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The response of arboreal marsupials to long-term changes in forest disturbance

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ABSTRACT

Quantifying the long-term population trajectory of species and the factors affecting these trends is a fundamental part of animal conservation. We describe the results of a long-term investigation of temporal changes in the occurrence of arboreal marsupials in the wet eucalypt forests of south-eastern Australia. The assemblage includes habitat specialists such as the vulnerable greater glider (*Petauroides volans*) and the critically endangered Leadbeater's possum (*Gymnobelideus leadbeateri*), as well as common and widespread taxa. Using data gathered between 1997 and 2018, we quantified relationships between site occupancy of four marsupial species and spatio-temporal site and landscape-level variables, including the number of hollow-bearing trees at a site, and the extent of fire and logging in the surrounding landscape. We found evidence that: **(1)** The number of hollow-bearing trees (which are critical den sites for arboreal marsupials) has declined substantially in the past two decades. **(2)** There was a decline in all species of arboreal marsupials. **(3)** The presence of all species of arboreal marsupials was positively linked to the number of large old hollow-bearing trees at a site. **(4)** The extent of logging disturbance in the landscape surrounding a site had a positive impact on the sugar glider (*Petaurus breviceps*) but a negative effect on Leadbeater's possum, suggesting that ongoing logging will have further negative impacts on the Leadbeater's possum. **(5)** The presence of the greater glider and sugar glider declined with increasing amounts of fire in the landscape. Negative fire effects are a concern as montane ash forests are increasingly susceptible to high-severity wildfires. Stronger efforts are needed to reduce the extent and frequency of logging and fire disturbance in mountain ash forests to protect arboreal marsupial populations.

KEYWORDS: Arboreal marsupials, logging, clearcutting, wildfire, landscape ecology, south-eastern Australia, Mountain Ash forest, biotic homogenization, long-term studies

INTRODUCTION

The world is experiencing a biodiversity crisis, with large numbers of species at risk of decline and extinction (Ceballos, Ehrlich & Dirzo, 2017; IPBES, 2019). While global assessments of biodiversity show major declines (e.g. Maxwell *et al.*, 2016), some species are increasing at regional and local levels, while others are declining (Inger *et al.*, 2014; Lindenmayer *et al.*, 2018b; Nielsen *et al.*, 2019). Quantifying and understanding such variation in the trajectories of species is dependent on long-term population data. Analyses of long-term population trajectories can be particularly powerful when they are linked with drivers of change such as the impacts of invasive species (e.g. Savidge, 1987), the spread of disease (e.g. Scheele *et al.*, 2019), modifications to local habitat suitability (Morrison, Marcot & Mannan, 2006), or changes in landscape cover (Fahrig, 2017; Tschamntke *et al.*, 2012).

Investigations that couple patterns of temporal change in populations of species with potential drivers of those changes are critical for guiding effective conservation management (e.g. Betts *et al.*, 2019; Haddad *et al.*, 2015). In the study reported here, we use a dataset gathered between 1997 and 2018 on Australian arboreal marsupials, to quantify temporal changes in animal occurrence at 158 long-term sites. We examined these changes in the context of spatio-temporal changes in key habitat and landscape attributes. Our work focused on the montane ash forests of the Central Highlands of Victoria, which is a heavily disturbed native forest environment that supports several species of arboreal marsupials (and other plant and animal taxa) of conservation concern (Taylor & Lindenmayer, 2019). The arboreal marsupial assemblage includes specialist species such as the vulnerable folivore, the greater glider (*Petauroides volans*), the vulnerable exudivore, the yellow-bellied glider (*Petaurus australis*), and the range-restricted and Critically Endangered Leadbeater's possum (*Gymnobelideus leadbeateri*). The assemblage also includes widespread generalist taxa such as the mountain brushtail possum (*Trichosurus cunninghami*) and sugar glider (*Petaurus*

breviceps) (see Appendix Table S1). Our overarching aim was to quantify patterns of temporal change in these species and determine which site and landscape-level factors were associated with such temporal changes. Our study tested four inter-related questions:

Q1. What are the temporal trends in critical denning resources for arboreal marsupials?

Almost all species of arboreal marsupials in montane ash forests are cavity-dependent and require large old hollow-bearing trees for shelter and reproduction (Lindenmayer *et al.*, 2017a). We sought to determine if the trend for declines in populations of these trees documented in past studies (e.g. see Lindenmayer *et al.*, 2011) has continued.

Q2. What are the temporal trends in the occurrence of arboreal marsupials?

We predicted a decline in the occurrence of all species of arboreal marsupials, in line with an expected decline in denning resources. However, we anticipated that declines would be most pronounced in range-restricted species such as Leadbeater's possum and the dietary specialist, the greater glider (which consumes only eucalypt leaves).

Q3. Is the number of hollow-bearing trees related to land tenure and landscape levels of wildfire and logging?

The landscapes surrounding our long-term sites have been subject to extensive disturbance as a result of clearcutting (VicForests, 2019) as well as a major wildfire in 2009. These disturbances can alter patterns of wind movement leading to elevated tree fall (e.g. Savill, 1993). We sought to quantify relationships between the abundance of hollow-bearing trees on sites and the amount of logging and fire in the surrounding landscape. We predicted there would be negative relationships between these measures; that is, fewer trees on sites where more of the surrounding landscape had been logged or burnt.

Q4. Is the occurrence of arboreal marsupials related to the number of hollow-bearing trees, land tenure, and landscape-levels of wildfire and logging?

Past investigations have established strong statistical relationships between the number of hollow-bearing trees at a site and the occurrence of arboreal marsupials (Lindenmayer *et al.*, 2017a). We predicted that such relationships would persist and, hence, that changes in the number of hollow-bearing trees (see Q1) would underpin changes in the occurrence of arboreal marsupials.

Animal species may be adapted to the fire regimes with which they have co-evolved (Frelich, 2005; Whelan, 1995). Montane ash forests and associated animal species have evolved under a fire regime characterized by rare, high-severity wildfire (Ashton, 1981). High-severity wildfire can affect habitat structure and food resources and we therefore anticipated that the occurrence of arboreal marsupials would be negatively related to the amount of fire that occurred in the landscape during the 2009 wildfires. Clearcutting can substantially modify forest and landscape structure and, in turn, reduce habitat suitability for many species, including cavity-dependent taxa. We predicted that the occurrence of animals at a site would be negatively associated with an increasing amount of logging in the surrounding landscape.

Quantifying temporal patterns of change in animal occurrence, and the factors influencing those changes, is fundamental to the development of informed strategies for effective biodiversity conservation (Scheele *et al.*, 2018). The results of the work reported here are therefore important for guiding forest management strategies that aim to conserve communities of arboreal marsupials.

