RESEARCH PAPER
https://doi.org/10.1071/WR23129
WILDLIFE RESEARCH

The influence of severe wildfire on a threatened arboreal mammal

Mikayla C. Green[A,B], Damian R. Michael[B], James M. Turner[C], Lucy J. Wright[A,B] and Dale G. Nimmo[A,B,*]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
Dale G. Nimmo
School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Albury, NSW, Australia
Email: mcg99@xtra.co.nzdnimmo@csu.edu.au

Handling Editor:
Natasha Robinson

Received: 12 October 2023
Accepted: 28 June 2024
Published: 26 July 2024

Cite this: Green MC *et al.* (2024) The influence of severe wildfire on a threatened arboreal mammal. *Wildlife Research* **51**, WR23129. doi:10.1071/WR23129

ABSTRACT

Context. Fire regimes are changing with ongoing climate change, which is leading to an increase in fire frequency and severity. Australia's Black Summer wildfires burned >12 million hectares in 2019–2020, affecting numerous threatened animal species. One of the species predicted to be most impacted was the threatened southern greater glider, an arboreal, hollow-dependent folivore, endemic to eastern Australia's eucalypt forests. **Aims.** This study aimed to assess how the 2019–2020 wildfires affected greater glider abundance and the resources they depend on in Woomargama National Park, New South Wales, Australia. **Methods.** We categorised 32 sites into four fire severity treatments with eight sites for each treatment: unburned (continuous unburned vegetation); refuges (unburned patches within the fire's perimeter); low-moderate severity; and high severity. We carried out two spotlight surveys per site using the double-observer method, beginning 21 months after the fires. We also conducted vegetation assessments on the same transects. To analyse the data, we used Generalised Linear Models to compare habitat differences based on fire severity, and N-mixture models to model greater glider detectability and abundance in relation to habitat and fire severity. **Key results.** We found that fire severity depleted several habitat variables including canopy cover and the number of potentially hollow-bearing trees, a resource that greater gliders rely on. Greater glider abundance also decreased in all burn categories, with the greatest decline experienced in areas burned at high severity. We also found that greater glider abundance was much lower in fire refuges than unburned habitat outside of the fire zone. **Conclusions.** Greater glider declines following severe wildfire can be at least partly attributed to the level of vegetation loss and the associated loss of key habitat resources. The contribution of direct mortality to population declines remains unknown. **Implications.** Greater glider conservation will rely heavily on protecting expansive unburned areas of suitable habitat and maintaining hollow-bearing trees.

Keywords: Black Summer, fire regime, fire severity, habitat, hollows, marsupial, megafire, threatened species, wildfire.

Introduction

Fire is one of Earth's most widespread abiotic disturbances and has caused significant ecological change over millions of years (Bowman *et al.* 2009). Fire consumes plant matter, affecting resources for plants and animals over years, decades, and centuries (Haslem *et al.* 2011; Bassett *et al.* 2017). Fire regimes have shifted (Rogers *et al.* 2020) and are projected to change further due to climate change (Wu *et al.* 2021). Fire activity in many parts of the world is increasing (Bowman *et al.* 2020). For example, climate change is prolonging fire seasons, increasing fuel dryness and exacerbating fire risk (Bowman *et al.* 2020; Duane *et al.* 2021; Jain *et al.* 2022). A series of recent extreme wildfire events around the world underscore Earth's changing fire regimes (Duane *et al.* 2021), culminating in megafires (>10,000 ha burned) and gigafires (>100,000 ha burned) (Linley *et al.* 2022).

Fire severity is an important aspect of fire regimes that affects animal survival and population persistence through direct mortality (Jolly *et al.* 2022) and by causing changes in habitat structure (Chia *et al.* 2015; Lindenmayer *et al.* 2021*a*). Fire severity is the consumption of organic matter during fire: high severity fire, by definition, consumes more organic matter than low severity fire (Keeley 2009; May-Stubbles *et al.* 2022). In forest ecosystems, low to moderate severity fires burn the understorey and midstorey, whereas high severity fires consume understorey, midstorey, and canopy vegetation (Keeley 2009; Collins *et al.* 2021; May-Stubbles *et al.* 2022). High severity fires can cause the depletion of habitat resources, even in landscapes with adaptations to fire, such as eucalypt forests (Possingham *et al.* 1994; Lindenmayer *et al.* 2004; Legge *et al.* 2022). For example, hollow bearing trees – which are used by over 300 vertebrate species in Australia (Lindenmayer *et al.* 2004) – can be destroyed by high severity fire, and may not form again for decades or longer (Possingham *et al.* 1994; Lindenmayer *et al.* 2004; Legge *et al.* 2022). This loss is detrimental to many species, such as birds and arboreal mammals that are dependent on hollows as refuges for nesting and breeding (Gibbons *et al.* 2002; McLean *et al.* 2018). By contrast, low to moderate severity fire can aid the formation of tree hollows by causing limbs to fall off trees, creating areas for hollows to form in the future (Haslem *et al.* 2016). Therefore, high severity fires may present a particular risk to hollow dependent fauna species (Roberts *et al.* 2008; Lindenmayer *et al.* 2014; May-Stubbles *et al.* 2022).

Australia's 'Black Summer' bushfires were a series of large, severe fires that occurred across southern and eastern Australia during the 2019–2020 spring and summer. The fires followed a prolonged drought (Abram *et al.* 2021), and displayed unprecedented fire behaviour, including a record number of firestorms (Kablick *et al.* 2020). Landscape features that usually act as barriers to fire – wet gullies, rocky outcrops, riparian strips, rivers and cliffs – failed to do so under such extreme conditions (Wintle *et al.* 2020).

The southern greater glider (*Petauroides volans*, herein 'greater glider') is an Australian endemic, arboreal marsupial that inhabits eucalypt forests across eastern Australia (McGregor *et al.* 2020). Populations of greater gliders are declining due to deforestation, habitat degradation, climate change, and fire (Smith and Smith 2020; Wagner *et al.* 2020; Ashman *et al.* 2021). The greater glider is listed as Endangered under the Australian Government's *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) (Australian Government 2022*b*). Greater gliders are Australia's largest gliding mammals (with a weight range of 900–1700 g) and can glide up to 100 m between trees (Van Dyck and Strahan 2008). They have a specialised folivore diet, consisting primarily of eucalypt leaves (Kavanagh and Lambert 1990). Greater gliders shelter in tree hollows, and when hollow-bearing trees are lost from an area, their abundance declines by up to 40% (McLean *et al.* 2018). Greater gliders are particularly vulnerable to ecological disturbance and following the 2019–2020 wildfires, experts identified them as one of the most impacted species. Local population losses have been estimated to be between 25 and 85% immediately following high severity fires (Legge *et al.* 2022) and it is estimated that more than 54% of greater glider location records since 2000 were burned in the 2019–2020 wildfires (Ashman *et al.* 2021). Isolated populations of greater gliders since these bushfires have concerningly been found to have low genetic diversity (Knipler *et al.* 2023). Their reliance on tree hollows and their folivorous diet makes them highly vulnerable to the spatial patterns of high severity fires (McLean *et al.* 2018; Wagner *et al.* 2021).

This study aimed to investigate the impacts of the 2019–2020 wildfires on greater gliders in a eucalypt forest in Woomargama National Park (NP), in southern New South Wales. Woomargama NP burned as part of a mixed severity fire that started on 29 December 2019 and was not extinguished until close to 2 months later. The western section of the park largely escaped the fire, whereas the eastern section burned at a range of severities, including high severity patches (Fig. 1) (Australian Government 2020). Furthermore, several patches within the perimeter of the fire remained unburned, and therefore could act as fire refuges (Fig. 1). These fire patterns make Woomargama NP an ideal location to study how greater gliders respond to fire, while providing baseline population information for the park. Greater gliders are known to occur in Woomargama NP (NPWS 2009); although records are relatively evenly distributed across the park, they are generally restricted to fire trails (ALA 2022).

This study specifically aimed to address the following questions:

1. How did the severity of the 2019–2020 wildfires affect habitat structure within Woomargama NP?
2. Which habitat structure variables influence greater glider abundance?
3. Does greater glider abundance differ between fire severity treatments (unburned, low-moderate, high) and does the species occur within fire refuges at similar abundances to continuous unburned areas?

