models, we allowed the covariates to have different effects for the zero and count parts of the models. Once a distribution was chosen, we then employed a backward elimination procedure guided by WAIC to assess whether the full model could be simplified further.

To assess the effect of spatial dependence on our conclusions for the abundance of large old trees per site, we fitted a spatial model to the final model selected by the WAIC criteria. However, due to software limitations, we were able to fit only a Poisson distribution and hence could not account for over-dispersion or an over-abundance of zeros.

Tree form (Figure 1) is an ordinal response variable and hence ordinal logistic regression (Agrestiit, 2010) initially appeared to be appropriate for statistical analysis.

However, we did not employ ordinal logistic regression for two reasons. First, the choice of logits that are generally available in software packages did not correspond to our research hypotheses. Second, preliminary analysis indicated that the proportionality of the odds ratio assumption did not hold. Therefore, we elected to analyze the following four binary response variables: the abundance of large old living hollow-bearing trees (forms 1+2), the abundance of collapsed trees (form 9), the abundance of glider-suitable trees (forms 2-4), and the abundance of possum-suitable trees (forms 5-8). We used generalized linear mixed model (GLMM) with a binomial distribution with the same set of covariates as above to each of the response variables and did a backward elimination guided by WAIC to choose a final model for interpretation. To account for site-level effects, we included site as a random effect in each of the models.

For all analyses, we set vague prior distributions for all model parameters and we report posterior medians and the upper and lower values of the 95% credible intervals. We also report posterior tail areas (Btail) for each model parameter. Btail is the fraction of the posterior distribution that is to the left (posterior median > 0) or the right (posterior median < 0) of zero. Small values of Btail indicate support for non-zero parameter values, that is, posterior distributions that are shifted away from zero. Btail values < 0.10 indicate weak evidence that a parameter is different from zero, values < 0.05 given marginal evidence and values < 0.01 indicate strong evidence.

We completed all analyses in R version 3.2.3 (R Core Team, 2015) using the following packages: brms (Buerkner, 2015), spBayes (Finley et al., 2015), and CODA (Plummer et al., 2006).

1.4 Results

Q1. What factors influence the abundance of large old hollow-bearing trees at a site?

The abundance of hollow-bearing trees varied from zero to 29 per site. Approximately, 50% of our 166 sites supported two or fewer large old hollow-bearing trees; there were no such trees on 27 sites, only one large old hollow-bearing tree on 28 sites, and two large old hollow-bearing trees on 25 sites.

The first stage of our modelling revealed that the best fitting model was the negative binomial model (Table 3), although the zero inflated negative binomial model was a close second according to WAIC. We present results only for the negative binomial model as the added complication of the zero-inflated negative binomial was not warranted.

Our analyses revealed the model for the abundance of hollow-bearing trees contained six predictor variables. The abundance of hollow-bearing trees was greatest on sites with high values for TWI (Btail = 0.004). Sites dominated by old-growth supported the highest abundance of large old hollow-bearing trees, with mixed aged stands supporting the next nearest levels of abundance to old-growth (old-growth vs mixed aged, Btail = 0.002; old-growth vs 1939, Btail < 0.001; old-growth vs 1960-1990s, Btail < 0.001; mixed-aged vs 1939, Btail < 0.001; mixed-aged vs 1960-1990s, Btail < 0.001). Mixed species forest supported the highest abundance of hollow-bearing trees (Btail = 0.014). There also was evidence that more large old hollow-bearing trees occurred on sites located within reserves than sites in wood production forest (Btail = 0.002). We also found evidence of a quadratic relationship for **P** (i.e. the combination of eastern aspect and slope) (Btail = 0.033), with the highest abundance of large old hollow-bearing trees on steep slopes with either an easterly or westerly aspect. In addition, there was evidence that sites subject to moderate severity fire in 2009 supported the fewest large old hollow-bearing trees (moderate severity vs unburned, Btail < 0.001 and moderate severity vs high severity, Btail = 0.019). We summarize effects in Figure 3 with the accompanying model given in Table A.1 in Appendix A.

We assessed the effect of spatial dependence on our conclusions and found that, qualitatively, the spatial results were very similar to the negative binomial model (i.e. in the absence of spatial effects) (Table A.6). The exception was forest type which was characterized by weak support in the spatial model while the non-spatial model was characterized by moderate support. The associated semi-variogram is given in Figure A.1 and the effective range was approximately 2km (Table A.6). This suggests that the results of the non-spatial model are valid with the possible exception of forest type for which the results might be over stated.

Q2. Do different factors or combinations of factors influence the abundance of different forms of large old trees?

Our data showed that 41% of large old hollow-bearing trees standing in 1997 had collapsed by 2015. Our initial sample of trees in 1997 contained no collapsed trees, yet by 2015 a total of 57% of large old hollow-bearing trees were in form 9 (collapsed) on young-aged forest sites. The equivalent values for old-growth sites, 1939 aged sites, and mixed aged sites were 16%, 53% and 26%, respectively. From our cross-sectional analyses of the abundance of collapsed trees in 2015, we found that sites characterized by the most collapsed large old hollow-bearing trees had low values for TWI (Btail = 0.012) and were subject to moderate severity fire in 2009 (moderate severity vs unburned, Btail = 0.001; moderate severity vs high severity, Btail = 0.032). In addition, sites characterized by the largest number of collapsed large old trees were dominated by young forest (dating from 1960-1990) and stands dating from the 1939 fires (old-growth vs 1939, Btail < 0.001; old-growth vs 1960-1990s, Btail < 0.001; mixed-aged vs 1939, Btail < 0.001; mixed-aged vs 1960-1990s, Btail < 0.001). Finally, we uncovered evidence of quadratic effects of **P** (Btail = 0.039) and Q (Btail = 0.040), with the highest number of collapsed trees on flatter sites. We present trend patterns for these effects in Figure 4 and the associated model in Table A.2.

