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Contrasting the influence of extent and severity of fire on the occupancy of two marsupial gliders in New South Wales

Natasha M. Robinson[A,*], Chad T. Beranek[B], Darren M. Southwell[B] and Jane L. DeGabriel[A]

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

***Correspondence to:**
Natasha M. Robinson
Conservation and Restoration Science Branch, NSW Department of Climate Change, Energy, the Environment and Water, Parramatta, NSW 2150, Australia
Email:
Natasha.Robinson@environment.nsw.gov.au

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ABSTRACT

Context. The 2019–2020 Australian wildfires were the largest and most severe fires recorded for south-eastern Australia. Two glider species, the southern greater glider *Petauroides volans* and the yellow-bellied glider *Petaurus australis*, were predicted to be severely affected due to widespread habitat loss and vulnerability to the scale and severity of the fires. However, despite similar ecological requirements, differences in species traits were expected to influence their response to fire. **Aim.** Our aim was to investigate the probability of occupancy of each species following the 2019–2020 wildfires in relation to fire severity and spatial extent, and other environmental covariates. We predicted different fire responses for each species, according to their individual species traits. **Methods.** We surveyed for gliders using spotlighting and call-playback, 3 years post-fire across 223 sites, covering the breadth of their ranges in New South Wales. We used occupancy-detection models of each species to compare model fit with four extents (site, 300 m, 500 m and 1000 m) across three severity classes (unburnt, low-moderate and high) while controlling for other factors that are correlated with glider occupancy (e.g. forest disturbance and mean temperatures). **Key results.** Our results reveal strong negative relationships between occupancy of both glider species and high-severity fire. This effect was most significant for the southern greater glider at the largest spatial scale (1000 m), whereas for the yellow-bellied glider the response was more significant at the site level. For both species, low-moderate severity fire at all spatial scales was less predictive than other covariates. **Conclusions.** Southern greater gliders, with their highly specialised diet, small home ranges and limited dispersal capacity, are particularly sensitive to high-severity fire that consumes essential canopy resources at large scales. Yellow-bellied gliders likely have greater resilience to landscape fire due to greater mobility and a broader, more generalised diet. **Implications.** Both glider species are sensitive to forest disturbance, including canopy consuming fire. Low-moderate fire is less disruptive, in line with expectations that both species are resilient to partial canopy scorch, where essential resources remain. Species traits can be used to predict species responses to disturbances beyond the natural disturbance regime.

Keywords: 2019–2020 Black Summer wildfires, arboreal marsupial, biological traits, ecological traits, fire response traits, fire severity, life history, *Petauroides volans*, *Petaurus australis*.

Introduction

Fire is a major driver of ecological communities (Bowman *et al.* 2009; He *et al.* 2019). How a species responds to fire is defined by their biological and ecological requirements, the type of fire or fire regime experienced (Pocknee *et al.* 2023) and, for fauna, their evolutionary exposure to fire as a threat and their behavioural response (Nimmo *et al.* 2021; Ensbey *et al.* 2023). In the absence of knowledge on species-specific fire responses, species trait information can help predict their responses to varying aspects of a fire regime (Gallagher *et al.* 2021; Ensbey *et al.* 2023; Pocknee *et al.* 2023). Species traits such as increased mobility, high fecundity and more generalised dietary and habitat requirements are predicted to result in greater survival and post-fire persistence; although responses are nuanced within species and fire types (Pocknee *et al.* 2023). Fires characterised by mixed severity enhance the survival and persistence of a broader range of species, with unburnt patches being particularly important for facilitating the persistence of fire-sensitive fauna (Robinson *et al.* 2013; Chia *et al.* 2015).

Within fire-prone landscapes, species assemblages generally reflect the fire regime experienced, with individual species having evolved adaptations to persist (He *et al.* 2019). However, an extreme fire event outside the bounds of this fire regime (e.g. in terms of severity, extent, frequency and season) can have negative consequences, with certain species having reduced capacity to survive and persist long term (Nimmo *et al.* 2021; Pocknee *et al.* 2023). Severe fire has greater impact on fauna through increased mortality, habitat loss and displacement (Ensbey *et al.* 2023), while large severely burnt areas exacerbate this by reducing the number of refuges (Robinson *et al.* 2013) and limiting recolonisation (Ensbey *et al.* 2023).