METHODS

Study area

This study was focused on the Mountain Ash (*Eucalyptus regnans*), Alpine Ash (*E. delegatensis*) and Shining Gum (*E. nitens*) forest ecosystems in the Central Highlands of

Victoria, south-eastern Australia (Fig. 1). Forests dominated by these three tree species are collectively termed montane ash forest. We have established 164 long-term monitoring sites, each measuring 1 ha in the Central Highlands region. These sites have been surveyed on a repeated basis for arboreal marsupials and vegetation attributes since 1997.

Our long-term field sites encompass a wide range of environmental conditions including the age of stands, slope, aspect, and whether a site was burned in the 2009 Black Saturday fires (the only wildfire to occur in the region during our study). Our 164 sites spanned two key forms of land tenure in approximately equal proportion. These were areas broadly designated for pulpwood and timber production (hereafter ‘wood production forests’) and reserves and closed water catchments where logging is excluded (hereafter called ‘protected forests’). This large dataset on hollow-bearing trees was representative of broader montane ash environment in our study region.

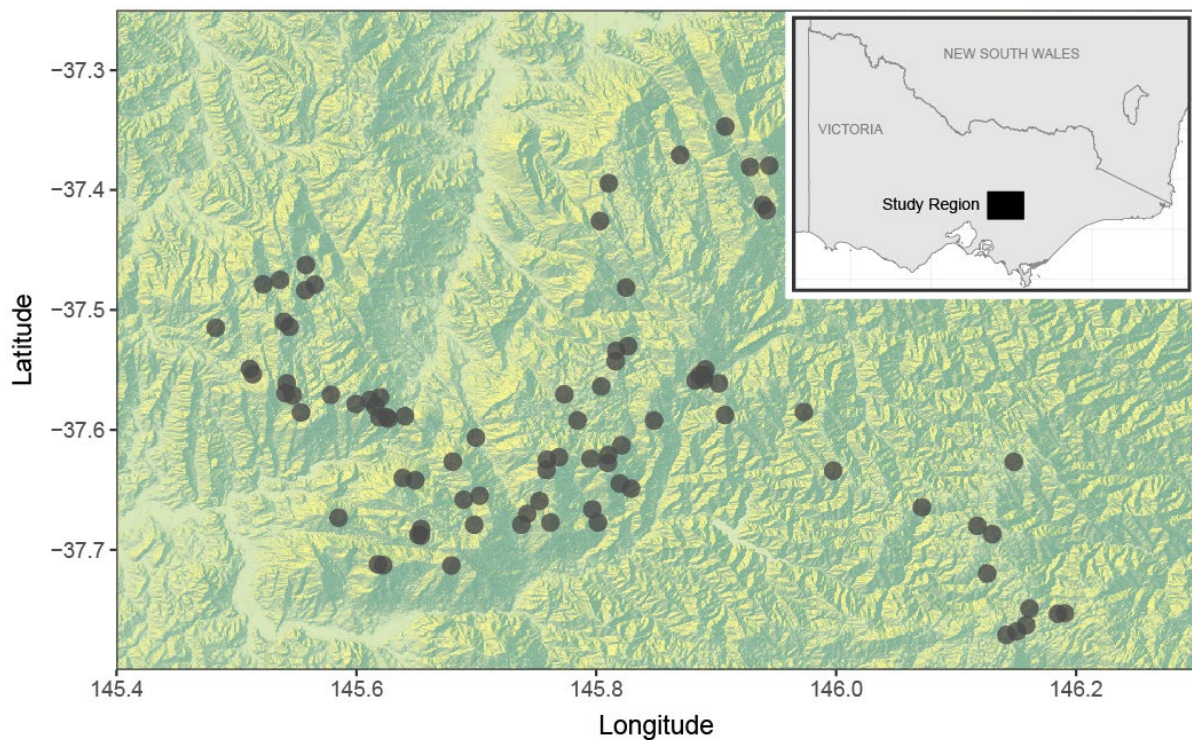


Fig. 1. The location of the study area in the Central Highlands of Victoria, south-eastern Australia. The black dots show the location of field survey sites.

Site-level surveys of hollow-bearing trees

We mapped the location of all hollow-bearing trees at each of our 164 long-term sites in 1997, 2003, 2009, 2011, 2012, 2015 and 2017. We defined a hollow-bearing tree as any tree > 80 cm DBH and containing obvious hollows as determined by scanning using binoculars. During each survey, we conducted a full reconnaissance of each field site and assessed the condition of each hollow-bearing tree, including whether it had collapsed or remained standing. Importantly, there has been very little recruitment of hollow-bearing trees over the 20+ years of repeated surveys at our long-term sites (Lindenmayer *et al.*, 2018a). Limited recruitment was expected given that the forest at most sites is dominated by trees that are 80 years or younger and it will be at least another 40 years before we would expect these trees to develop cavities (Ambrose, 1982).

Site-level survey of arboreal marsupials

We surveyed arboreal marsupials on 158 of our 164 field sites using the stagwatching method (*sensu* Lindenmayer *et al.*, 1991a). We did not survey six sites with this method because of logistical constraints in accessing parts of the forest. The stagwatching survey approach entails observers scanning each hollow-bearing tree on a given site for the emergence of arboreal marsupials for an hour before and after dusk. Thus, we documented the number of individuals of each species that was recorded emerging from a hollow-bearing tree on a given long-term monitoring site.

Stagwatching surveys are labour-intensive because at least one observer is required to verify animal emergence from each hollow-bearing tree on each site. This is because all species of arboreal marsupials exhibit den-swapping behaviour whereby animals move

regularly between cavities in different hollow-bearing trees (Gibbons & Lindenmayer, 2002). This demands that all hollow-bearing trees on a given site are watched simultaneously by experienced volunteers (Lindenmayer *et al.*, 1991a). Given the logistical demands of our field survey method, in any given year we completed stagwatching surveys at an average of 35-45 of the 158 long-term field sites (see Lindenmayer *et al.*, 2003). We ensured that each year, the sites that we surveyed spanned a range of site and landscape conditions to avoid confounding year and other effects. We conducted stagwatching surveys in the following years: 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2006, 2007, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, and 2018.

As outlined above, observers are required to document the emergence of animals from each hollow-bearing tree on each site. However, since the 2009 wildfire, the number of sites with at least one hollow-bearing tree has been decreasing. When a site has no hollow-bearing trees, it was removed from the suite of sites targeted for surveys of arboreal marsupials (although still surveys for the presence of hollow-bearing trees). We subsequently made allowances for this procedure by using the predicted number of hollow bearing trees for the sites that were unobserved. Importantly, in past studies, we have used other methods to survey sites with no hollow-bearing trees and found that cavity-dependent arboreal marsupials are absent from these places (Lindenmayer *et al.*, 1991b).