Our analyses revealed three predictor variables – stand age, fire severity and P were associated with the abundance of large old living hollow-bearing trees per site. There was a higher proportion of large old living hollow-bearing trees in old-growth stands than sites dating from 1939, 1960-1990, and mixed aged forest (old-growth vs 1939, Btail = 0.004; old-growth vs 1960-1990s, Btail = 0.005; mixed-aged vs 1939, Btail < 0.001; mixed-aged vs 1960-1990s, Btail = 0.002). Our analyses revealed a higher abundance of living large old hollow-bearing trees on unburned sites versus those that burned at high severity (Btail < 0.001). In addition, there were fewer large old living hollow-bearing trees on sites burned at moderate severity vs those burned at moderate severity (Btail = 0.001). Finally, we identified a quadratic effect of **P** with a higher abundance of large old living hollow-bearing trees on flatter sites (Btail = 0.044) (Figure 5, Table A.3).

Our analyses revealed that sites with the greatest fraction of trees potentially suitable for marsupial gliders (i.e. forms 2-4 in Figure 1) were old-growth and mixed aged stands (old-growth vs 1939, Btail < 0.001; old-growth vs 1960-1990s, Btail < 0.001; mixed-aged vs 1939, Btail < 0.001; mixed-aged vs 1960-1990s, Btail = 0.002). In addition, sites with the greatest fraction of trees potentially suitable for marsupial gliders had been subject to high severity fire in 2009 (high severity vs unburned, Btail = 0.002 and high severity vs moderate severity, Btail = 0.008) and were at low elevation (Btail = 0.019) (Figure 6, Table A.4).

The model for the abundance of possum-suitable large old hollow-bearing trees on a site (i.e. trees in forms 5-8; see Figure 1) included fire severity, P and TWI as predictor variables. There was a higher proportion of possum-suitable large old hollow-bearing trees on unburned sites versus those that burned at moderate severity (Btail < 0.001) and at high severity (Btail < 0.001). We found evidence of a quadratic effect of **P** (Btail = 0.068) corresponding to a lower proportion of possum-suitable large old hollow-bearing trees on steeper east and west-facing sites. There also was a higher proportion of possum-suitable large old hollow-bearing trees on sites with high values for TWI (Btail = 0.057) (Figure 7, Table A.5).

1.5 Discussion

Large old hollow-bearing trees have pivotal ecological roles in numerous natural and human-modified terrestrial ecosystems worldwide (Manning et al., 2006; Fischer et al., 2010; Lindenmayer et al., 2014b). Understanding where such trees occur and the factors which influence their abundance has significant implications for determining where their various ecological roles will be most effectively played. This information can, in turn, influence where additional management actions might be required such as efforts to restore populations of large old hollow-bearing trees where they have been depleted. We found the abundance of large old hollow-bearing trees is governed by a suite of factors including measures of topography, age of the surrounding forest, the severity of past fire, and human disturbance history (as reflected by land tenure). Different sets of environmental and other factors affect the abundance of different morphological forms of large old hollow-bearing trees. That is, different parts of landscapes are most likely to support different kinds of trees, for example, as reflected through measures such as TWI, **P**, **Q**, and elevation.

1.5.1 Factors affecting the abundance of large old hollow-bearing trees

Statistical analyses revealed that models of the abundance of large old hollow-bearing trees as well as the abundance of particular forms of these trees contained a combination of environmental, human disturbance and natural disturbance covariates. Previous work has modeled the environmental domains occupied by different species of trees in montane ash forests (Lindenmayer et al., 1996) and the analyses we report here suggest that the large old hollow-bearing tree stage occupies a subset of the overall climatic and environmental envelope for a given tree species. That is, large old hollow-bearing trees occur in parts of landscapes that are relatively predictable based on environmental and other information (see also Smith et al., 2012). However, rare and episodic events such fires also have marked effects on the abundance of large old trees, but the precise timing and severity of fires is notoriously difficult to predict accurately.

Many of the response variables in the statistical models were broadly consistent with expectations. For example, old forest supported the greatest overall abundance of large old hollow-bearing trees (irrespective of morphological form). Old-growth forest also was where the greatest abundance of large old living hollow-bearing trees occurred. Both of these results are broadly congruent with the known ontogeny of increasing cavity development and increasing tree age in montane ash forests (Ambrose, 1982; Lindenmayer et al., 1993). Conversely, young forest supported the fewest large old hollow-bearing trees. Relatively recent fire and/or logging is likely to have reduced the abundance of these trees in young forest, congruent with some of our other findings such as those indicating that the greatest number of collapsed trees occurred in young forest (Figure 4, Table A.2). This is reflected in the simplified conceptual model in Figure 8 which shows relationships between disturbance and large old tree abundance. Essentially, large old trees in young forest are more likely to collapse because they are in a later decay state than those in old forest, typically being biological legacies of the previous forest generation killed by the most recent fire.

The highest abundance of large old hollow-bearing trees was on the wettest sites as reflected by high values for TWI. Such places are typically those with the highest rates of tree growth and also where previous analyses indicated old-growth forests are most likely to occur (Mackey et al., 2002). They also may be where fire frequency and/or fire severity may be the lowest.

An initially surprising result was that fewer large old hollow-bearing trees were found on sites subject to moderate severity fire compared with sites where there had been a high-severity fire. This finding can be attributed to differential fire severity effects on living vs dead trees (Figure 8). Moderate severity fire may leave large living trees relatively intact but consume pre-existing dead trees on a site, possibly as a result of the flammability of dead standing wood. High severity fire may not only consume dead trees but also create a new cohort of dead trees as a result of killing large living trees (Figure 8). Finally, forest in protected areas (such as that managed by Parks Victoria) supported more large old hollow-bearing trees (as well as more dead trees) than State Forests where timber harvesting is permitted. This result was expected given the long history of logging in forests broadly designated for wood production and the effects of harvesting, which historically targeted the largest trees and, more recently, has focused on cutting regrowth trees (thereby impairing the recruitment of new cohorts of large old hollow-bearing trees). In addition, there is a prolonged history in logged areas of poor protection of large old hollow-bearing trees from mechanical disturbance by harvesting machinery and from high-intensity regeneration burns deliberately lit to promote the regeneration of cutblocks (Lindenmayer et al., 2015).