The 2019–2020 Australian wildfires were an extreme event, and significantly affected ecological communities across southern and eastern Australia (Ward *et al.* 2020; Legge *et al.* 2022*a*). Approximately 7 M ha of land was affected (Collins *et al.* 2021), with more than 20% of Australian eucalypt forest burnt (Boer *et al.* 2020; Bowman *et al.* 2020). In the south-east fire-prone region of Australia, the fires were the largest ever reported (Bowman *et al.* 2020; Ward *et al.* 2020; Collins *et al.* 2021), and the largest area of high-severity fire (~1.8 M ha) recorded in more than three decades (Collins *et al.* 2021). In New South Wales (NSW) alone, ~5.8 M ha burnt, the largest area burnt in a fire season during the last 20 years (Filkov *et al.* 2020). The extent and severity of these fires were particularly devastating for animals who could not escape the immediate impact or survive in the aftermath, with an estimated three billion native vertebrates killed, injured or displaced by the 2019–2020 fires (Van Eeden *et al.* 2020; Van Eeden and Dickman 2023).

Threatened arboreal marsupials, in particular the southern greater glider *Petauroides volans* (hereafter greater glider) and the yellow-bellied glider *Petaurus australis*, were identified as species substantially impacted by the 2019–2020 fires (Legge *et al.* 2022*a*, 2022*b*). This was due to large parts of their distributions being fire affected, with an estimated 28% of greater glider habitat, including the range of all three subsequently re-classified *Petauroides* species (McGregor *et al.* 2020), and 29% of yellow-bellied glider habitat burnt by the fires (Ward *et al.* 2020). Following the 2019–2020 fire season and in response to the predicted impact and new classification, the threat status of the greater glider was uplisted to Endangered under both the NSW Biodiversity Conservation Act 2016 and the Commonwealth Environment Protection and Biodiversity Conservation Act 1999. The predicted fire-induced declines of the two glider species have likely increased the trajectory of on-going declines associated with changing climatic conditions, habitat loss and fragmentation, and reductions in habitat quality, particularly the loss of large, hollow-bearing trees (Gibbons and Lindenmayer 2002; Goldingay 2012; McLean *et al.* 2018; Wagner *et al.* 2020).

The two glider species have similar distributions, habitat requirements and ecology but differ in other traits such as mobility and dietary specialisation, which may influence their responses to fire (Legge *et al.* 2022*b*). Both occupy mature eucalypt forest from Queensland through to Victoria from 0 to 1400 m elevation, but greater gliders show a greater preference for wet forests of high elevation (Kavanagh 2000; Smith and Smith 2018; Wagner *et al.* 2020; DAWE 2022). Both species require hollow-bearing trees for denning (Goldingay 2012). However, yellow-bellied gliders have a greater preference for dens found in mature, live, smooth barked eucalypt trees (Goldingay 2012). Greater gliders have small home ranges (typically 1–2 ha) with limited dispersal capacity (Tyndale-Biscoe and Smith 1969; Pope *et al.* 2004; McGregor *et al.* 2023) and have a highly specialised diet, feeding almost exclusively on eucalypt foliage, supplemented with buds and flowers (Kavanagh and Lambert 1990; Comport *et al.* 1996). In contrast, yellow-bellied gliders have large home ranges (20–85 ha) and are highly mobile (Goldingay and Kavanagh 1993; Goldingay and Possingham 1995). They have a broad diet and forage on foliage, insect exudate, arthropods and pollen (Goldingay and Kavanagh 1991). This dietary breadth and greater mobility may give the yellow-bellied glider greater resilience to fire compared to the greater glider as more food sources may be available post-fire, and their mobility enables them to access resources more easily.

Using species trait information, experts predicted increasing declines in both species with increasing severity. Severe fire (or fire with substantial canopy impact) was predicted to result in declines of ~85–91% in greater gliders and 82–85% in yellow-bellied gliders during the first weeks to months, with little long-term recovery (Legge *et al.* 2022*a*). This outlook reflected immediate fire-induced mortality coupled with ongoing population declines due to habitat loss. Mild fire (or fire with no to moderate impact to canopy) was predicted to cause smaller declines of 25–35% in greater gliders and 14–23% in yellow-bellied gliders in the first week to 10 years (Legge *et al.* 2022*a*). Populations in unburnt areas were expected to decline by 18% in greater gliders and 10% in yellow-bellied gliders for up to 10 years post fire, reflecting other threatening processes in the absence of fire (Legge *et al.* 2022*a*). These predictions provided important direction to post-fire recovery efforts. However, actual post-fire data are still rare and are often reported at a local scale (e.g. Bilney *et al.* 2022; May-Stubbles *et al.* 2022; Green *et al.* 2024) or using presence only data (e.g. Ridley *et al.* 2024).