Measurement of landscape disturbance

None of our 1 ha sites was logged, but the landscape surrounding some of our sites has been subject to clearcutting. The amount of logged forest in the landscape increased over time (Department of Environment, 2019). The exception was deep within closed water catchments and reserves (i.e. protected forests) where logging is excluded. We calculated a spatially-weighted proportion of 25 m x 25 m pixels logged within a 2500 m x 2500 m square surrounding each survey site in the previous 20 years. We selected landscapes of this size for

two reasons. First, radio-tracking studies indicate that animals such as Leadbeater's possum may move at least 600 m from their nest sites (Lindenmayer *et al.*, 2017b) with other species also making occasional long distance movements (e.g. the mountain brushtail possum; (How, 1972)). Second, multiple interconnected colonies and groups of animals with home ranges spanning 1-60 ha in size are likely to respond to forest conditions in the landscape surrounding our sites.

For each site, we defined the following spatially weighted proportion of a square subject to logging:

$$L_{it} = \frac{\sum_k \sum_l w_{kl} lp_{itkl}}{\sum_k \sum_l w_{kl}}$$

where L_{it} is the calculated amount of logging at site i in survey year t , lp_{itkl} is 1 if the $(k,l)^{th}$ 25 m x 25 m pixel of site i in year t is logged and 0 if not, and the weights, w_{kl} , are constructed from two different Gaussian kernel weight functions, that is,

$$w_{kl} = e^{-\phi d_{kl}} e^{-\tau \Delta_{kl}}$$

where d_{kl} is the distance between pixel (k,l) and the origin (i.e. the centre of the 2500 m x 2500 m square) with spatial kernel scale parameter, ϕ , and Δ_{kl} is the time lag in years between the current survey and the logging that occurred in pixel (k,l) with associated temporal kernel scale parameter, τ . Details of our choice of scale parameters are given in Appendix 2, and they were set based on the assumption that logged areas close to our long-term sites would have a stronger effect on animals than more distant logged places. We set the scale parameters so that effects would diminish over time (as logged stands regenerated) with advanced regrowth forests potentially supporting animals or facilitating their movement through the landscape. We therefore set the temporal weighting factor to be 1 in the year after an area was logged and 0.01 30 years after a site had been harvested. Notably, we used

different scale parameters for the hollow bearing tree analysis compared to that for the occurrence of animals.

The wildfire that burnt during February-March 2009 was the only major fire that occurred during our study. Using spatial data obtained from the Government of Victoria on forest cover following the 2009 fires (Department of Environment and Primary Industries, 2014), we calculated a spatially-weighted proportion of 25 m x 25 m pixels burned 2500 m x 2500 m square surrounding each survey site in a broadly analogous fashion to that described above for logging with similar Gaussian kernel scale parameters (see Appendix 2). Specifically, the definition is as follows:

$$F_{it} = \frac{\sum_k \sum_l w_{kl} f p_{itkl}}{\sum_k \sum_l w_{kl}}$$

where F_{it} is the calculated amount of fire in the landscape at site i in survey year t , $f p_{itkl}$ is 1 if the $(k,l)^{\text{th}}$ 25 m x 25 m pixel of site i in year t was burned and 0 if not, and the weights, w_{kl} are defined in an analogous fashion to the logging weights.

Prior to 2009, all sites were assigned a value of zero for this variable. Although we measured whether each 1 ha site had been burned (or not) in the 2009 wildfires, we did not include this covariate in subsequent statistical analyses. This was because it was highly correlated with the extent of fire in the surrounding landscape.

STATISTICAL ANALYSES

We describe the analysis of two-distinct, but inter-related processes; **(1)** the factors associated with the number of hollow bearing trees at a site (Q1 and Q3), and **(2)** how the number of hollow bearing trees and other factors influenced the occurrence of arboreal marsupials (Q2 and Q4). We conducted these analyses separately due to differences in the sampling regime for hollow-bearing trees and marsupial occurrence. These differences in

sampling were unavoidable because **(1)** the labour-intensive nature of stagwatching means it was not possible to undertake marsupial surveys at all sites in each year (see above for more details), and **(2)** stagwatching surveys cannot be conducted at sites that no longer support at least one hollow bearing tree. The removal of sites lacking hollow-bearing trees from the sampling regime for marsupials introduced a slight, but unavoidable, positive bias to the marsupial occurrence probability of occurrence through time. For this reason, we retained all sites in our analysis of hollow-bearing trees, which allows us to draw inference across the broader landscape and remove the bias induced by our method of sampling arboreal marsupials. As a final step in our analysis we combined estimates from both the hollow-bearing tree and marsupial occurrence analyses in order to draw a landscape-level inference about marsupial occurrence.

Full model for count of hollow-bearing trees (Q1 and Q3)

The count of the number of hollow bearing trees on sites occurred in 1997, 2005, 2009 (post fire), 2011, 2012, 2015 and 2017. Each site was surveyed on average 6.8 times with a low of two visits and a high of seven visits. Let HBT_{it} represent the number of hollow bearing trees occurs on site i ($i = 1, \dots, 164$) in year t . We modelled this process with a Bayesian Poisson regression with the following predictors: land tenure (1 if protected, 0 if wood production), survey year, amount of fire in the surrounding landscape and the amount of harvesting in the surrounding landscape. Thus, our model can be expressed as a generalized linear model as follows: Let:

$$\begin{aligned}
 HBT_{it} &\sim \text{Poisson}(\mu_{it}) \\
 \eta_{it} &= \beta_0 + u_i + \beta_1 F_{it} + \beta_2 L_{it} + \beta_3 LT_{it} + \beta_4 rs^1(SY_{it}) + \beta_5 rs^2(SY_{it}) + \beta_6 rs^3(SY_{it}) \\
 &\quad + \beta_7 rs^4(SY_{it}) \\
 u_i &\sim N(0, \sigma_u)
 \end{aligned}$$

$$\log(\mu_{it}) = \eta_{it}$$

where, F_{it} is the fraction of forest burned in 2009, L_{it} is the fraction of forest that was logged, LT_t is the land tenure of site I , SY_{it} is the survey year, $rs^1(SY_{it})$ to $rs^4(SY_{it})$ are the basis functions for a cubic regression spline of survey year with four degrees of freedom, u_i is the site level random intercept with standard deviation σ_u and η_{it} is the linear predictor. We note that F_{it} was zero prior to the 2009 wildfire. For the models that included a survey year effect (see section on Model fitting & selection), we also looked at whether the spline could be simplified to a linear function of time. In addition, for the models with linear year effects, we also examined whether or not the addition of a random slope effect for year improved the model, with the slope of year allowed to vary according to site. Specifically, our linear predictor for this model is given by:

$$\eta_{it} = \beta_0 + u_i + \beta_1 F_{it} + \beta_2 L_{it} + \beta_3 LT_{it} + (\beta_4 + b_{i4}) SY_{it}$$

$$u_i \sim N(0, \sigma_u)$$

$$b_{i4} \sim N(0, \sigma_{SY})$$

where u_i is the site level random intercept with standard deviation σ_u and b_{i4} is the site level random slope for survey year with standard deviation σ_{SY} .