Large old hollow-bearing trees occur in different morphological forms in montane ash forests (Figure 1) and we found that both: (1) different factors can influence large old hollow-bearing trees at different stages of decay, and (2) the same factors can affect different kinds of trees in different ways. This finding is broadly similar to the results of studies of the regeneration niche of Victorian Mountain Ash (Smith et al., 2016) which demonstrated how different factors affect the prevalence of post-fire germinants. Fire is a useful illustrative case, especially as it was an important predictor in each of the models we constructed but its effects varied among morphological classes. Its effects also varied depending on whether the fire was moderate or high severity at a given site. Fire may kill living trees and create a pulse of large dead trees (Figure 8). Conversely, existing dead trees may be consumed by a moderate or high severity fire. This, in turn, explains why burned sites supported a higher proportion of glider-suitable trees but a lower proportion of possum-suitable trees (Figure 6 vs Figure 7), although we re-iterate that such trees were only considered to be potentially suitable for animals as other factors such as direct mortality resulting from fire and the development of post-fire natural regeneration also can influence both site occupancy and the suitability of burned sites for colonization (Lindenmayer et al., 2013). The pervasive effects of fire on both the overall abundance of large old hollow-bearing trees and the abundance of different morphological forms of such trees underscores its importance as a key ecological process in montane ash forests.

1.5.2 Management implications

Large old hollow-bearing trees can be a robust surrogate for the occurrence of cavity-dependent animals such as arboreal marsupials in montane ash forests, including the critically endangered Leadbeater's Possum (Lindenmayer et al., 2014a). At the same time, logging operations can significantly reduce the abundance of large old trees, either directly through harvesting or indirectly via the impacts of fires lit to regenerate cutover areas or edge effects like windthrow created by cutting stands adjacent to retained forest (Lindenmayer et al., 1997). Collectively, these outcomes mean it can be valuable to better understand where large old hollow-bearing trees are most likely to occur in the landscape. Such places can then be critical ones to protect, especially as populations of large old hollow-bearing trees are declining rapidly across much of the montane ash forest estate in the Central Highlands of Victoria (Lindenmayer et al., 2012a; Burns et al., 2015). Indeed, more than more than 40% of trees have collapsed in the 18 years since we commenced monitoring. Burns et al. (2015) considered that the decline of large old hollow-bearing trees was so precipitous and the subsequent impacts on key ecosystem processes sufficiently serious that they classified Mountain Ash forests as Critically Endangered under the formal IUCN Ecosystem Assessment protocol. Approximately 80% of montane ash forest estate is broadly designated for wood production and our analyses can help identify potential candidate areas within these State Forests for protection of large old hollow-bearing trees.

The greatest number of collapsed trees was found in young forest that is ~30-50 years old, followed by 75 year old forest that regenerated after the 1939 fires (Figure 4), yet these age cohorts of forest comprise the vast majority of the existing montane ash forest estate in the Central Highlands of Victoria. Conversely, only 1.16% of the forest estate is old-growth where the greatest overall abundance of large old hollow-bearing trees occurs. Stands of old-growth forest that are 5 ha or larger are currently not logged. However, the vast majority of old-growth montane ash forest stands are far smaller than this, including individual large old trees within younger regrowth (Lindenmayer et al., 2015). The importance of the remaining (but rapidly declining) large old hollow-bearing tree cohort means these smaller areas of old-growth and individual trees need to be protected. Similarly, areas with high values for TWI might be prioritized for protection as these are where the abundance of large old hollow-bearing trees is currently the greatest. Old-growth stands are currently not logged directly, but large old trees continue to be lost across the landscape as a result of the indirect impacts of timber harvesting operations.

Unburned sites supported the greatest number of large old hollow-bearing trees (Figure 3) as well as the greatest number of possum-suitable trees (Figure 7). It is well established that large old hollow-bearing trees are critical nest sites for critically endangered cavity-dependent species like Leadbeater's Possum (Lindenmayer et al., 1991b) and the abundance of these trees underpins habitat suitability for such animals (Lindenmayer et al., 2014a), although we acknowledge other factors like the mortality of animals following fire will mean that potentially suitable trees will remain unoccupied on recently burned sites (Lindenmayer et al., 2013). We suggest that, along with large and small patches of old-growth forest, unburned areas of montane ash forests are strong candidates for protection from logging to ensure the maintenance of relatively high numbers of large old hollow-bearing trees and to facilitate the maturation of younger regrowth stands such as those that regenerated after the 1939 fires into future old-growth forest.

1.6. Conclusions

Large old hollow-bearing trees are critical structures in forest ecosystems worldwide and identifying the factors which influence their abundance is important for informed forest management practices. We constructed statistical models of the environmental, human disturbance and natural disturbance factors influencing the abundance of different morphological forms of large old hollow-bearing trees in the montane ash forests of the Central Highlands of Victoria, south-eastern Australia. Our detailed analyses revealed that different sets of environmental factors, as well as variables associated with fire severity and land tenure, had important effects on the abundance of four key kinds of large old hollow-bearing trees in these forests – large old living trees, collapsed trees, large old glider-suitable trees, and large old possum-suitable trees. Our models, in turn, can be valuable for identifying parts of montane ash forest landscapes to protect and hence best conserve large old hollow-bearing trees. These areas include old-growth stands, unburned forest, and locations with high values for the TWI.

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Foundation, and the Long-term Ecological Research Network within the Terrestrial Ecosystem Research Network.