Materials and methods

Study area

This study was conducted in Woomargama NP (Supplementary material 1), located in the South Western Slopes bioregion of New South Wales. The park covers approximately 24,000 ha (NPWS 2009), comprised of wet and dry old growth sclerophyll forest (NPWS 2004; Benson 2008) on hilly and mountainous terrain, ranging from ~200 m to ~1000 m elevation. Dominant tree species include a variety of eucalypts capable of epicormic sprouting, including broad-leaved peppermint (*E. dives*), narrow-leaved peppermint (*E. radiata*), long-leaved box (*E. goniocalyx*), red stringybark (*E. macrorhyncha*), and brittle gum (*E. mannifera*) (Kavanagh and Stanton 1998). Wet sclerophyll forests in the park are typically dominated by narrow-leaved and broad-leaved peppermint, and dry sclerophyll forests are dominated by brittle gum and broad-leaved peppermint (Keith and Simpson 2018).

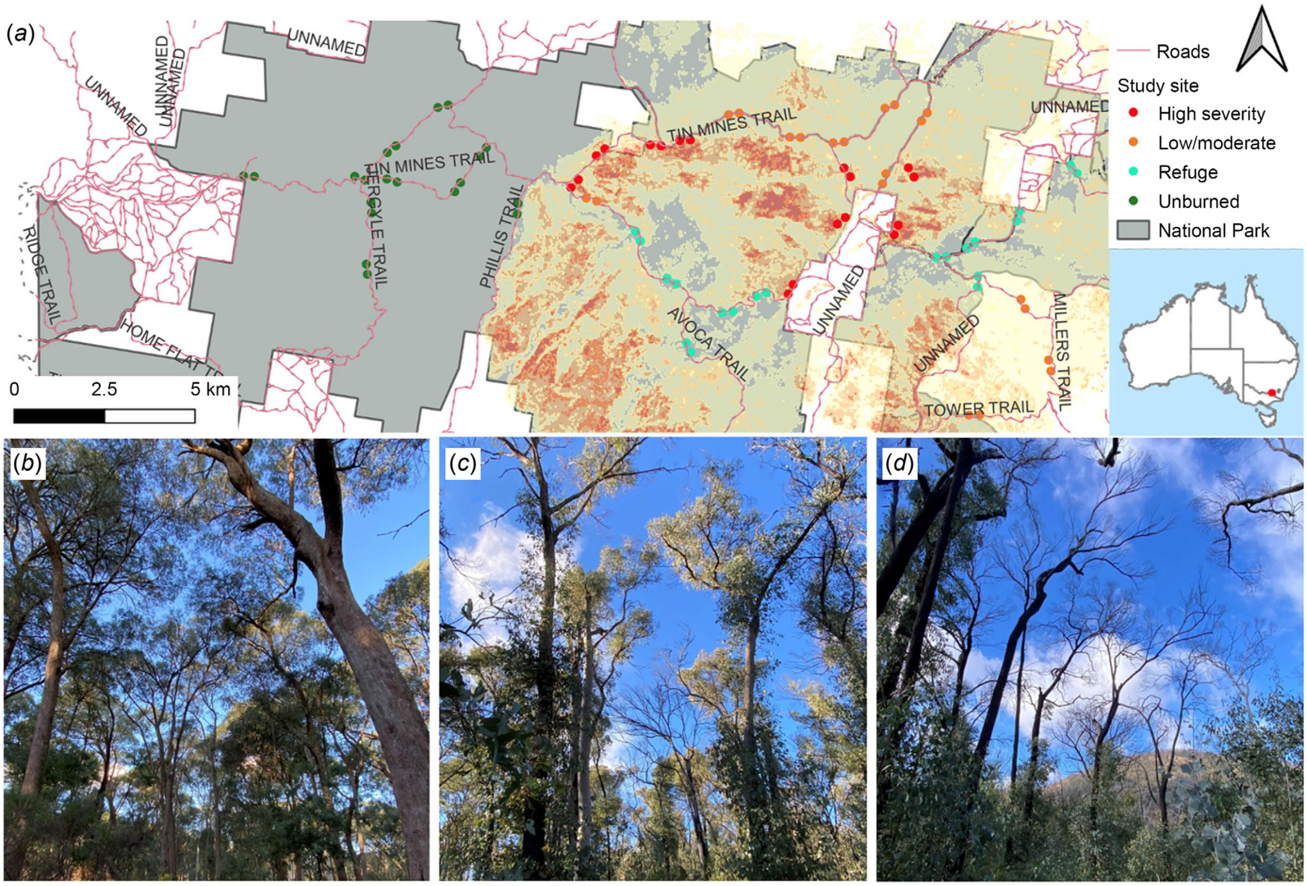

Fig. 1. Woomargama NP (grey) showing (*a*) the location of the 32 transects (circles, marking the start and end of each transect), stratified and colour-coded according to fire severity. The 2019–2020 wildfire severity is shown: light (yellow) areas burned at low to moderate fire; darker (orange/red) areas burned at high and very high severity. Photographs show examples of (*b*) unburned, (*c*) low-moderately burned, and (*d*) high severity burned sites. Photos: M. Green.

Mean monthly temperatures range between 4.4°C in July to 31.2°C in January and the average annual rainfall is 697.4 mm (Elders Weather 2022). Woomargama NP was severely affected by the Australian 2019–2020 summer wildfires, which burned ~18,000 ha of the park and the adjacent Woomargama State Forest as part of the ~630,000 ha Green Valley/Tunnel Road gigafire (*sensu* Linley *et al*. 2022). Greater gliders inhabit these forests with records distributed evenly across the park, although no previous population estimates have been made (Kavanagh and Stanton 1998; ALA 2022; Australian Government 2022*b*).

Experimental design and fire severity classification

This study used fire severity categories adapted from the Australian Google Earth Engine Burnt Area Map (GEEBAM) classification of the 2019–2020 wildfires developed by the Department of Agriculture, Water and the Environment (Australian Government 2020). GEEBAM has five severity categories ranging from unburned to very high, as well as an added 'no data' category. We combined low and medium sites as 'low-moderate severity', and high and very high as 'high severity'. The combination of fire severity classes was undertaken because differences between the combined fire severity classes (i.e. between high and very high) were not always clear in the field, and to increase samples sizes within each treatment. In total, we had four fire severity treatments: unburned (continuous unburned vegetation), refuges (unburned patches within wildfire perimeter), low-moderate severity (burned with some regrowth and intact canopy), and high severity (high canopy scorch).

Eight sites were established in each of the four fire severity classes, totalling 32 sites (Fig. 1). At each site, a 300 m transect was established and ground-truthed to confirm the on-ground fire severity matched the GEEBAM map. Sites were located in the desired fire severity class within a short walking distance of nearby dirt tracks for accessibility. Sites were separated by a minimum of 500 m. Where fire severity did not conform with the map, the transect was moved to a nearby area of desired fire severity. Sites were selected to be within sclerophyll forest (the preferred greater glider habitat) at elevations between 492 m and 786 m, with most sites located in dry forests (25/32) and a smaller number (7/32) occurring in wet sclerophyll forests (based on Keith and Simpson 2018). The number of sites in each vegetation type within each fire severity treatment varied: unburned was comprised of one wet and seven dry sclerophyll transects; refuge had three wet and five dry sclerophyll transects; low-moderate had all dry sclerophyll transects; and high severity had three wet and five dry sclerophyll transects. All transects were within a single fire severity treatment (i.e. not crossing from one into another) and typically ran parallel to dirt four-wheel drive tracks. Refuge transects were within small patches of vegetation that escaped the fire, and were therefore usually close to the boundary of the fires (average distance of transect mid-point to nearest burned edge = 105 m).