Full model for marsupial occurrence (Q2 and Q4)

Conditional on their being at least one hollow bearing tree on a site (necessary to conduct stag-watching), we modelled the presence of each individual species of arboreal marsupial with a Bayesian logistic regression model. Specifically, let y_{it} represent the presence of the species on site i ($i = 1, \dots, 158$) in year t ($t=1997, 1998, 1999, 2000, 2001, 2002, 2003, 2006, 2007, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018$) and

let $\pi_{it} = \text{Prob}(y_{it} = 1)$. Each site was surveyed on average 4.8 times with a low of one and a high of ten visits. Our full logistic regression model is specified as follows:

$$y_{it} \sim \text{Bernoulli}(\pi_{it})$$

$$\psi_{it} = \beta_0 + v_i + \beta_1 F_{it} + \beta_2 L_{it} + \beta_3 LT_{it} + \beta_4 \log(HBT_{it}) + \beta_5 rs^1(SY_{it}) + \beta_6 rs^2(SY_{it}) + \beta_7 rs^3(SY_{it}) + \beta_8 rs^4(SY_{it})$$

$$v_i \sim N(0, \sigma_v)$$

$$\text{logit}(\pi_{it}) = \left(\frac{\pi_{it}}{1 - \pi_{it}} \right) = \psi_{it}$$

where HBT_{it} is the number of hollow bearing trees, v_i is site level random intercept with standard deviation σ_v . Note we are using $\log(HBT_{it})$ instead of HBT_{it} as preliminary analysis showed a better fit to the presence of arboreal marsupials. We note that F_{it} was zero prior to the 2009 wildfire. For the models that included a survey year effect, we also examined whether the spline could be simplified to a linear function of time.

Model fitting & selection

As the landscape factors we were interested in were time-varying, each analysis included two steps: **(1)** Fitting of a model including time as the only fixed effect (i.e. excluding landscape variables), to describe the temporal trends in HBT (Q1) and arboreal marsupials (Q2). And; **(2)** A model selection process to choose the best-fitting model of the effects of landscape factors on numbers of hollow-bearing trees (Q3) and arboreal marsupial occurrence (Q4). We completed model selection for each stage of our analysis using the widely applicable information criteria (WAIC) (Vehtari, Gelman & Gabry, 2017) to choose the best fitting model for each response variable. For the analysis of temporal trends in the number of hollow bearing trees and the occurrence of each species of arboreal marsupial (Q1 and Q2), we performed a model selection amongst various combinations of year discussed

above, i.e. none, linear, linear with random slopes (number of hollow bearing trees only) and cubic regression spline of year with four degrees of freedom. For the full analysis (Q3 and Q4), we performed model selection on a set of 32 candidate models for the Poisson regression for the number of hollow bearing trees on a site (see Table S6) and 48 models for the occurrence of each species of arboreal marsupial (see Tables S8-S11). We elected to interpret the best fitting model (i.e. the one with the lowest WAIC) and the most parsimonious model (the simplest model within two WAIC units of the best fitting model) in each case.

All continuous variables were standardized to have zero mean and standard deviation one, this was done to aid with convergence of Markov Chain Monte Carlo (MCMC) algorithms and to aid with prior specification. We performed a prior sensitivity analysis for Bayesian logistic regression parameters on the logit scale using the following priors: 1) Student-t distribution with 7 degrees of freedom, zero mean and scale parameter of 2. (<https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations>); 2) Student-t distribution with 7 degrees of freedom, zero mean and scale parameter of 1.414 (Northrup & Gerber, 2018); 3) Gaussian (normal) distribution with zero mean and standard deviation 1.414 (Northrup & Gerber, 2018); 4) Logistic distributions with zero mean and scale parameter of 1 (Northrup & Gerber, 2018); and 5) “flat” or non-informative priors. We used a half student-t distribution with three degrees of freedom, centred at zero and a scale parameter of ten, for the random effect standard deviation. The results of the prior sensitivity analysis are reported in Figs. S1-S4 and we proceeded with our model selection procedure with the “flat” or non-informative priors.

We constructed all models using the brms package (Bürkner, 2017; Bürkner, 2018) in R 3.6.1 (R Core Team, 2018). We ran four Markov chains for 10,000 iterations, discarding a warmup of 2,000 with a thinning factor of eight giving a total 4,000 samples for posterior

inference. We assessed convergence of the chains using the Rhat statistic (Gelman & Rubin, 1992), values less than 1.01 were deemed to have been adequately converged.

The best fitting logistic regression model for each species was used to predict the occurrence of each species for all years and sites. In order to account for the sites that unobserved (for a given year site combination) we used the predicted number of hollow bearing trees from the best fitting Poisson regression model.

Model synthesis

We combined the hollow bearing tree analyses and the animals species occurrence analyses to quantify the overall effect of temporal changes in the hollow bearing tree resource on the occurrence of individual species of arboreal marsupials. Combining these analyses allowed us to account for the fact that not all sites were stag-watched in every year and also the conditional nature of the stagwatch sampling (i.e. if a site no longer supports any hollow-bearing trees, then we no longer conducted stagwatching surveys). Combining these analyses required that we assume sites with zero hollow-bearing trees supported zero arboreal marsupials.

To combine these analyses, we first generated posterior samples of the annual numbers of hollow-bearing trees for each of the 164 sites that were stagwatched between 1997 and 2018. These were generated from the posterior samples of the best fitting model for the number of hollow-bearing trees. Thus, we developed a complete, albeit model-based, data set of the number of hollow-bearing trees at each site from 1997-2018. We obtained values for tenure, amount of fire in the surrounding landscape, and amount of logging in the surrounding landscape for each site in each year; using the same methods as for the original models. We then derived posterior samples of the probability of occurrence for each species of arboreal marsupial for each posterior sample of the number of hollow bearing trees for

each site and year combination. If the estimated number of hollow bearing trees at a site was zero, we assumed that site had a zero probability of animal occurrence. For computational reasons, we used 500 posterior samples for each stage and we present the annual estimate of occupancy for each species by averaging across the 158 sites.

RESULTS

We detected eight species of arboreal marsupials over the duration of this study (Table S2). There were sufficient data available for detailed analyses of four species; Leadbeater's possum, greater glider, mountain brushtail possum, and sugar glider. The yellow-bellied glider, common ringtail possum, eastern pygmy possum, and feathertail glider were too rarely recorded to allow statistical analyses. Descriptive information on the species of arboreal marsupials and the associated covariates is given in Tables S2 and S3. We provide descriptive information on the number of sites at which enumeration of hollow bearing trees was performed as well as basic information on covariates in Table S4 and Figs. S5-S7.