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Table 1. Descriptive statistics for elevation, topographic wetness Index (TWI), and **P** and **Q**. **P** and **Q** are continuous functions of landscape position, with largest magnitude on steepest slopes, and reducing to zero on flat areas in valley bottoms and on flat ridgetops. **P** can be viewed as an aspect adjusted slope in the east-west direction (negative values correspond to westward facing slopes, values near zero correspond to valley bottoms and ridges and positive values correspond to eastward facing slopes). **Q** can be viewed as the aspect adjusted slope in the north-south direction (negative values correspond to southward facing slopes, values near zero correspond to valley bottoms and ridges and positive values correspond to northward facing slopes).

	Mean	**SD**	**Median**	**Min**	**Max**
Elevation	951.73	185.82	854.3	303	1227
TWI	-1.15	0.96	-0.83	-3.06	1.64
P	-0.04	0.14	-0.02	-0.39	0.47
Q	-0.06	0.12	-0.01	-0.35	0.39

Table 2. Descriptive statistics for the number of hollow-bearing trees (HBT) per site and the proportions of alive, collapsed, and glider and possum-suitable hollow-bearing trees by fire severity, stand age, land tenure and forest type.

	No. Sites	Number of Hollow-bearing trees					Tree form			
		Mean	SD	Median	Min	Max	Live	Collapsed	Glider	Possum
Overall	166	5	5	3	0	29	21	41	31	23
Fire Severity										
Unburned	90	5	4	4	0	15	24	39	23	31
Moderate	46	3	4	2	0	20	25	55	29	11
Severe	30	7	9	2	0	29	9	33	52	14
Stand Age										
Old-growth	15	15	8	13	2	29	28	17	64	16
1939	102	3	4	2	0	14	16	54	16	25
1960-1990s	25	2	2	2	0	6	11	57	24	16
Mixed	24	8	4	8	1	17	33	26	43	24
Land Tenure										
State Forest	81	3	3	2	0	14	20	49	21	25
National Park	85	6	6	4	0	29	21	37	36	22
Forest Type										
Mountain Ash	127	5	5	3	0	27	22	40	33	21
Alpine Ash	28	5	6	2	0	29	15	46	26	24
Mixed	11	6	5	4	0	12	29	41	17	31

Table 3. Model selection results for the choice of distribution via WAIC. Note that the full model was fit in each case with quadratic effects of the continuous variables. The full model in each case is: Stand Age + Fire Severity + Land Tenure + Forest Type + Elevation + TWI (topographic wetness index) + P + Q + Elevation^2 + TWI^2 + P^2 + Q^2.

Distribution	**WAIC**
Poisson	976.91
Hurdle Poisson	958.76
Zero Inflated Poisson	959.77
Negative Binomial	**829.21**
Hurdle Negative Binomial	897.89
Zero Inflated Negative Binomial	830.15

Figure 1. Sequential development of tree forms in Mountain Ash trees. Form 1: Ecologically mature, living tree; 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. In subsequent surveys we added a ninth category – Form 9: Collapsed tree.

Figure 2. The location of the Central Highlands region of south-eastern Australia where studies of the abundance and transitions of large old hollow-bearing trees have been conducted.

Figure 3. Factors affecting the number of large old hollow-bearing trees (HBT) per hectare. In each panel, the other categorical variables are held fixed at the most common level and the continuous variables are set at the mean value. Posterior medians and 95% point-wise credible intervals are displayed on the original scale (the number of trees per sites). Panel A) Stand Age (OG = old-growth, 1939 = 1939 regrowth, Y = 1960-1990s regrowth, Mixed = Mixed age regrowth); B) Fire Severity (U = unburned, M = moderate, S = severe); C) Land Tenure (SF = State Forest and NP = National Park); D) Forest Type (MA = Mountain Ash, AA = Alpine Ash, M = Mixed Forest); E) P (east-west component of aspect adjusted slope: negative values correspond to westward facing slopes, values near 0 correspond to flat slopes and positive values correspond to eastward facing slopes); F) TWI (topographic wetness index, lower values correspond to drier conditions), and; G) Elevation.

Figure 4. Factors affecting the proportion of collapsed large old hollow-bearing trees (HBT) per site. In each panel, the other categorical variables are held fixed at the most common level and the continuous variables are set at the mean value. Posterior medians and 95% point-wise credible intervals are displayed on the proportional scale. Panel A) Stand Age (OG = old-growth, 1939 = 1939 regrowth, Y = 1960-1990s regrowth, Mixed = mixed-age regrowth); B) Fire Severity (U = unburned, M = moderate, S = severe); C) P (east-west component of aspect adjusted slope: negative values correspond to westward facing slopes, values near 0 correspond to flat slopes and positive values correspond to eastward facing slopes); D) Q (north-south component of aspect adjusted slope: negative values correspond to southward facing slopes, values near 0 correspond to flat slopes and positive values correspond to northward facing slopes), and; E) TWI (topographic wetness index, lower values correspond to drier conditions).

Figure 5. Factors affecting the abundance of large old living hollow-bearing trees (HBT) per site. In each panel, the other categorical variables are held fixed at the most common level and the continuous variables are set at the mean value. Posterior medians and 95% point-wise credible intervals are displayed on the proportional scale. Panel A) Stand Age (OG = old-growth, 1939 = 1939 regrowth, Y = 1960-1990s regrowth, Mixed = mixed-age regrowth); B) Fire Severity (U = unburned, M = moderate, S = severe), and; C) P (east-west component of aspect adjusted slope: negative values correspond to westward facing slopes, values near 0 correspond to flat slopes and positive values correspond to eastward facing slopes).