Greater glider surveys

Greater glider surveys were conducted between November 2021 and March 2022 on fine/partly cloudy nights. Surveys were not undertaken during strong winds, rain, or fog, which reduce detectability (Laurance 1990; Wayne *et al.* 2005; Wintle *et al.* 2005). Thirty-two transects, separated by a minimum of 500 m, were marked with flagging tape prior to surveys. Spotlighting commenced 45 min after dusk when greater gliders were foraging (Lindenmayer *et al.* 1991*a*). We employed the double-observer method to increase detectability (Cripps *et al.* 2021). Two observers (observer 1 = MG, observer 2 = LW) commenced surveys approximately 10–20 min apart, depending on vegetation and visibility of the first observer's spotlight to the second observer (Cripps *et al.* 2021). Transect lines were walked for ~30 min, using a handheld spotlight and binoculars to detect greater gliders. The direction, distance from transect, and colouring (light or dark) of all gliders was noted by each observer. Upon completing the transect, observers compared notes, identifying individuals based on those factors. This was done to verify how many greater gliders were recorded by both observers and how many were recorded by one observer. From there, an abundance tally of greater gliders could be formulated for the survey site. Each of the 32 transects were surveyed twice (approximately 2–3 months apart) using the double-observer method. Occupancy detection models verified that two nights of sampling was sufficient to detect greater glider presence with 95% confidence (following Kéry 2002).

Habitat surveys

Habitat surveys were conducted at all sites approximately one month after completion of fauna surveys. Habitat variables were selected based on previous research on greater gliders (see Table 1). A description and justification for each habitat variable is provided in Table 1. All variables were measured at various points along the same 300 m transect line that was used for the greater glider surveys (see Table 1 for details). Elevation was derived from a Geographic Information System (GIS) spatial layer.

Data analysis

How did the 2019–2020 wildfires affect habitat structure?

We used Linear Models (LMs) and Generalised Linear Models (GLMs) to examine differences in habitat variables across the fire severity classes. LMs were developed for continuous response variables including average tree height, average midstorey height, the number of strata at each site, and the basal area for overstorey and midstorey trees. GLMs were developed for modelling canopy cover, which is a proportion and hence modelled assuming a binomial distribution, and the number of large potentially hollow-bearing trees was modelled assuming a quasi-Poisson distribution (to account for overdispersion). Fire severity was a categorical predictor variable with four levels: unburned, refuge, low-moderate severity, and high severity. Unburned sites were specified as the reference category. Differences were regarded as significant if the 95% confidence interval did not overlap zero (for coefficient estimates from LMs) or one (for odds ratios and incidence rate ratios from GLMs).

How does habitat structure affect greater glider detectability and abundance?

We created a correlation matrix to assess whether habitat variables exhibited collinearity >0.7 (Dormann *et al.* 2013). The number of vegetation strata was correlated with the proportion of canopy cover >0.7. Therefore, we included only canopy cover in the N-mixture models.

In order to identify habitat variables related to the abundance of greater gliders – and which therefore might explain differences in greater glider abundance between fire severity classes – we used N-mixture models in R's unmarked package (Fiske and Chandler 2011; Schmidt *et al.* 2015). N-mixture models predict abundance at sites while considering factors affecting detection probability (Fiske and Chandler 2011; Schmidt *et al.* 2015; Kidwai *et al.* 2019). While our research questions are not focused on detectability, accounting for detectability is important when surveying animals under varying weather conditions, at varying distances from the observer, and in the presence of features that can visually obstruct animals. N-mixture models rely on repeated counts, which was appropriate in our instances because we had counts of greater gliders (i.e. the total number of individual greater gliders observed by the two observers) from two repeat surveys (Keever *et al.* 2017). We compared N-mixture models fit with Poisson, negative binomial, and zero inflated Poisson distributions using Akaike's Information Criterion (AIC).

Table 1. Description of habitat variables and justification for their inclusion.

Variable	Description	Justification
Average midstorey height (mid height)	Height of closest midstorey plant (m) measured with range finder every 10 m along transect (30 times over 300 m) and then averaged.	The midstorey layer creates a distinct second canopy between the overstorey canopy and shrub layers which can facilitate movement but also affect detectability (Incoll *et al.* 2001).
Basal area of midstorey species (basal mid)	Measured three times per transect (0 m, 150 m, 300 m) using the Bitterlich-stick method and then averaged.	Midstorey vegetation can aid in movement and impact detectability of arboreal mammals (Lindenmayer *et al.* 1991*b*).
Number of vegetation strata (strata)	Number of vegetation strata (1–4) i.e. overstorey, tree midstorey, understorey/shrub layer, ground layer), determined visually three times per transect (0 m, 150 m, 300 m) and averaged.	Old growth forests, which are favoured by greater gliders, tend to have a higher number of vegetation strata (Lindenmayer *et al.* 1990).
Canopy cover (canopy)	Determined visually (present or absent) directly above observer every 10 m along the 300 m transect. Calculated as a proportion of canopy cover for each transect.	Greater gliders forage and spend most of their time within the canopy (Cunningham *et al.* 2004; Berry *et al.* 2015).
Average tree height (tree height)	Height of closest overstorey tree (m) measured with a range finder every 10 m along the transect (30 times over 300 m) and then averaged. Tree height was measured for both burned and unburned trees from the highest point, regardless of whether or not the canopy was intact.	Greater gliders are typically found in old growth eucalypt forests with tall trees for launching (Vinson *et al.* 2021).
Large potentially hollow-bearing trees (large trees)	The number of potentially hollow-bearing (>80 cm trunk diameter (Lindenmayer *et al.* 2021*b*)) trees were counted along a 40 × 300 m belt transect (20 m either side of the transect line). Trunk diameter was determined using a tape measure.	Tree size was used as proxy for hollow potential. Greater gliders are dependent on tree hollows for protection from predators and shelter (Lindenmayer *et al.* 2021*b*, 2022; May-Stubbles *et al.* 2022).
Elevation	Determined using a layer on GIS.	Greater gliders attain higher abundance at elevations >500 m (Smith and Smith 2018). Elevation corresponds to changes in temperature, rainfall, soil types, and vegetation composition.

We fit an N-mixture model with habitat variables (Table 1) as predictors of greater glider detection and abundance. We expected that rain (mm within 24 h of the survey) and minimum temperature (within 24 h of the survey) could impact greater glider behaviour. In addition, we expected that basal midstorey, midstorey height, and tree height could influence greater glider detection due to their impact on the level of visual obstruction and distance between the surveyor and greater gliders in the canopy. We also expected that canopy cover, tree height, the number of potentially hollow-bearing trees, midstorey height, midstorey basal area, and elevation would influence greater glider abundance.

We developed a model that included all predictor variables using the dredge function in R package '*MuMIn*' to fit all combinations of predictors and compared support for each model using Akaike's Information Criterion (AIC). The Akaike weight (wi) for each model was calculated, and if no model had a weight of <0.9, model averaging was undertaken using the 95% confidence set (Burnham and Anderson 1998). We considered a variable as important to greater glider detectability or abundance when the 85% confidence interval of the coefficient did not include zero (Arnold 2010). All statistical analyses were performed within R ver. 4.3.2 using the unmarked package for N-mixture models (Fiske and Chandler 2011), MuMIn for model selection (Barton and Barton 2015) and ggplot2 for plotting the models (Wickham 2016).

How does fire severity affect greater glider abundance?

To test how fire severity affects greater glider abundance, the same procedure as above was followed although the predictors were changed. The predicter variables included fire severity (unburned, refuge, low-moderate and high) as well as tree height, elevation, and vegetation type (wet or dry sclerophyll). These latter variables acted as covariates to account for pre-existing differences among sites, and were able to be included alongside the fire severity treatment because they were not colinear with fire severity.

Results

In total, 101 greater glider observations were made at 17 out of 32 (53%) sites over the two survey rounds. Overall, 39 greater gliders were recorded during the first survey round and 62 were recorded during the second survey round (Supplementary material 2). The double observer method proved effective in identifying individuals that single observers missed. In the first round of surveys, this approach resulted in the detection of an additional 7–14 individuals (depending on the individual observer). In the second round, it helped identify between 13 and 15 more individuals. The average number of greater gliders observed during an individual survey was 21.8–55.9% and 26.52–31.95% higher (due to the double observer method) for survey rounds one and two, respectively (Supplementary material 2). More greater gliders were recorded in the second than in the first round, perhaps due to the timing of the second round coinciding with the emergence of independent young. During both surveys, greater gliders were recorded at all unburned sites (8/8), half of the refuge sites (4/8) and low-moderate sites (4/8), and one high severity site (1/8).

How did the 2019–2020 wildfires affect habitat structure?