Q1 and Q2: What are the temporal trends in hollow-bearing trees and arboreal marsupials?

Analysis of time effects only revealed that the expected number of hollow bearing trees per site declined between 1997 and 2018 (Fig. 2a), as did the expected probability of occurrence of the four individual species of arboreal marsupials (Fig. 2b-2e), although the effect of time was marginal for the mountain brushtail possum (as measured by WAIC, Table S5).

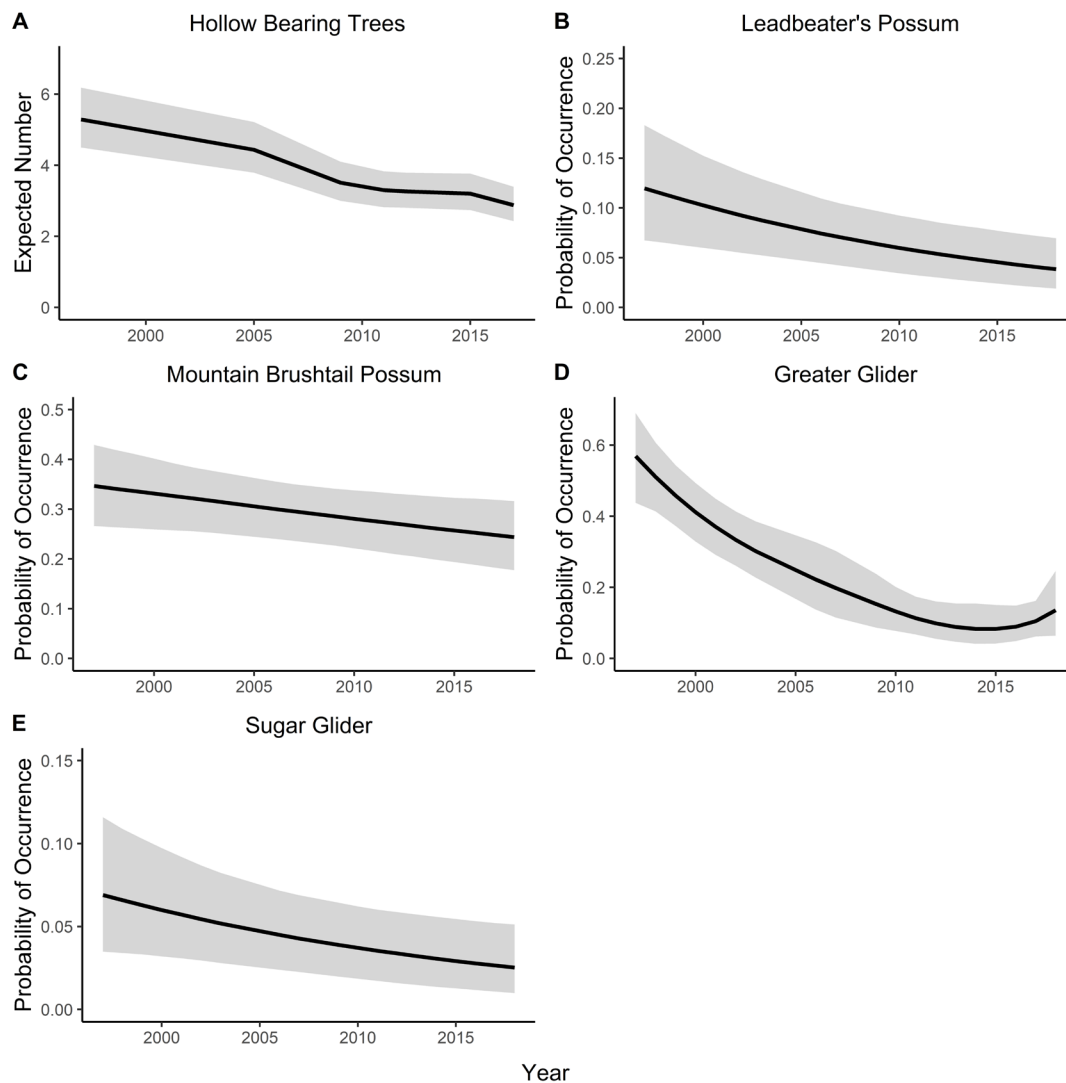


Fig. 2: Estimated temporal trends in the number of hollow bearing trees, and the occurrence of each species of arboreal marsupial. The grey shaded areas represent 95% credible intervals.

Q3: Is the number of hollow-bearing trees related to land tenure and landscape levels of wildfire and logging?

When landscape factors were included in the model, the best-fitting model still included a downward temporal trend in the number of hollow-bearing trees (Fig. 3a). This model also revealed fewer hollow-bearing trees on sites where high proportions of the

surrounding landscape had been burned (Fig. 3b), and on sites located in wood production forest (Fig. 3c).