Figure 6. Factors affecting the proportion of glider-suitable large old hollow-bearing trees (HBT) per site. In each panel, the other categorical variables are held fixed at the most common level and the continuous variables are set at the mean value. Posterior medians and

95% point-wise credible intervals are displayed on the proportional scale. Panel A) Stand Age (OG = old-growth, 1939 = 1939 regrowth, Y = 1960-1990s regrowth, Mixed = mixed-age regrowth); B) Fire Severity (U = unburned, M = moderate, S = severe), and; C) Elevation.

Figure 7. Factors affecting the abundance of possum-suitable large old hollow-bearing trees (HBT) per site. In each panel, the other categorical variables are held fixed at the most common level and the continuous variables are set at the mean value. Posterior medians and 95% point-wise credible intervals are displayed on the proportional scale. Panel A), Fire Severity (U = unburned, M = moderate, S = severe); B) P (east-west component of aspect adjusted slope: negative values correspond to westward facing slopes, values near 0 correspond to flat slopes and positive values correspond to eastward facing slopes), and; C) TWI (topographic wetness index, lower values correspond to drier conditions).

Figure 8. Conceptual model of the inter-relationships between stand age, disturbance and the abundance of different forms of large old hollow-bearing trees.

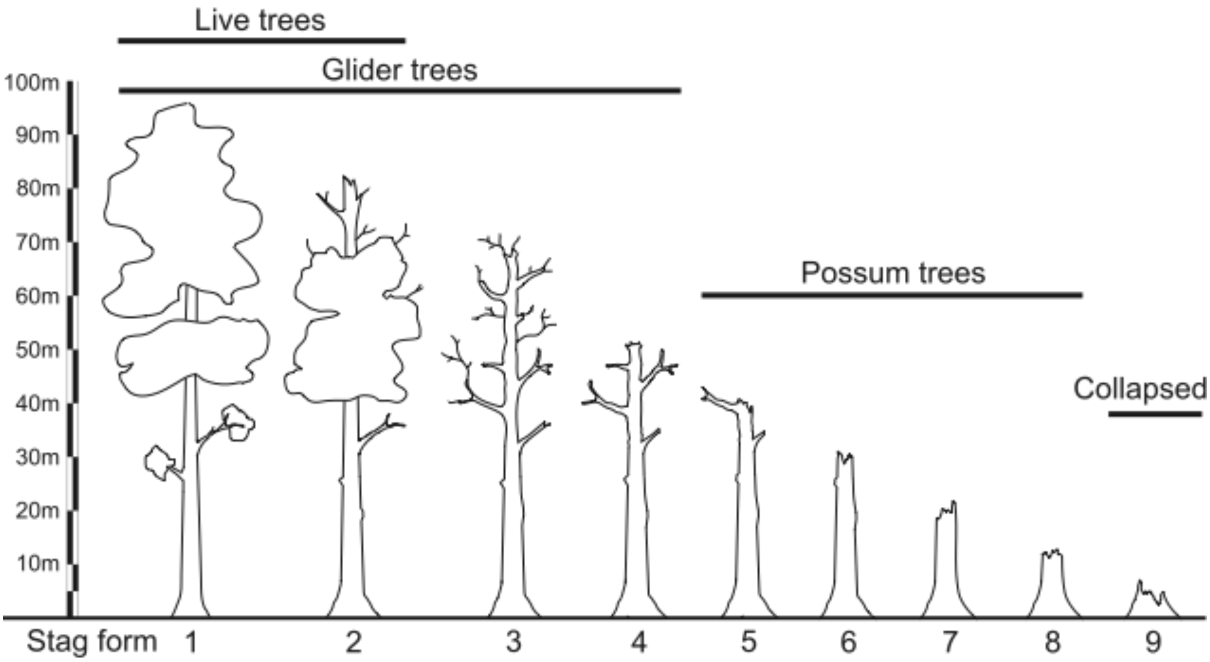

Live trees
Glider trees
Possum trees
Collapsed
100m
90m
80m
70m
60m
50m
40m
30m
20m
10m
Stag form 1 2 3 4 5 6 7 8 9