The 2019–2020 wildfires provided an opportunity to compare the impact of fire severity at large scales for two similar but different species. We investigated the probability of occupancy of the greater glider and yellow-bellied glider within NSW in response to different fire severity classes (unburnt, low-moderate and high) and at varying spatial scales (site, 300 m, 500 m and 1000 m) to determine which scale is most appropriate for understanding impacts of fire on the distribution of each species.

We tested several hypotheses relating to each species' response to fire severity and scale. We predicted that occupancy would be reduced at severely burnt sites for both species. We reasoned this as both species rely on canopy resources and would be negatively affected by fire that consumes the canopy. Next, we predicted that the greater glider would have a stronger negative response to increasing extents of high-severity fire surrounding a site, than the yellow-bellied glider (Kavanagh and Lambert 1990; Pope *et al.* 2004; McGregor *et al.* 2023). In contrast, we predicted that the yellow-bellied glider would have the strongest response to local fire severity, where we anticipate they would select unburnt habitats and their response to larger spatial scales would be less clear (Goldingay and Kavanagh 1993; Goldingay and Possingham 1995). Finally, we predicted that low-moderate severity fire, regardless of spatial scale, would not be predictive of the occupancy of either species. Both glider species have evolved in fire-prone forest systems, characterised by mixed severity wildfires at ~5–100 year intervals (Murphy *et al.* 2013) and likely have resistance to such fires that do not affect canopy resources.

Materials and methods

Study area

Our study was conducted in the eucalypt forests of the east coast and inland ranges of NSW, Australia. This region is largely described by wet or dry eucalypt forest, intermixed with rainforest, and other vegetation types (e.g. wetland, woodland and cleared land; Keith 2004). Wet sclerophyll forests are characterised by tall trees (~30–70 m), moderately fertile soils and high rainfall (Keith 2004). In NSW, wet sclerophyll forest is typically found on coastal ranges and the eastern side of the escarpment (Keith 2004). Dry sclerophyll forests occur on extremely low nutrient soils, resulting in shorter trees (~10–30 m tall), with canopies that are less dense than wet sclerophyll forest (Keith 2004). They are characterised by a particularly high diversity of eucalypt species, reflecting the variable topography, geology, climate and geographical range where they are found (Keith 2004). Rainfall and temperature vary greatly across this region, with average historical precipitation ranging from ~600 mm on the inland range through to >1500 m along parts of the coast (BOM 2024). Temperatures are cool at high elevations (average annual range 3–15°C), becoming warmer at coastal, low elevation sites (average annual range 12–24°C).

Forests across this region have been fragmented and degraded following the European occupation and the associated removal of Indigenous management including changes in fire regimes, and the introduction of forest harvesting, land clearing, livestock grazing and invasive pest species (Keith 2004; Bradshaw 2012). From September 2019 through to March 2020, multiple wildfires burnt across south-eastern Australia, including large swathes of NSW, to collectively contribute to what is now known as 2019–2020 Black Summer wildfires (Filkov *et al.* 2020; Collins *et al.* 2021). Large areas of forest burnt at high intensity, resulting in severely burnt forest, with few unburnt 'refuge' areas remaining (Collins *et al.* 2021). The fires followed a period of extended drought (Filkov *et al.* 2020), causing areas of dieback and reduced tree health before the fires commenced (Losso *et al.* 2022).

Design

We designed a landscape-scale study to investigate the responses of greater gliders and yellow-bellied gliders to 2019–2020 fire severity and environmental characteristics. We stratified 223 sites across both species' distributions in NSW and according to three main variables: fire severity (unburnt, low-moderate and high), forest type (wet or dry) and elevation (<500 and >500 m) (Fig. 1, Table 1). These 12 treatments were spatially represented and replicated across NSW. Fire severity was defined using the local fire extent and severity mapping (FESM) score that was extracted from the FESM layer and grouped into three fire severity categories: unburnt (FESM 0), low-moderate (FESM 2–3) and high (FESM 4–5), where 0 = unburnt, 2 = burnt surface with unburnt canopy, 3 = partial canopy scotch, 4 = full canopy scotch with some canopy consumption and 5 = full canopy consumption (Gibson *et al.* 2020).