Several habitat variables differed across the fire severity classes. Compared to unburned sites, burned sites had fewer vegetation strata and large trees, less canopy cover, and a shorter, denser midstorey (Table 2). Often, differences were most pronounced (i.e. larger effect sizes) when comparing unburned and high severity sites (Table 2). Unburned sites and refuges did not differ in the number of large trees, canopy cover, tree height, mid height or midstorey basal area. However, refuge sites tended to have fewer strata than unburned sites (Table 2). There was no significant difference in elevation between unburned sites and any other treatment (Table 2), probably due to the relatively narrow elevation range (~300 m) that the study sites encompassed.

How does habitat structure affect greater glider detectability and abundance?

The Poisson model had the lowest AIC value and was therefore used throughout. No model was identified clearly as best during model selection (i.e. $w_i < 0.9$), so model averaging was undertaken. Greater gliders were less detectable at sites with a denser midstorey and were more abundant at sites with greater canopy cover, more large trees, taller midstorey, and with taller trees (Fig. 2). Greater gliders were also more abundant at sites at higher elevation (Table 3).

How does fire severity affect greater glider abundance?

No model was identified clearly as best (i.e. $w_i < 0.9$). Model averaging showed minimum temperature and rainfall within 24 h of the survey had a positive effect on greater glider detectability (Table 4). Unburned sites had a higher abundance of greater gliders than refuge sites, low-moderate, and high fire severity sites (Table 4). Greater gliders were most abundant on unburned sites, with a predicted abundance of 11.24 individuals per site (Fig. 3). Abundance was lower in all other treatments, including refuge sites, ranging between 0.31 and 0.96 gliders (Fig. 3), although the effect size was greatest in high severity sites (indicative of greater reductions in abundance) (Table 4). Tree height and elevation had a positive association with greater glider abundance and greater glider abundance was similar between dry and wet sclerophyll forest types (Table 4).

Table 2. Results from GLMs and LMs examining the association between fire severity and vegetation structure and elevation.

Variable	Predictors		CI
Mid height		*Estimates*	
	(Intercept)	8.18	7.29–9.06
	Refuge	−1.07	−2.33 – 0.18
	Low-moderate severity	**−1.45**	**−2.70 – −0.19**
	High severity	−1.09	−2.35 – 0.17
	R^2	0.169	
Basal mid		*Estimates*	
	(Intercept)	4.12	2.47–5.78
	Refuge	1.83	−0.51 – 4.17
	Low-moderate severity	0.92	−1.42 – 3.26
	High severity	**2.83**	**0.49–5.17**
	R^2	0.182	
Strata		*Estimates*	
	(Intercept)	3.63	3.44–3.81
	Refuge	**−0.38**	**−0.64 – −0.11**
	Low-moderate severity	**−0.58**	**−0.85 – −0.32**
	High severity	**−1.54**	**−1.81 – −1.27**
	R^2	0.833	
Large trees		*Incidence rate ratios*	
	(Intercept)	52.63	41.23–65.94
	Refuge	0.7	0.48–1.00
	Low-moderate severity	**0.51**	**0.34–0.76**
	High severity	**0.31**	**0.19–0.50**
	R^2	0.995	
Canopy cover		*Odds ratios*	
	(Intercept)	3.8	2.81–5.24
	Refuge	0.69	0.45–1.06
	Low-moderate severity	**0.25**	**0.17–0.38**
	High severity	**0**	**0.00–0.01**
Tree height		*Estimates*	
	(Intercept)	18.97	16.99–20.95
	Refuge	1.98	−0.82 – 4.77
	Low-moderate severity	0.63	−2.17 – 3.42
	High severity	−0.14	−2.94 – 2.65
	R^2	0.09	
Elevation		*Estimates*	
	(Intercept)	686.21	631.92–740.50
	Refuge	−68.47	−145.25 – 8.31
	Low-moderate severity	−46.93	−123.71 – 29.85
	High severity	−52.13	−128.91 – 24.65
	R^2	0.108	

Bold = 95% confidence intervals do not overlap zero or one.

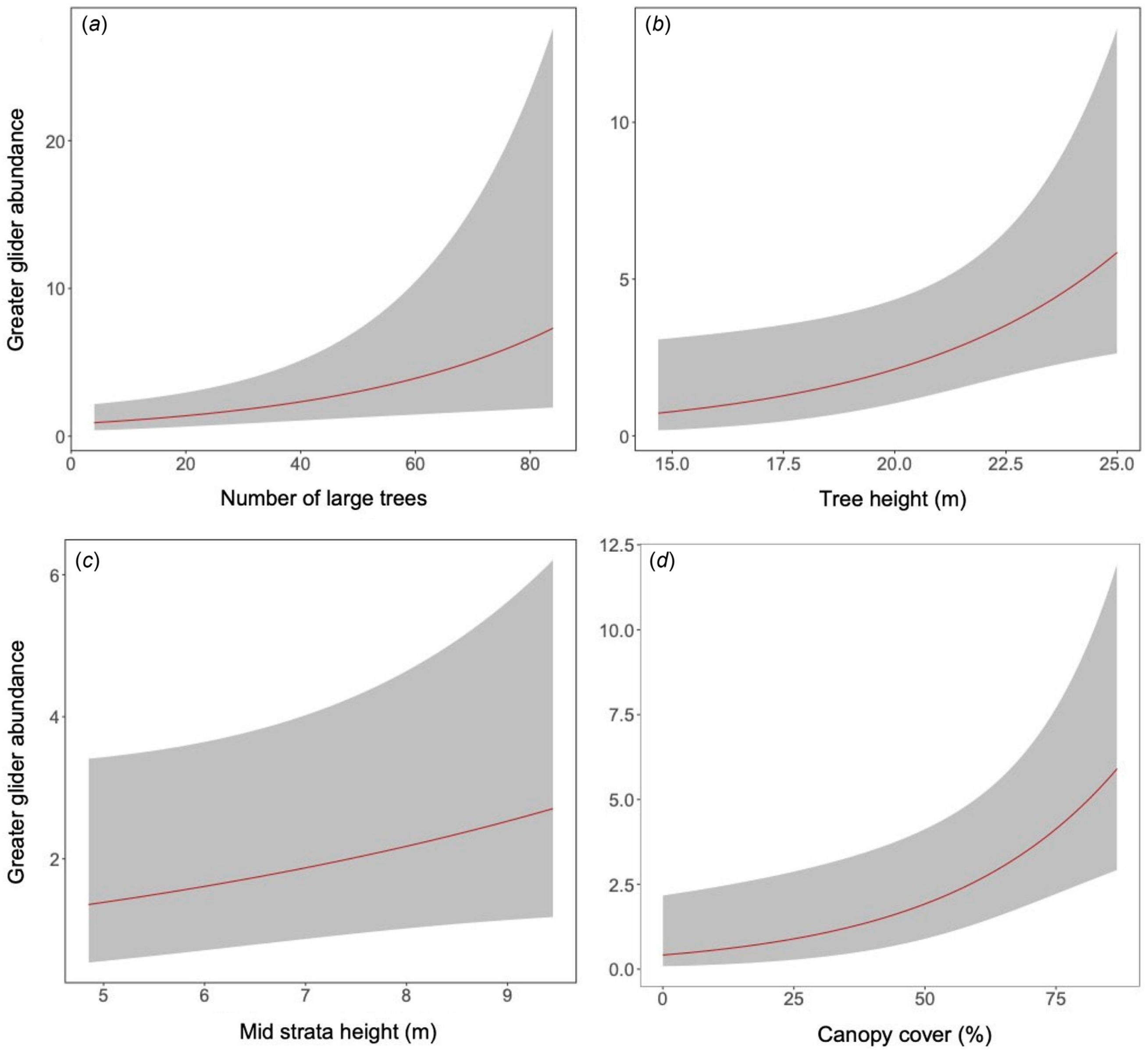

Fig. 2. Effect of (*a*) number of large potentially hollow-bearing trees, (*b*) average tree height, (*c*) average midstorey height and (*d*) proportion of canopy cover on greater glider abundance (λ).

Discussion

How did the 2019–2020 wildfires affect habitat structure?

The 2019–2020 bushfires significantly affected various vegetation attributes in Woomargama NP, the most noticeable being the impact on overstorey vegetation. Large trees and canopy cover saw considerable reductions, and the number of vegetation layers decreased. These changes were most pronounced at sites that experienced high severity fires. Changes in the midstory were less pronounced, but generally indicated a higher density of shorter plants, most likely rapid regrowth of shrubs and eucalypts stimulated by the fires. Of the five key factors influencing greater glider abundance, three (large trees, canopy cover, and midstorey height) were negatively impacted by the bushfires.