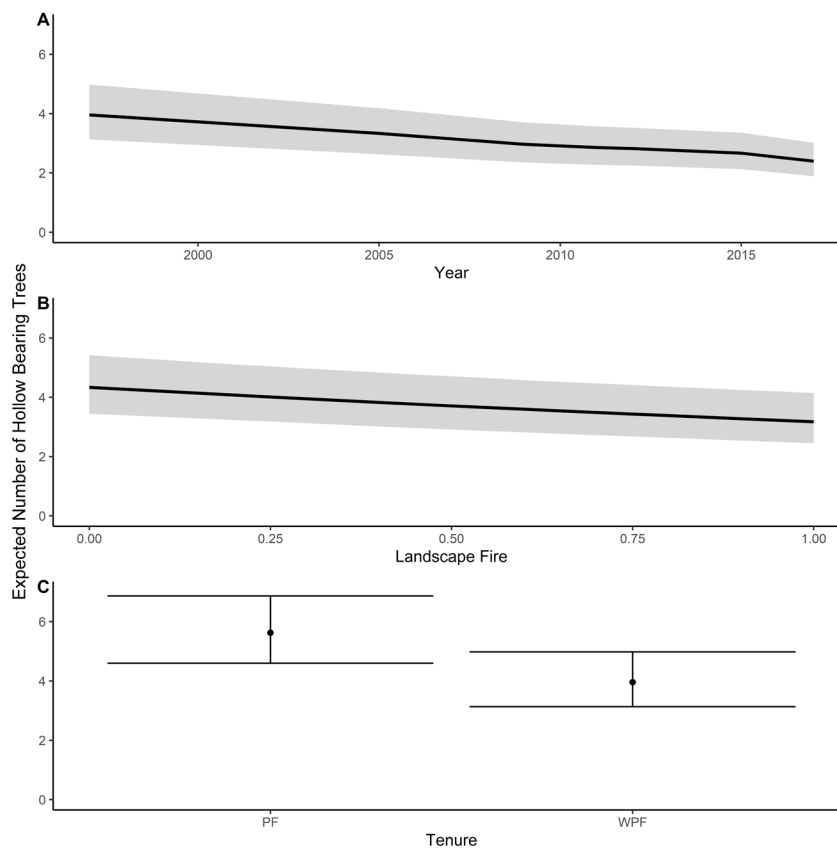
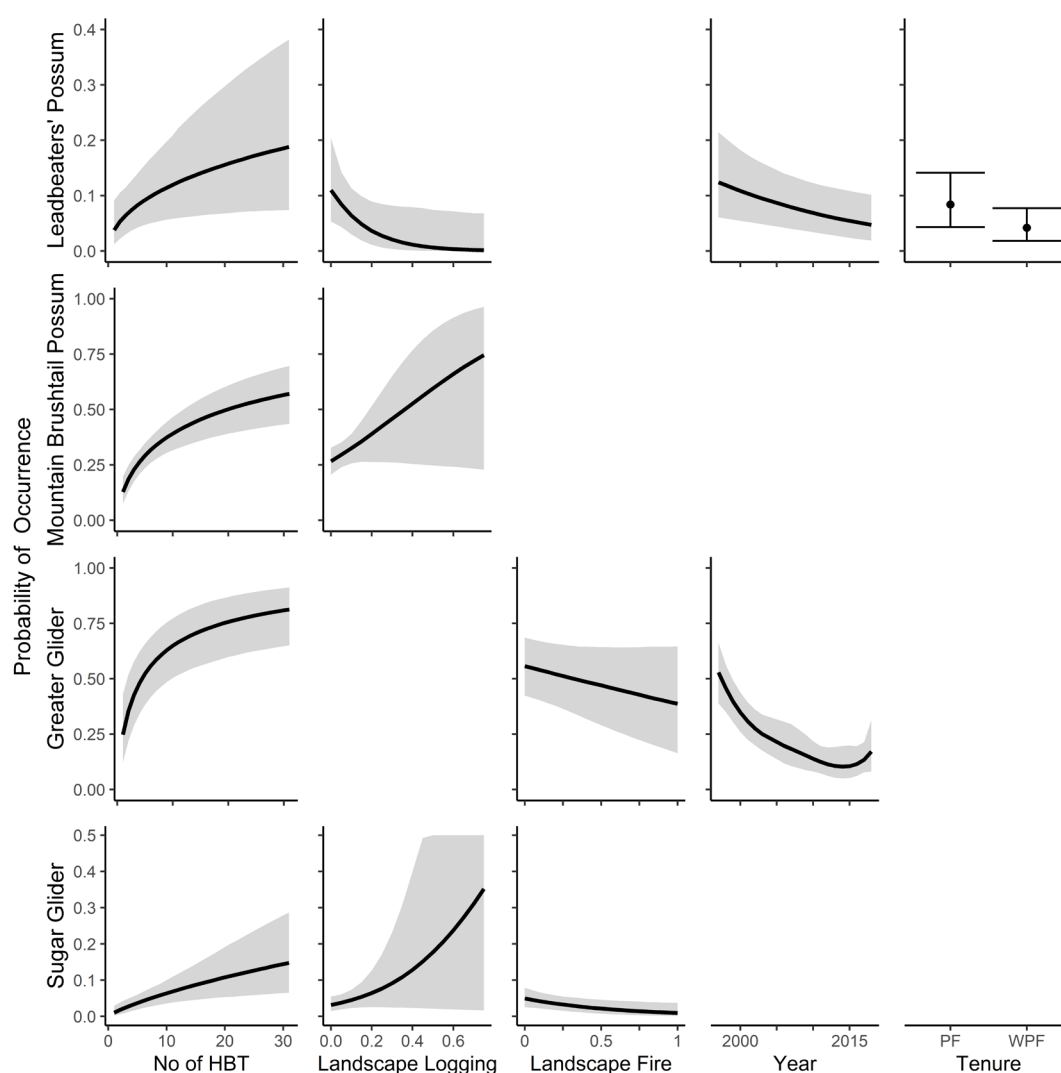


Fig. 3. Factors influencing the number of hollow-bearing tree (HBT) in the montane ash forests of the Central Highlands of Victoria. Values for other covariates in each of the models are held to the mean value. PF = protected forest. WPF = wood production forest. The grey shaded areas represent 95% credible intervals.

Q4: Is the occurrence of arboreal marsupials related to the number of hollow-bearing trees, land tenure, and landscape-levels of wildfire and logging?

We found evidence of a strong positive relationship between the occurrence of all species of arboreal marsupials and the number of hollow-bearing trees at a site (Fig. 4; Tables S8-S15). The probability of occurrence of Leadbeater's possum declined with increasing amounts of logging in the surrounding landscape, whereas we found the opposite effect for

the sugar glider and the mountain brushtail possum (Fig. 4). The presence of Leadbeater's possum was higher on sites in wood production forests compared to protected forests (Fig. 4). Finally, the probability of occurrence of the two glider species was negatively associated with increasing amounts of fire in the landscape (Fig. 4). Top-ranked models for each species indicated that temporal trends in mountain brushtail possums and sugar gliders observed under Q2 (Fig. 2) were no longer important once landscape factors were included in the model, but remained important for Leadbeater's possum and the greater glider.



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Fig. 4. The effects of the number of hollow bearing trees, landscape logging, landscape fire and year on the occurrence of four species of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria. The analysis for each species was

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ash forests of the Central Highlands of Victoria. The analysis for each species was

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conditional on the presence of at least one hollow bearing tree at the site. Values for other covariates in each of the models are held to the mean value. Blank plots in the grid correspond to where a particular covariate was not included in the top-ranked model for that species. Note that we have used different y-axis scales for each species. The grey shaded areas represent 95% credible intervals.

Model synthesis

The final part of our analysis combined the model for the number of hollow-bearing trees with the analysis of the factors influencing the occurrence of each species of arboreal marsupial to estimate marsupial occurrence at all sites in all years of the study to estimate each species' temporal trend at the landscape scale. The results of this combined analysis closely resembled results from analysis of temporal trends in the marsupial occurrence data alone, and shows a decline in the occurrence of each of the four species of arboreal marsupial (Fig. 5). The combined analysis indicated a slightly stronger decline for the Leadbeater's possum than the occurrence only analysis, and also highlighted marked declines in the occurrence of both the sugar glider and greater glider, coincident with the 2009 wildfire.