Selected sites met the following criteria: on or <100 m from minor roads and tracks within public land; outside of known historical intensive forest harvest areas; and not burnt since 2019–2020. In consultation with four Local Aboriginal Land Councils (LALCs) on the NSW south coast, additional sites were selected on Batemans Bay, Jerrinja, Merrimans and Bega LALC land. Final selected sites were spatially separated by >1 km to minimise pseudo-replication since yellow-bellied glider calls can be heard >400 m (Goldingay and Kavanagh 1991). All sites were verified on ground prior to fauna surveys to ensure the site was consistent with the designated treatment.

Fauna surveys

A site consisted of a 200 m transect along a road or track, with 50 m visibility either side of the transect. Each site was surveyed two to three times between September 2022 and April 2023 (mean = 2.71, s.e. = 0.05); 3–4 years since the 2019–2020 Black Summer fires. We did not expect seasonal effects over this time period but any effects would have been taken into account by temperature and rainfall terms in our models. At least three repeat surveys provide ~80% confidence in either species being detected if present (Wintle *et al.* 2005; Bilney *et al.* 2022). Repeat surveys were typically conducted on different nights. Surveys commenced >1 h after sunset and concluded >1 h before sunrise. Surveys were avoided during poor weather (e.g. heavy rain, strong winds and fog) due to

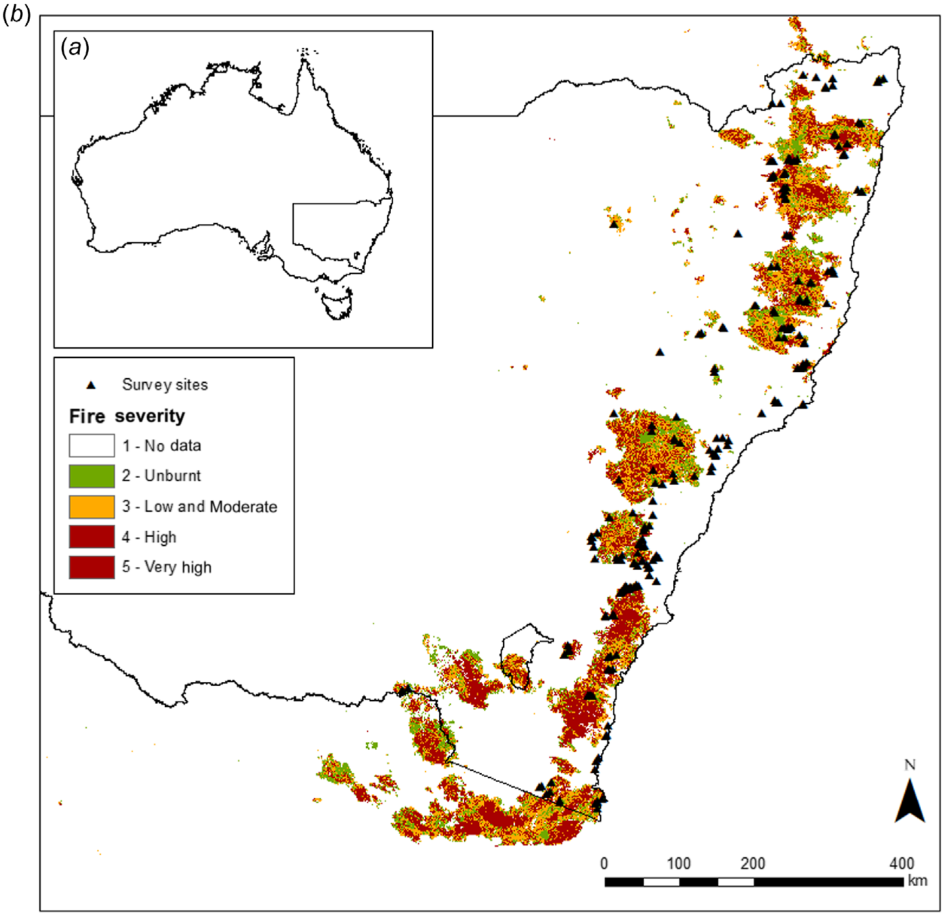

Fig. 1. (*a*) Inset showing the study region of NSW within Australia. (*b*) Severity of the 2019–2020 fires and locations of sites surveyed within NSW. Data sources: NSW DCCEEW (2020) and DCCEEW (2024).