Several studies have documented that fire severity exerts detrimental effects on tree hollow abundance in eucalypt forests (Collins *et al*. 2012; Lindenmayer *et al*. 2012; May-Stubbles *et al*. 2022). High severity fire can damage tree hollows or consume hollow-bearing trees entirely (Collins *et al*. 2012), and may also trigger the collapse of hollow-bearing trees (Gibbons *et al*. 2008). During vegetation surveys in Woomargama, large fallen trees were often seen in areas that were subjected to high severity fire. Formation of hollows in eucalypts can take over 150 years (Banks *et al*. 2011); hence,

Table 3. The effect of habitat structure on greater glider detectability (*P*) and abundance (λ) derived from model averaging of N-mixture models.

	Estimate	s.e.	*Z* value	Pr(>|z|)	CI
P(Int)	−0.882428	0.400946	2.201	0.0277	−1.47 – −0.28
P(rainfall)	0.420568	0.565119	0.744	0.4567	−0.43 – 1.32
***P*(basal mid)**	**−0.471602**	**0.304145**	**1.551**	**0.1210**	**−0.92 – −0.02**
P(tree height)	0.130546	0.373024	0.35	0.7263	−0.36 – 0.68
P(min temp)	0.088155	0.209666	0.42	0.6741	−0.22 – 0.39
λ(Int)	**0.713474**	**0.35922**	**1.986**	**0.0470**	**0.23–1.25**
λ(canopy prop)	**0.863911**	**0.36604**	**2.36**	**0.0183**	**0.32–1.30**
λ(large trees)	**0.656422**	**0.181488**	**3.617**	**0.0003**	**0.50–0.92**
λ(mid height)	**0.25284**	**0.125177**	**2.02**	**0.0434**	**0.06–0.41**
λ(tree height)	**0.386298**	**0.203274**	**1.9**	**0.0574**	**0.08–0.61**
λ(elevation)	**0.300241**	**0.20839**	**1.441**	**0.1497**	**0.00–0.60**
λ(basal mid)	0.005698	0.331419	0.017	0.9863	−0.33 – 0.54

Bold = 85% confidence intervals did not overlap zero.

Table 4. The effect of detection covariates, fire severity treatments, tree height, elevation, and vegetation type on greater glider detectability (*P*) and abundance (λ) derived from model averaging of N-mixture models.

	Estimate	s.e.	*Z* value	Pr(>|z|)	CI
P(Int)	−1.997815	2.027463	0.985	0.3244	−4.92 – 0.92
***P*(min temp)**	**0.19147**	**0.091925**	**2.083**	**0.0373**	**5.91–0.32**
P(basal midstorey)	0.045202	0.107784	0.419	0.6749	−0.1 – 0.20
***P*(rainfall)**	**0.011596**	**0.008042**	**1.442**	**0.1494**	**0.00–0.023**
P(tree height)	0.059877	0.160479	0.373	0.7091	−0.17 – 0.29
λ(Int)	**2.450027**	**0.260043**	**9.422**	**<2e-16**	**2.08–2.82**
λ(refuge)	**−2.364303**	**0.403566**	**5.859**	**<2e-16**	**−2.95 – −1.78**
λ(low-moderate severity)	**−2.484345**	**0.44557**	**5.576**	**<2e-16**	**−3.13 – −1.84**
λ(high severity)	**−3.601912**	**0.747643**	**4.818**	**1.50e-06**	**−4.68 – −2.53**
λ(tree height)	**0.644317**	**0.157756**	**4.084**	**4.42e-05**	**0.41–0.87**
λ(elevation)	**0.245798**	**0.170705**	**1.44**	**0.1499**	**0.00–0.49**
λ(wet sclerophyll)	0.558264	0.475695	1.174	0.2406	−0.12 – 1.24

Bold = 85% confidence intervals did not overlap zero.

the impact of the 2019–2020 fires on greater gliders and other hollow-dependent fauna are likely to perist for decades. Canopy vegetation is typically consumed in high severity fires (Smucker *et al.* 2005), and recurrent severe fires can culminate in the loss of canopy cover, and extensive charring can impede recovery (Haslem *et al.* 2016).

How does fire severity affect greater gliders?

We found a positive association between greater glider abundance and several habitat factors that are typical of unburned habitat, including the number of large trees, high canopy cover, a taller midstorey, and a more complete canopy. The 2019–2020 bushfires negatively impacted many of these habitat features. Consequently, we observed a marked decrease in the greater glider abundance in all burned areas, with the greatest decline in areas that experienced high severity fires. Similar results have been observed in other studies investigating the impacts of fire on greater glider populations (Berry *et al.* 2015; McLean *et al.* 2018; Campbell-Jones *et al.* 2022), including a recent study that found greater glider occurrence decreased with increasing fire severity in the Southern Tablelands of New South Wales (May-Stubbles *et al.* 2022).

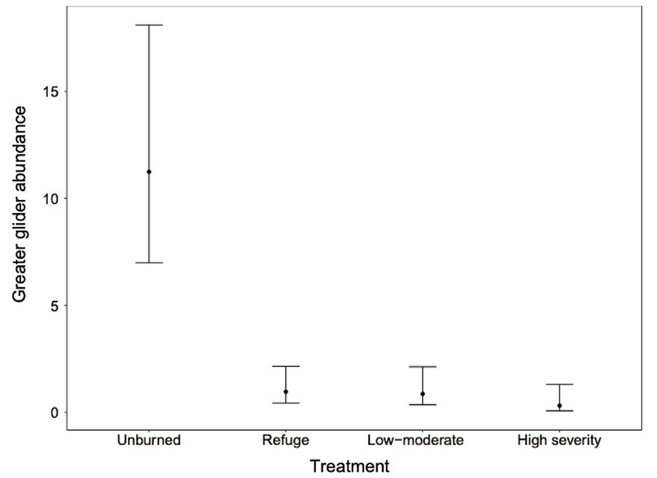

Fig. 3. Predictions from N-mixture models of the effect of different fire severity treatments on greater glider abundance in Woomargama NP, New South Wales.

Fire negatively affects animals through direct mortality (Bradstock *et al.* 2005; Jolly *et al.* 2022), and indirect mortality by altering habitat, reducing availability of resources, and causing increased rates of predation in the post-fire landscape (Whelan *et al.* 2002; Engstrom 2010; Jolly *et al.* 2022). A systematic review that explored the fate of individual animals before and after fire found that animal mortality during fire is often lower than assumed (1–9%), but that mortality is higher during high severity fires (Jolly *et al.* 2022). Recent modelling by Zylstra (2023) estimated that the critically endangered arboreal mammal, ngwayir (western ringtail possum, *Pseudocheirus occidentalis*), suffered 77% mortality during a prescribed burn in a woodland in Western Australia. By contrast, a study that directly tracked the fate of mountain brushtail possums (*Trichosurus cunninghami*) through Victoria's Black Saturday fires found no direct mortality (Banks *et al.* 2011). It has previously been found that greater gliders can often initially survive severe disturbances when their home range has only partially been destroyed, by either remaining in hollows or fleeing. Tyndale-Biscoe and Smith (1969) marked greater gliders at the point of felling during logging, with over 70% of individuals being re-captured within 1 week of logging. This number dropped below 7% of the original capture rate just 1 year after felling (Tyndale-Biscoe and Smith 1969). It is estimated that the intensity of disturbance and spatial distribution of critical habitat and feeding resources drives these population dynamics over time (Wagner *et al.* 2021). Untangling the relative contributions of direct mortality and fire-induced habitat changes that lead to reductions in greater glider abundance warrants further research.