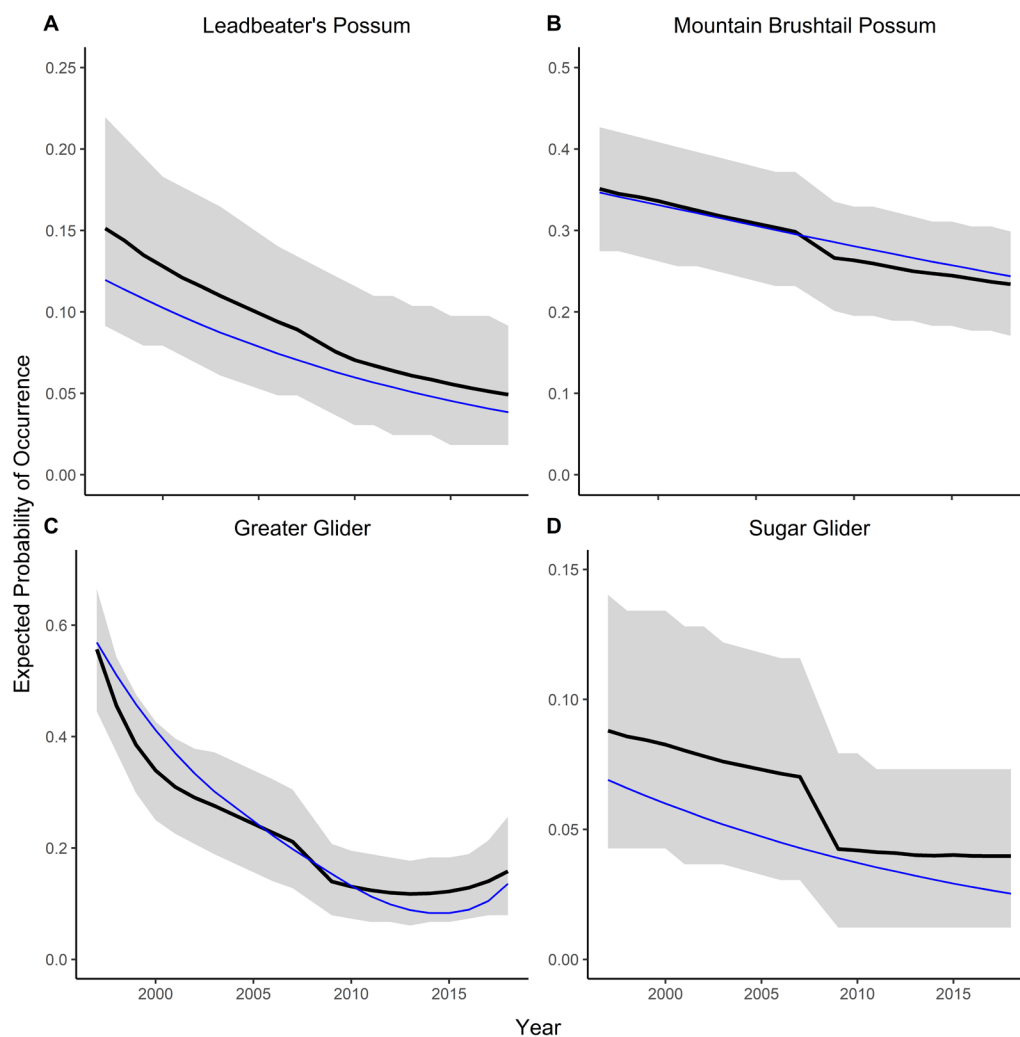


Fig. 5. The combined effects (shown by the black line) of the Poisson regression model for the number of hollow bearing trees at a site and the logistic regression model for the occurrence of each individual species of arboreal marsupial (see Methods). We also include the temporal trend from Fig. 2 (shown by the blue line) for each species. The grey shaded areas represent 95% credible intervals.

DISCUSSION

We examined long-term, large-scale temporal changes in the occurrence of arboreal marsupials and how they are associated with site-level and landscape-level variables. Our

analyses revealed that: **(1)** The number of hollow-bearing trees on sites has declined since 1997 (Fig. 2). The number of these trees was lower on sites located in wood production areas compared to sites in water catchment areas. It was also lower where a large proportion of the surrounding landscape had burnt. **(2)** Populations of arboreal marsupials have declined since 1997 (Fig. 2) and also after accounting for other factors (e.g. the decline in hollow-bearing trees and the amount of disturbance in the landscape) as well as the inherent biases associated with the stagwatching method (Fig. 5). **(3)** The occurrence of all species of arboreal marsupials was strongly, positively linked to the number of large old hollow-bearing trees at a site. **(4)** There were marked inter-specific differences in species responses to landscape disturbance such as the amount of logging and the amount of fire surrounding a site. We further describe these findings in the remainder of this paper and conclude with commentary on the implications of our work for the conservation of arboreal marsupials.

Q1 and Q3. What are the temporal trends in critical denning resources for arboreal marsupials? And: Is the number of hollow-bearing trees related to land tenure and landscape levels of wildfire and logging?

Our analyses contained strong evidence of a decline in the abundance of hollow-bearing trees (Fig. 2). This is a particular concern for the long-term persistence of arboreal marsupials, given the strong positive relationships between the number of hollow-bearing trees and the occurrence of all species that we modelled (see below). Previous work has shown that the fastest losses of hollow-bearing trees occur in regrowth stands aged 80 years or younger (Lindenmayer *et al.*, 2018a), where such trees are legacies of past old growth stands that were disturbed by wildfires (Lindenmayer *et al.*, 2019). Conversely, the slowest rate of decline is in old growth forests, but these comprise only 1.16% of the Mountain Ash estate and 0.47% of the Alpine Ash estate in the Central Highlands region.

We found that the decline in numbers of hollow-bearing trees was associated with the amount of fire in the landscape and land tenure. These results were expected given that fires can consume a large amount of forest, leading to altered microclimatic conditions (such as elevated windspeeds) which can increase the loss of large old trees (Lindenmayer *et al.* 2011). We recorded fewer large old trees on sites within wood production forests. Timber harvesting in logged landscapes intersperses cutblocks with uncut stands (including areas supporting our long-term sites). This can lead to landscape-level changes in windspeeds and increases windthrow (Lindenmayer, Cunningham & Donnelly, 1997), which is likely to be one of the key reasons for reduced numbers of large trees in such areas.

Q2. What are the temporal trends in the occurrence of arboreal marsupials?

We found evidence for a decline in the occurrence of all species of arboreal marsupials (Figs. 2 and 5). The effects remained after accounting for other factors (e.g. the decline in hollow-bearing trees and the amount of disturbance in the landscape) as well as the inherent biases associated with the stagwatching method (Fig. 5). The inter-specific patterns observed were broadly consistent with our predictions at the outset of this investigation. That is, the feeding specialist greater glider and range-restricted Leadbeater's possum exhibited the most marked declines (Figs. 2 and 5), whereas there was a marginal effect of time in the best fitting model for the widespread generalist, the mountain brushtail possum (Fig. 2). The most pronounced decline we observed was for the greater glider (Figs. 2 and 5). This trend is of considerable concern as it is mirrored in other parts of eastern Australia (Lindenmayer *et al.*, 2018c; Smith & Smith, 2018). Indeed, the greater glider used to be one of the most commonly detected species in field surveys in many areas of wet forest in eastern Australia. Its decline appears to be an example of a formerly common – but specialist species – rapidly becoming rare (Lindenmayer *et al.*, 2011). Losses in specialist species suggest that not only will the future arboreal marsupial assemblage in montane ash forests be characterized by

fewer species, but also that it will be simplified with key niches vacated, such as those for a specialist arboreal folivore (greater glider). Other niches may have already been vacated, such as the large exudivore niche that would formerly have been occupied by the yellow-bellied glider, a species which is now rarely recorded (with only 59 animals detected in the past 20 years of surveys; see Table S5). There may well be cascading impacts of these losses on other species, such as large forest owls for which arboreal marsupials can be important prey items (Debus, Davies & Hollands, 2009).