Figure 1

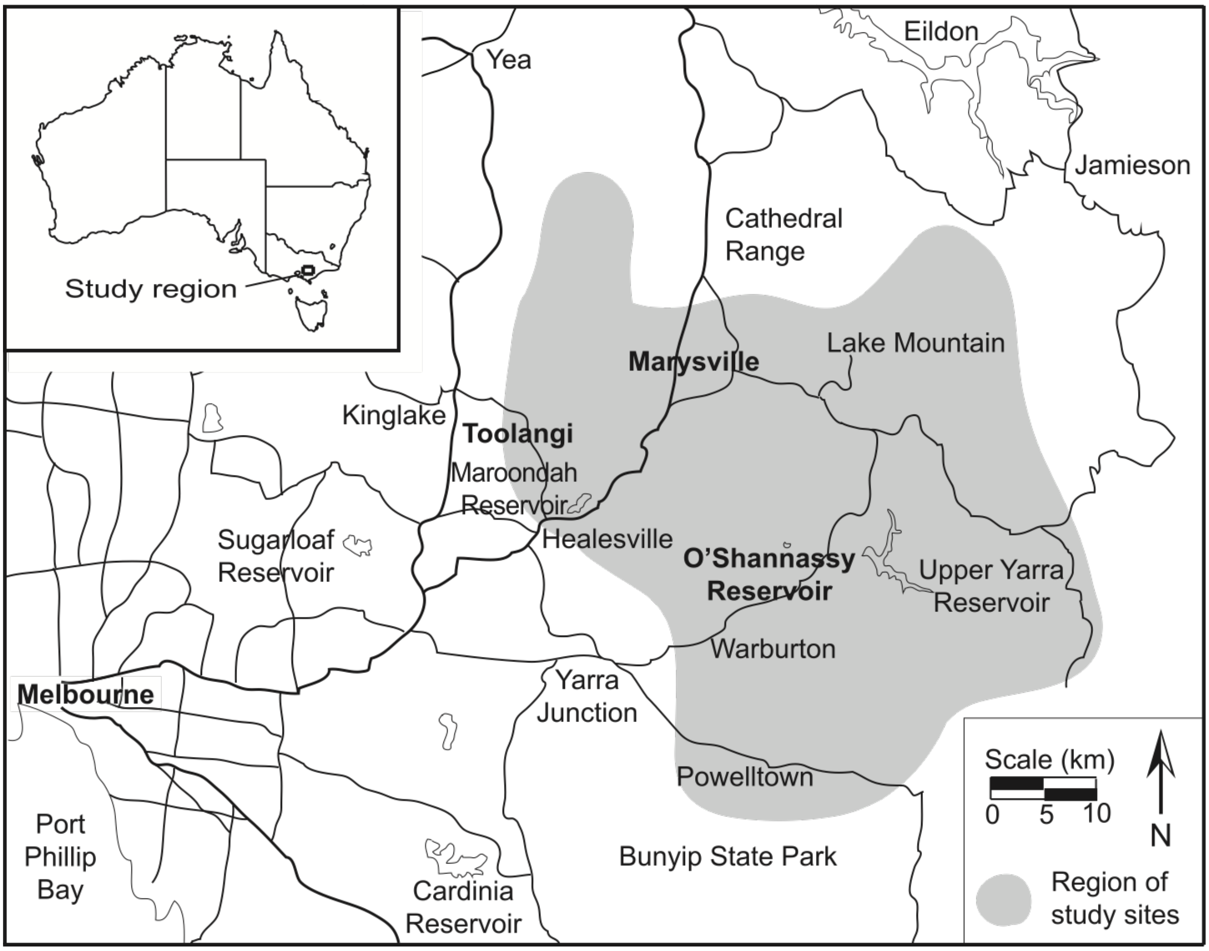

Study region
Yea
Eildon
Jamieson
Cathedral
Range
Lake Mountain
Marysville
Kinglake
Toolangi
Maroondah
Reservoir
Healesville
Sugarloaf
Reservoir
O'Shannassy
Reservoir
Upper Yarra
Reservoir
Warburton
Yarra
Junction
Melbourne
Scale (km)
0
5
10
N
Powelltown
Port
Phillip
Bay
Bunyip State Park
Cardinia
Reservoir
Region of
study sites