Fire refuges are areas within the fire zone which could allow animals to persist while burned areas recover (Robinson *et al.* 2013; Wintle *et al.* 2020; Mackey *et al.* 2021). Results from studies on the effectiveness of refugia for population recovery often vary, particularly due to differences in species' mechanisms for survival, connectivity, dispersal and persistence during and after fire (Meddens *et al.* 2018). Previous research has shown that small mammals (Griffiths and Brook 2014), birds (Robinson *et al.* 2014) and some reptile species (Doherty *et al.* 2015) are able to persist after fire by moving into unburned patches. Our study found that greater glider abundance in fire refuges was significantly lower than in areas of continuously unburned forest outside of the fire zone. A study from the Victorian mountain ash forests found similar results for greater gliders as well as Leadbeater's possum (*Gymnobelideus leadbeateri*) and inland sugar glider (*Petaurus notatus*; previously sugar glider (*Petaurus breviceps*)) (Lindenmayer *et al.* 2013). While pre-existing differences between unburned and refuge sites may have plausibly contributed to the observed differences, this is unlikely in our view. Refuge sites were similar to unburned sites in most aspects, including those identified as drivers of greater glider abundance (large trees, canopy cover, mid height, tree height, and elevation). Our refuge sites were mostly unburned strips surrounded by high proportions of burned areas on either side. While our study was not designed to examine the influence of refuge patch size, this may be an important consideration for future studies. With an average distance of ~100 m from refuge transects to the nearest burned edge, it is possible, even likely, that the refuges that we surveyed are too small or narrow to conserve populations of greater gliders after severe fire. The current findings suggest that small unburned refuges within the fire footprint seem to play a minimal role in the conservation of greater gliders in Woomargama NP, and that large expanses of unburned vegetation are vital for their long-term persistence.

While our study offers insight into the effects of severe fire on greater gliders, it is not without limitations. First, our study is a control-impact study, rather than a before-after-control-impact study, and hence our inference assumes that sites were similar prior to the fires. It is possible that differences existed prior to the fires, and that we are interpreting these differences as being driven by fire when they are pre-existing. This underscores the importance of long-term monitoring of threatened species so that before data is available when large disturbances like the 2019–2020 wildfires occur. However, given the consistency between our findings and previous studies of greater glider responses to wildfire, we believe the patterns observed are largely attributable to fire. Second, our study analysed greater glider abundance in relation to broad environmental drivers. Further variation in greater glider abundance would probably be explained by variables that we did not measure, such as the distribution of preferred eucalypt species within transects (Youngentob *et al.* 2011).

Conclusion

Our study confirms that fire, and particularly high severity fire, transforms vegetation structure and diminishes habitat quality for the greater glider. This likely leads to a reduction in greater glider abundance in burned sites. The conservation of greater gliders in tall eucalypt forests will depend on protecting large expanses of old growth vegetation from severe fire events (Lindenmayer *et al.* 2013; Andrus *et al.* 2021; Australian Government 2022*a*).

Supplementary material

Supplementary material is available online.

References

Abram NJ, Henley BJ, Sen Gupta A, Lippmann TJR, Clarke H, Dowdy AJ, Sharples JJ, Nolan RH, Zhang T, Wooster MJ, Wurtzel JB, Meissner KJ, Pitman AJ, Ukkola AM, Murphy BP, Tapper NJ, Boer MM (2021) Connections of climate change and variability to large and extreme forest fires in southeast Australia. *Communications Earth & Environment* **2**, 8. doi:10.1038/s43247-020-00065-8

ALA (2022) Atlas of living Australia greater glider occurrence records. ALA.

Andrus RA, Martinez AJ, Jones GM, Meddens AJH (2021) Assessing the quality of fire refugia for wildlife habitat. *Forest Ecology and Management* **482**, 118868. doi:10.1016/j.foreco.2020.118868

Arnold TW (2010) Uninformative parameters and model selection using akaike's information criterion. *The Journal of Wildlife Management* **74**, 1175–1178. doi:10.1111/j.1937-2817.2010.tb01236.x

Ashman KR, Watchorn DJ, Lindenmayer DB, Taylor MFJ (2021) Is Australia's environmental legislation protecting threatened species? A case study of the national listing of the greater glider. *Pacific Conservation Biology* **28**, 277–289. doi:10.1071/PC20077

Australian Government (2020) Australian Google earth engine burnt area map. Department of Agriculture, Water and the Environment.

Australian Government (2022*a*) Conservation advice for *Petauroides volans* (greater glider (southern and central). Department of Climate Change, Energy, the Environment and Water.

Australian Government (2022*b*) Species profile and threats database. Department of Climate Change, Energy, the Environment and Water.

Banks SC, Knight EJ, McBurney L, Blair D, Lindenmayer DB (2011) The effects of wildfire on mortality and resources for an arboreal marsupial: resilience to fire events but susceptibility to fire regime change. *PLoS ONE* **6**, e22952. doi:10.1371/journal.pone.0022952

Barton K, Barton MK (2015) Package 'mumin'. Version 1(18), p. 439.

Bassett M, Leonard SWJ, Chia EK, Clarke MF, Bennett AF (2017) Interacting effects of fire severity, time since fire and topography on vegetation structure after wildfire. *Forest Ecology and Management* **396**, 26–34. doi:10.1016/j.foreco.2017.04.006

Benson J (2008) New South Wales vegetation classification and assessment: Part 2 plant communities of the NSW south-western slopes bioregion and update of NSW western plains plant communities, version 2 of the NSWVCA database. *Cunninghamia* **10**, 599–673.

Berry LE, Driscoll DA, Banks SC, Lindenmayer DB (2015) The use of topographic fire refuges by the greater glider (*Petauroides volans*) and the mountain brushtail possum (*Trichosurus cunninghami*) following a landscape-scale fire. *Australian Mammalogy* **37**, 39–45. doi:10.1071/AM14027

Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Marston JB, Moritz MA, Prentice IC, Roos CI, Scott AC, Swetnam TW, van der Werf GR, Pyne SJ (2009) Fire in the earth system. *Science* **324**, 481–484. doi:10.1126/science.1163886

Bowman DMJS, Kolden CA, Abatzoglou JT, Johnston FH, van der Werf GR, Flannigan M (2020) Vegetation fires in the anthropocene. *Nature Reviews Earth & Environment* **1**, 500–515. doi:10.1038/s43017-020-0085-3

Bradstock RA, Bedward M, Gill AM, Cohn JS (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* **32**, 409–423. doi:10.1071/WR02114

Burnham KP, Anderson DR (1998) Practical use of the information-theoretic approach. In 'Model selection and inference'. (Eds KP Burnham, DR Anderson) pp. 75–117. (Springer)

Campbell-Jones MM, Bassett M, Bennett AF, Chia EK, Leonard S, Collins L (2022) Fire severity has lasting effects on the distribution of arboreal mammals in a resprouting forest. *Austral Ecology* **47**, 1456–1469. doi:10.1111/aec.13231

Chia EK, Bassett M, Nimmo DG, Leonard SWJ, Ritchie EG, Clarke MF, Bennett AF (2015) Fire severity and fire-induced landscape heterogeneity affect arboreal mammals in fire-prone forests. *Ecosphere* **6**, 1–14. doi:10.1890/ES15-00327.1

Collins L, Bradstock RA, Tasker EM, Whelan RJ (2012) Impact of fire regimes, logging and topography on hollows in fallen logs in eucalypt forest of south eastern Australia. *Biological Conservation* **149**, 23–31. doi:10.1016/j.biocon.2012.01.065

Collins L, Hunter A, McColl-Gausden S, Penman TD, Zylstra P (2021) The effect of antecedent fire severity on reburn severity and fuel structure in a resprouting eucalypt forest in Victoria, Australia. *Forests* **12**, 450. doi:10.3390/f12040450

Cripps JK, Nelson JL, Scroggie MP, Durkin LK, Ramsey DSL, Lumsden LF (2021) Double-observer distance sampling improves the accuracy of density estimates for a threatened arboreal mammal. *Wildlife Research* **48**, 756–768. doi:10.1071/WR19136

Cunningham RB, Pope ML, Lindenmayer DB (2004) Patch use by the greater glider (*Petauroides volans*) in a fragmented forest ecosystem. III. Night-time use of trees. *Wildlife Research* **31**, 579–585. doi:10.1071/WR02112

Doherty TS, Davis RA, van Etten EJB, Collier N, Krawiec J (2015) Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire. *International Journal of Wildland Fire* **24**, 534–543. doi:10.1071/WF14115

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46. doi:10.1111/j.1600-0587.2012.07348.x

Duane A, Castellnou M, Brotons L (2021) Towards a comprehensive look at global drivers of novel extreme wildfire events. *Climatic Change* **165**, 43. doi:10.1007/s10584-021-03066-4

Elders Weather (2022) 'Woomargama climate history.' (Elders Weather)