Q4. Is the occurrence of arboreal marsupials related to the number of hollow-bearing trees, land tenure, and landscape-levels of wildfire and logging?

Our analyses contained evidence of a positive relationship between the number of hollow-bearing trees at a site and the occurrence of all four species of arboreal marsupials (Fig. 4). This result was expected given that arboreal marsupials are cavity-dependent and cannot persist in areas where hollow-bearing trees are absent.

The landscape surrounding our long-term field sites has undergone considerable change in the past 20 years as a result of wildfire (primarily in 2009) and ongoing clearcutting. Our analyses revealed that temporal patterns of site occurrence by some species of arboreal marsupials have been associated with these spatio-temporal changes in forest cover. We found evidence of a negative association between the occurrence of Leadbeater's possum at a site and the amount of logged forest in the surrounding landscape (Fig. 4). Such relationships are of considerable concern. Recent studies have indicated that proposed future logging in Victoria over the next 5-10 years (VicForests, 2019) will be focused disproportionately in high conservation value forests (Taylor & Lindenmayer, 2019). Therefore, additional planned logging will add to the extent of logged forest in the landscape and hence magnify logging-induced disturbance impacts on species such as Leadbeater's possum.

Whilst there was a negative relationship between the amount of logging in the
 landscape and Leadbeater's possum, both the mountain brushtail possum and the sugar glider
 exhibited a positive association with this covariate (Fig. 4). Indeed, a potential reason for the
 negative relationship between Leadbeater's possum and the amount of logging in the
 surrounding landscape may be competition with the sugar glider. Leadbeater's possum and
 the sugar glider are functionally similar species and have even been known to co-occupy the
 same nest trees (Lindenmayer & Meggs, 1996). However, the sugar glider is one of the most
 widely distributed marsupials globally, including being introduced to a number of areas
 outside its natural range (Lindenmayer, 2002). It is possible that negative responses of
 Leadbeater's possum to the amount of logged forest is linked with the positive response of
 the sugar glider to the same landscape attribute. Indeed, work in logged forests on the
 Australian island of Tasmania (where the sugar glider is an introduced species) has shown it
 often colonizes logged and regenerated forests (Allen *et al.*, 2018). A detailed co-occurrence
 analysis, coupled with radio-tracking and behavioural studies, would be required to determine
 if there are negative relationships between the two species in Victorian forests, although data
 for both species in montane ash forests were too sparse to allow such work to be completed
 for this investigation.

Our analyses indicated that sites in wood production forests were more likely to
 support Leadbeater's possum than sites in protected areas. This was an unexpected outcome,
 especially as wood production forests support fewer hollow-bearing trees than protected areas
 (Fig. 3) and such areas are subject to more logging. It is possible that this result occurred
 because, relative to protected areas, wood production forests tend to be located in more
 productive environments (Braithwaite, Turner & Key, 1984). Moreover, sites in wood
 production forests earmarked for future logging are also those which have high conservation
 value, including for species such as Leadbeater's possum (see Taylor & Lindenmayer, 2019).

We identified a negative relationship between the extent of fire in the landscape and the occurrence of the greater glider and sugar glider (Fig. 3). We suggest that this effect may be related to the high likelihood that animals are killed on-site by the high-intensity conflagrations that typically occur in montane ash forests, or indirectly through the loss of feeding resources in canopy consuming fire. In addition, increasing rates of collapse of hollow-bearing trees are associated with increasing areas of burned forest in the landscape (Fig. 3) and this may deplete nesting and den sites for cavity-dependent animals.

We found evidence of a decline for the mountain brushtail possum and the sugar glider (Fig 2), but the effects of time no longer remained in the best fitting model once other covariates were fitted. Hence, declines in the number of hollow-bearing trees and the amount of fire and logging in the landscape explained temporal declines in these species. Conversely, in the case of Leadbeater's possum and the greater glider, an effect of time was retained in the best fitting model after other covariates were fitted. This suggests that other factors that were not modelled are contributing to the ongoing decline of these species. For example, the greater glider is known to be heat-sensitive (Rubsamen *et al.*, 1984) and elevated temperatures in recent decades in this region may be contributing to declines (Lindenmayer *et al.*, 2011). Similarly, recent studies have indicated that Leadbeater's possum may be preyed upon by feral predators like cats (McComb *et al.*, 2018) although whether this threat has increased in recent decades within the study region remains unclear.

Management implications

The results of this study have important implications for conservation. First, our data highlight the major declines occurring in key species of conservation concern such as Leadbeater's possum and the greater glider. The strength and consistency of these declines demonstrate that it is important to take effective conservation action now and not simply monitor these species until they suffer regional or even global extinction (see Lindenmayer,

Piggott & Wintle, 2013). In the case of Leadbeater's possum, the importance of the amount of logged forest in the landscape indicates that ongoing logging will have further negative impacts on the species, as does our finding that this species is more likely to occur in areas earmarked for future logging. A moratorium on logging in landscapes where the species occurs is urgently required. The recent decision by the Victorian Government to halt logging by 2030 (Office of the Premier of Victoria, 2019) is a proactive step. However, given the trajectory of declines in these species of conservation concern, a more rapid cessation of logging is needed.

The negative effects of the extent of fire in the landscape on numbers of hollow-bearing trees and the occurrence of arboreal marsupials is a second issue of concern arising from our analyses. Montane ash forests are increasingly susceptible to high-severity wildfires, with five major conflagrations in the region in the past century. This frequency has been elevated relative to the historical record (which was previously an average of one major fire every 75-150 years (McCarthy, Gill & Lindenmayer, 1999)). We suggest that greater efforts are needed to reduce the occurrence of wildfire in montane ash forests. This may entail both: **(1)** reducing the spatial extent of logging operations which creates large areas of flammable young forest (Zylstra, 2018) and can lead to regenerating stands being more prone to crown-scorching fires (Taylor, McCarthy & Lindenmayer, 2014) and **(2)** protecting existing advanced regrowth forest and allowing it to mature through to old growth, as fire severity is lower in such stands (Lindenmayer & McCarthy, 1998).

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