Figure 2

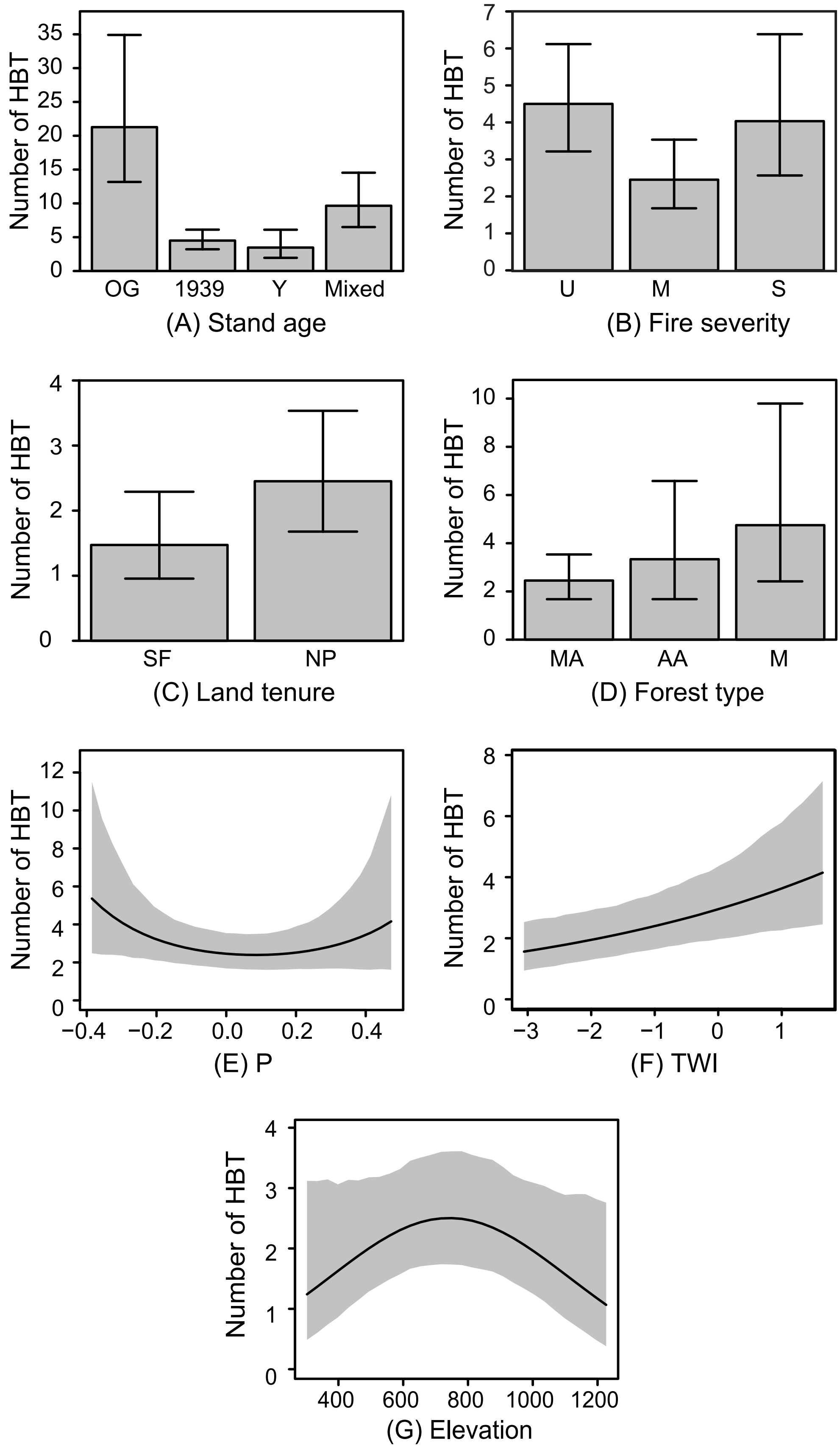
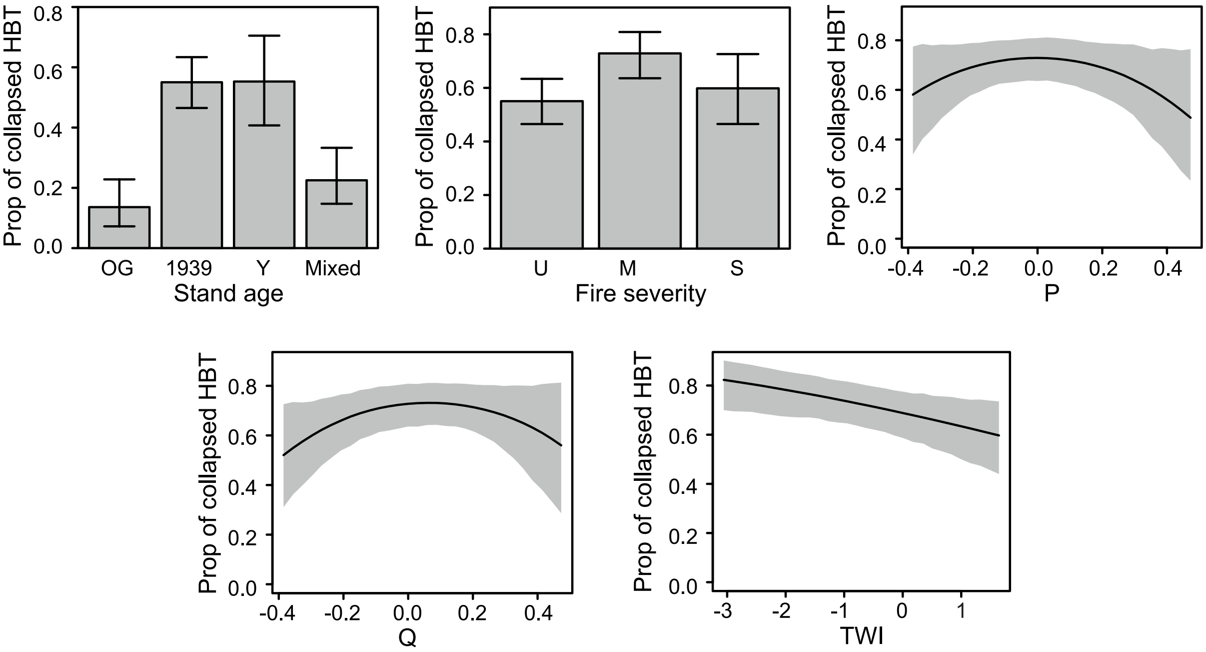
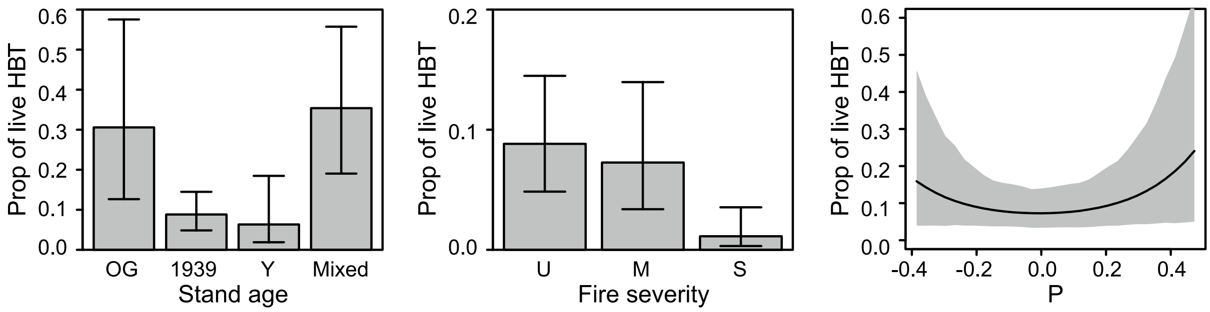

Number of HBT
35
30
25
20
15
10
5
0
OG
1939
Y
Mixed
(A) Stand age
7
6
5
4
3
2
1
0
U
M
S
(B) Fire severity
4
3
2
1
0
SF
NP
(C) Land tenure
10
8
6
4
2
0
MA
AA
M
(D) Forest type
12
10
8
6
4
2
0
−0.4
−0.2
0.0
0.2
0.4
(E) P
8
6
4
2
0
−3
−2
−1
0
1
(F) TWI
4
3
2
1
0
400
600
800
1000
1200
(G) Elevation

Figure 3



Prop of collapsed HBT
0.0
0.2
0.4
0.6
0.8
OG
1939
Y
Mixed
Stand age
U
M
S
Fire severity
-0.4
-0.2
0.0
0.2
0.4
P
Q
-3
-2
-1
0
1
TWI

Figure 4



Prop of live HBT
0.0
0.1
0.2
0.3
0.4
0.5
0.6
OG
1939
Y
Mixed
Stand age
Prop of live HBT
0.0
0.1
0.2
U
M
S
Fire severity
Prop of live HBT
0.0
0.1
0.2
0.3
0.4
0.5
0.6
-0.4
-0.2
0.0
0.2
0.4
P