Engstrom RT (2010) First-order fire effects on animals: review and recommendations. *Fire Ecology* **6**, 115–130. doi:10.4996/fireecology.0601115

Fiske I, Chandler R (2011) Unmarked: an r package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* **43**, 1–23. doi:10.18637/jss.v043.i10

Gibbons P, Lindenmayer DB, Barry SC, Tanton MT (2002) Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biological Conservation* **103**, 1–12. doi:10.1016/S0006-3207(01)00109-4

Gibbons P, Cunningham RB, Lindenmayer DB (2008) What factors influence the collapse of trees retained on logged sites?: a case-control study. *Forest Ecology and Management* **255**, 62–67. doi:10.1016/j.foreco.2007.08.020

Griffiths AD, Brook BW (2014) Effect of fire on small mammals: a systematic review. *International Journal of Wildland Fire* **23**, 1034–1043. doi:10.1071/WF14026

Haslem A, Kelly LT, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Avitabile SC, Callister KE, Spence-Bailey LM, Clarke MF, Bennett AF (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* **48**, 247–256. doi:10.1111/j.1365-2664.2010.01906.x

Haslem A, Leonard SWJ, Bruce MJ, Christie F, Holland GJ, Kelly LT, MacHunter J, Bennett AF, Clarke MF, York A (2016) Do multiple fires interact to affect vegetation structure in temperate eucalypt forests? *Ecological Applications* **26**, 2414–2423. doi:10.1002/eap.1399

Incoll RD, Loyn RH, Ward SJ, Cunningham RB, Donnelly CF (2001) The occurrence of gliding possums in old-growth forest patches of mountain ash (*Eucalyptus regnans*) in the Central Highlands of Victoria. *Biological Conservation* **98**, 77–88. doi:10.1016/S0006-3207(00)00144-0

Jain P, Castellanos-Acuna D, Coogan SCP, Abatzoglou JT, Flannigan MD (2022) Observed increases in extreme fire weather driven by atmospheric humidity and temperature. *Nature Climate Change* **12**, 63–70. doi:10.1038/s41558-021-01224-1

Jolly CJ, Dickman CR, Doherty TS, van Eeden LM, Geary WL, Legge SM, Woinarski JCZ, Nimmo DG (2022) Animal mortality during fire. *Global Change Biology* **28**, 2053–2065. doi:10.1111/gcb.16044

Kablick GP III, Allen DR, Fromm MD, Nedoluha GE (2020) Australian pyrocb smoke generates synoptic-scale stratospheric anticyclones. *Geophysical Research Letters* **47**, e2020GL088101. doi:10.1029/2020GL088101

Kavanagh RP, Lambert MJ (1990) Food selection by the greater glider, petauroides-volans – is foliar nitrogen a determinant of habitat quality. *Wildlife Research* **17**, 285–299. doi:10.1071/WR9900285

Kavanagh R, Stanton M (1998) Nocturnal forest birds and arboreal marsupials of the southwestern slopes, New South Wales. *Australian Zoologist* **30**, 449–466. doi:10.7882/AZ.1998.012

Keeley JE (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* **18**, 116–126. doi:10.1071/WF07049

Keever AC, McGowan CP, Ditchkoff SS, Acker PK, Grand JB, Newbolt CH (2017) Efficacy of N-mixture models for surveying and monitoring white-tailed deer populations. *Mammal Research* **62**, 413–422. doi:10.1007/s13364-017-0319-z

Keith DA, Simpson CC (2018) Vegetation formations and classes of NSW (version 3.03–200 m Raster). NSW Department of Climate Change, Energy, the Environment and Water.

Kidwai Z, Jimenez J, Louw CJ, Nel HP, Marshal JP (2019) Using n-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis* L.) populations from aerial counts. *Global Ecology and Conservation* **19**, e00687. doi:10.1016/j.gecco.2019.e00687

Knipler ML, Gracanin A, Mikac KM (2023) Conservation genomics of an endangered arboreal mammal following the 2019–2020 Australian megafire. *Scientific Reports* **13**(1), 480. doi:10.1038/s41598-023-27587-3

Kéry M (2002) Inferring the absence of a species: a case study of snakes. *The Journal of Wildlife Management* **66**, 330–338. doi:10.2307/3803165

Laurance WF (1990) Effects of weather on marsupial folivore activity in a north Queensland upland tropical rainforest. *Australian Mammalogy* **13**, 41–47. doi:10.1071/AM90006

Legge S, Rumpff L, Woinarski JCZ, Whiterod NS, Ward M, Southwell DG, Scheele BC, Nimmo DG, Lintermans M, Geyle HM, Garnett ST, Hayward-Brown B, Ensbey M, Ehmke G, Ahyong ST, Blackmore CJ, Bower DS, Brizuela-Torres D, Burbidge AH, Burns PA, Butler G, Catullo R, Chapple DG, Dickman CR, Doyle KE, Ferris J, Fisher D, Gallagher R, Gillespie GR, Greenlees MJ, Hohnen R, Hoskin CJ, Hunter D, Jolly C, Kennard M, King A, Kuchinke D, Law B, Lawler I, Lawler S, Loyn R, Lunney D, Lyon J, MacHunter J, Mahony M, Mahony S, McCormack RB, Melville J, Menkhorst P, Michael D, Mitchell N, Mulder E, Newell D, Pearce L, Raadik TA, Rowley JJL, Sitters H, Spencer R, Valavi R, West M, Wilkinson DP, Zukowski S (2022) The conservation impacts of ecological disturbance: time-bound estimates of population loss and recovery for fauna affected by the 2019–2020 Australian Megafires. *Global Ecology and Biogeography* **31**, 2085–2104. doi:10.1111/geb.13473

Lindenmayer DB, Cunningham RB, Tanton MT, Smith AP, Nix HA (1990) The conservation of arboreal marsupials in the Montane ash forests of the central highlands of Victoria, Southeast Australia: I. Factors influencing the occupancy of trees with hollows. *Biological Conservation* **54**, 111–131. doi:10.1016/0006-3207(90)90137-E

Lindenmayer DB, Cunningham RB, Tanton MT, Nix HA (1991*a*) Aspects of the use of den trees by arboreal and scansorial marsupials inhabiting Montane ash forests in Victoria. *Australian Journal of Zoology* **39**, 57–65. doi:10.1071/ZO9910057

Lindenmayer DB, Cunningham RB, Tanton MT, Nix HA, Smith AP (1991*b*) The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, South-east Australia: III. The habitat requirements of leadbeater's possum *Gymnobelideus leadbeateri* and models of the diversity and abundance of arboreal marsupials. *Biological Conservation* **56**, 295–315. doi:10.1016/0006-3207(91)90063-F

Lindenmayer DB, Pope ML, Cunningham RB (2004) Patch use by the greater glider (*Petauroides volans*) in a fragmented forest ecosystem. II. Characteristics of den trees and preliminary data on den-use patterns. *Wildlife Research* **31**, 569–577. doi:10.1071/WR02111

Lindenmayer DB, Blanchard W, McBurney L, Blair D, Banks S, Likens GE, Franklin JF, Laurance WF, Stein JA, Gibbons P (2012) Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. *PLoS ONE* **7**, e41864. doi:10.1371/journal.pone.0041864

Lindenmayer DB, Blanchard W, McBurney L, Blair D, Banks SC, Driscoll D, Smith AL, Gill AM (2013) Fire severity and landscape context effects on arboreal marsupials. *Biological Conservation* **167**, 137–148. doi:10.1016/j.biocon.2013.07.028

Lindenmayer DB, Blanchard W, McBurney L, Blair D, Banks SC, Driscoll DA, Smith AL, Gill AM (2014) Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers. *Diversity and Distributions* **20**, 467–477. doi:10.1111/ddi.12172

Lindenmayer D, Taylor C, Blanchard W (2021*a*) Empirical analyses of the factors influencing fire severity in southeastern Australia. *Ecosphere* **12**, e03721. doi:10.1002/ecs2.3721

Lindenmayer DB, Blanchard W, Blair D, McBurney L, Taylor C, Scheele BC, Westgate MJ, Robinson N, Foster C (2021*b*) The response of arboreal marsupials to long-term changes in forest disturbance. *Animal Conservation* **24**, 246–258. doi:10.1111/acv.12634

Lindenmayer DB, McBurney L, Blanchard W, Marsh K, Bowd E, Watchorn D, Taylor C, Youngentob K (2022) Elevation, disturbance, and forest type drive the occurrence of a specialist arboreal folivore. *PLoS ONE* **17**, e0265963. doi:10.1371/journal.pone.0265963

Linley GD, Jolly CJ, Doherty TS, Geary WL, Armenteras D, Belcher CM, Bliege Bird R, Duane A, Fletcher M-S, Giorgis MA, Haslem A, Jones GM, Kelly LT, Lee CKF, Nolan RH, Parr CL, Pausas JG, Price JN, Regos A, Ritchie EG, Ruffault J, Williamson GJ, Wu Q, Nimmo DG (2022) What do you mean, 'megafire'? *Global Ecology and Biogeography* **31**, 1906–1922. doi:10.1111/geb.13499

Mackey B, Lindenmayer D, Norman P, Taylor C, Gould S (2021) Are fire refugia less predictable due to climate change? *Environmental Research Letters* **16**, 114028. doi:10.1088/1748-9326/ac2e88

May-Stubbles JC, Gracanin A, Mikac KM (2022) Increasing fire severity negatively affects greater glider density. *Wildlife Research* **49**, 709–718. doi:10.1071/WR21091

McGregor DC, Padovan A, Georges A, Krockenberger A, Yoon H-J, Youngentob KN (2020) Genetic evidence supports three previously described species of greater glider, *Petauroides volans*, *P. minor*, and *P. armillatus*. *Scientific Reports* **10**, 19284. doi:10.1038/s41598-020-76364-z

McLean CM, Kavanagh RP, Penman T, Bradstock R (2018) The threatened status of the hollow dependent arboreal marsupial, the Greater Glider (*Petauroides volans*), can be explained by impacts from wildfire and selective logging. *Forest Ecology and Management* **415-416**, 19–25. doi:10.1016/j.foreco.2018.01.048

Meddens AJ, Kolden CA, Lutz JA, Smith AM, Cansler CA, Abatzoglou JT, Meigs GW, Downing WM, Krawchuk MA (2018) Fire refugia: what are they, and why do they matter for global change? *BioScience* **68**, 944–954. doi:10.1093/biosci/biy103

NPWS (2004) Benambra National Park and tabletop nature reserve. NPWS.

NPWS (2009) Woomargama National Park and state conservation area plan of management. Department of Environment, Climate Change and Water.

Possingham HP, Lindenmayer DB, Norton TW, Davies I (1994) Metapopulation viability analysis of the greater glider *Petauroides volans* in a wood production area. *Biological Conservation* **70**, 227–236. doi:10.1016/0006-3207(94)90167-8

Roberts SL, van Wagtendonk JW, Miles AK, Kelt DA, Lutz JA (2008) Modeling the effects of fire severity and spatial complexity on small mammals in Yosemite National Park, California. *Fire Ecology* **4**, 83–104. doi:10.4996/fireecology.0402083

Robinson NM, Leonard SWJ, Ritchie EG, Bassett M, Chia EK, Buckingham S, Gibb H, Bennett AF, Clarke MF (2013) Review: Refuges for fauna in fire-prone landscapes: their ecological function and importance. *Journal of Applied Ecology* **50**, 1321–1329. doi:10.1111/1365-2664.12153

Robinson NM, Leonard SWJ, Bennett AF, Clarke MF (2014) Refuges for birds in fire-prone landscapes: the influence of fire severity and fire history on the distribution of forest birds. *Forest Ecology and Management* **318**, 110–121. doi:10.1016/j.foreco.2014.01.008

Rogers BM, Balch JK, Goetz SJ, Lehmann CER, Turetsky M (2020) Focus on changing fire regimes: interactions with climate, ecosystems, and society. *Environmental Research Letters* **15**, 030201. doi:10.1088/1748-9326/ab6d3a

Schmidt JH, Johnson DS, Lindberg MS, Adams LG (2015) Estimating demographic parameters using a combination of known-fate and open *N*-mixture models. *Ecology* **96**, 2583–2589. doi:10.1890/15-0385.1

Smith P, Smith J (2018) Decline of the greater glider (*Petauroides volans*) in the lower Blue Mountains, New South Wales. *Australian Journal of Zoology* **66**, 103–114. doi:10.1071/ZO18021

Smith P Smith J (2020) Future of the Greater Glider (*Petauroides volans*) in the Blue Mountains, New South Wales. *Proceedings of the Linnean Society of New South Wales* **142**, 55–66.

Smucker KM, Hutto RL, Steele BM (2005) Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* **15**(5), 1535–1549. doi:10.1890/04-1353

Tyndale-Biscoe CH, Smith RFC (1969) Studies on the Marsupial Glider, *Schoinobates volans* (Kerr): III. Response to habitat destruction. *The Journal of Animal Ecology* 651–659. doi:10.2307/3041

Van Dyck S, Strahan R (2008) 'The mammals of Australia.' 3rd edn. (Reed New Holland: Sydney)

Vinson SG, Johnson AP, Mikac KM (2021) Current estimates and vegetation preferences of an endangered population of the vulnerable greater glider at Seven Mile Beach National Park. *Austral Ecology* **46**, 303–314. doi:10.1111/aec.12979

Wagner B, Baker PJ, Stewart SB, Lumsden LF, Nelson JL, Cripps JK, Durkin LK, Scroggie MP, Nitschke CR (2020) Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits. *Ecosphere* **11**(10), e03262. doi:10.1002/ecs2.3262

Wagner B, Baker PJ, Nitschke CR (2021) The influence of spatial patterns in foraging habitat on the abundance and home range size of a vulnerable arboreal marsupial in southeast Australia. *Conservation Science and Practice* **3**(12), e566. doi:10.1111/csp2.566

Wayne AF, Cowling A, Rooney JF, Ward CG, Wheeler IB, Lindenmayer DB, Donnelly CF (2005) Factors affecting the detection of possums by spotlighting in Western Australia. *Wildlife Research* **32**, 689–700. doi:10.1071/WR04089

Whelan RJ, Rodgerson L, Dickman CR (2002) Developing a process-based understanding of population changes in fire-prone landscapes. In 'Flammable Australia: the fire regimes and biodiversity of a continent.' (Eds RA Bradstock, JE Williams, AM Gill) p. 94. (Cambridge University Press)

Wickham H (2016) 'Ggplot2: elegant graphics for data analysis.' (Springer-Verlag: New York) Available at https://ggplot2.tidyverse.org

Wintle BA, Kavanagh RP, McCarthy MA, Burgman MA (2005) Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *The Journal of Wildlife Management* **69**, 905–917.

Wintle BA, Legge S, Woinarski JCZ (2020) After the megafires: what next for Australian wildlife? *Trends in Ecology & Evolution* **35**, 753–757. doi:10.1016/j.tree.2020.06.009

Wu C, Venevsky S, Sitch S, Mercado LM, Huntingford C, Staver AC (2021) Historical and future global burned area with changing climate and human demography. *One Earth* **4**, 517–530. doi:10.1016/j.oneear.2021.03.002

Youngentob KN, Wallis IR, Lindenmayer DB, Wood JT, Pope ML, Foley WJ (2011) Foliage chemistry influences tree choice and landscape use of a gliding marsupial folivore. *Journal of Chemical Ecology* **37**, 71–84. doi:10.1007/s10886-010-9889-9

Zylstra P (2023) Quantifying the direct fire threat to a critically endangered arboreal marsupial using biophysical, mechanistic modelling. *Austral Ecology* **48**, 266–288. doi:10.1111/aec.13264

Data availability. Data will be made available upon reasonable request to authors.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. This project was supported by Murray Local Land Services, Holbrook Landcare and the Gulbali Institute at Charles Sturt University.

Acknowledgements. We acknowledge the Wiradjuri Traditional Owners of the land on which this study occurred. We thank Dave Pearce (NPWS) for access to Woomargama NP and are thankful to the reviewers for providing constructive feedback on the manuscript.

Author affiliations

[A]School of Agricultural, Environmental and Veterinary Sciences, Charles Sturt University, Albury, NSW, Australia.

[B]Gulbali Institute, Charles Sturt University, Albury, NSW, Australia.

[C]Institute of Biomedical and Environmental Health Research, School of Health and Life Sciences, University of the West of Scotland, South Lanarkshire, UK.