Figure 5

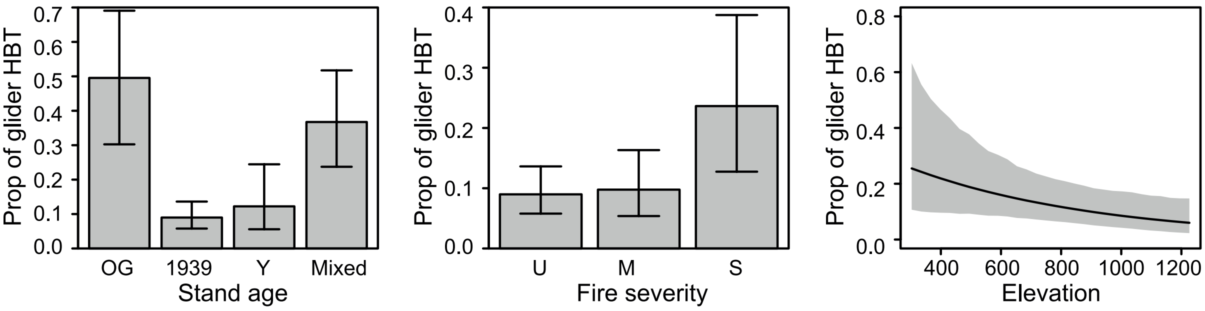

Prop of glider HBT
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
OG
1939
Y
Mixed
Stand age
Prop of glider HBT
0.0
0.1
0.2
0.3
0.4
U
M
S
Fire severity
Prop of glider HBT
0.0
0.2
0.4
0.6
0.8
400
600
800
1000
1200
Elevation

Figure 6

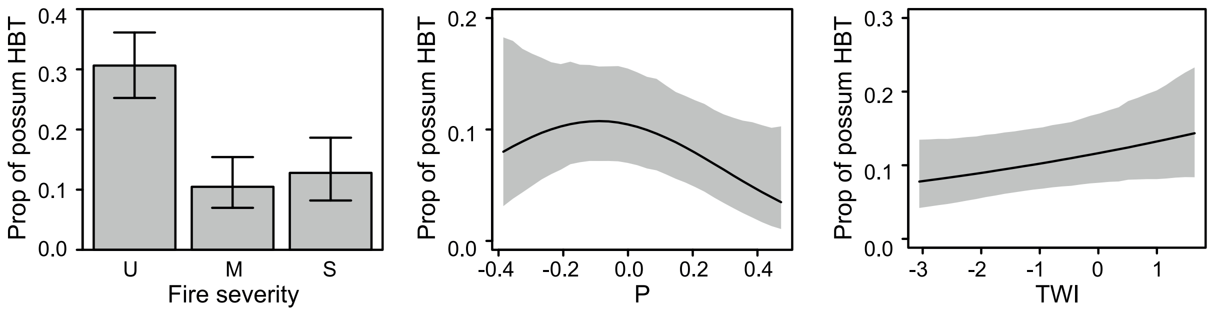

Prop of possum HBT
0.0
0.1
0.2
0.3
0.4
U
M
S
Fire severity
Prop of possum HBT
0.0
0.1
0.2
-0.4
-0.2
0.0
0.2
0.4
P
Prop of possum HBT
0.0
0.1
0.2
0.3
-3
-2
-1
0
1
TWI

Figure 7

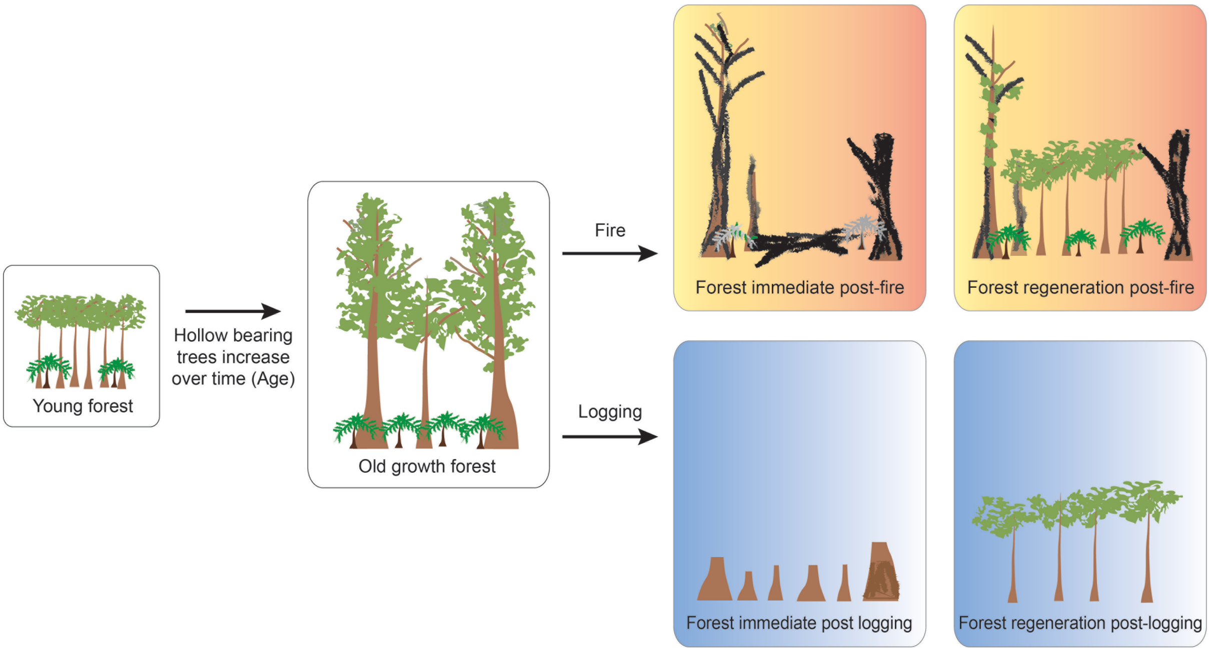

Young forest
Hollow bearing trees increase over time (Age)
Old growth forest
Fire
Logging
Forest immediate post-fire
Forest regeneration post-fire
Forest immediate post logging
Forest regeneration post-logging

Figure 8