Table 1. Number of sites surveyed for each fire severity, forest type and elevation.

Fire severity	Forest type	Elevation (m)	Sites
Unburnt	Dry	<500	28
Unburnt	Dry	>500	18
Unburnt	Wet	<500	12
Unburnt	Wet	>500	14
Low-moderate	Dry	<500	21
Low-moderate	Dry	>500	19
Low-moderate	Wet	<500	10
Low-moderate	Wet	>500	23
High	Dry	<500	25
High	Dry	>500	31
High	Wet	<500	12
High	Wet	>500	10

increased risks to observers, and reduced ability to detect animals (Wintle *et al.* 2005). If a predator, such as a forest owl was observed or heard on site, the surveys ceased (as per conditions on Animal Research Authority: AEC 220823/01).

Surveys consisted of a combination of listening, call playback and spotlighting. The survey commenced with 10 min of listening for calls of the yellow-bellied glider. This was followed by 15 min of spotlighting along the 200 m transect. Two observers walked side-by-side for 200 m, each observing one side of the transect, and then returned to the start of the transect within 15 min. Once an animal was detected, spotlights were switched from a high intensity lumen to lower (e.g. 500 lumens) for species identification of animals. The survey concluded with another 10 min of listening and call playback, commencing with active listening for yellow-bellied gliders (2 min), followed by call playback (2 min), repeated until 10 min was reached. If a response was heard, the playback was immediately turned off. Only calls of the powerful owl (*Ninox strenua*) were used for call playback as this species was found consistently across the survey range and is known to elicit a response by yellow-bellied gliders (Irish and Kavanagh 2011; Goldingay *et al.* 2022). Calls were played at approximately 100–120% of natural volume. During listening and call playback, spotlights were kept off unless an animal was detected nearby, and a spotlight was useful for confirming species identification.

Covariate data collation

We used five different covariates to model the variation in detection probability, which included linear and quadratic effects of temperature measured at the start of the survey (temp and temp^2, respectively), linear and quadratic effects of Julian date (jul and jul^2, respectively) and total rainfall on the day of each survey (rain). These covariates were considered because they effect detection and the behaviour of similar arboreal mammals (Wintle *et al.* 2005; Sharpe and Goldingay 2018; Goldingay 2021*a*). Air temperature was recorded at the beginning of each survey with a Kestrel weather meter (model: 3000 RH). Julian date was an integer, where the first day of September = 1 and the last day of August = 365 and was used to test for seasonal variation in detection. Total daily rainfall data were collated using the 'chirps' R package which allows extraction of global precipitation data at high resolution (0.05° × 0.05°) (De Sousa *et al.* 2020).

We extracted 15 spatial covariates to include in a base model (Table 2). Most of these covariates were used in recent species distribution modelling of the greater glider (Brizuela-Torres *et al.* 2024). Spatial covariates were extracted using the 'raster' R package (Hijmans 2024). Another eight fire covariates were computed to test fire-related hypotheses (Table 3). For example, we obtained the ecosystem disturbance index layer (EDI) from Brizuela-Torres *et al.* (2024) which represents ecosystem disturbances in the landscape such as wildfire, flooding, climate change and land use change (Table 2). Disturbances were derived from MODIS Aqua Land Surface Temperature and Terra Enhanced Vegetation. This included proportions of low-moderate and high-severity fire calculated at three different spatial scales from survey sites (300, 500 and 1000 m), distance to unburnt vegetation and local FESM score (i.e. the fire score at the survey site not including a neighbourhood). Fire buffers were computed using the 'raster' package in R with the FESM fire layer (down-scaled to a 20 m × 20 m resolution). Distance to unburnt vegetation (>20 m pixel, FESM 0) was calculated by creating an unburnt map, which coded all unburnt pixels as 1 and all burnt pixels as 'NA'. Then QGIS was used to measure the distance between each site and the nearest unburnt pixel.

Statistical analysis

Occupancy models were used to correlate site-based attributes with the occupancy of the greater glider and the yellow-bellied glider (MacKenzie *et al.* 2002). Occupancy models assume the detection of a target species from any given survey was the outcome of two binomial processes acting simultaneously: (1) the probability a species was present at a site (ψ) over long time periods; and (2) the probability a species was present within the site and observed in any given survey visit (ρ). The state process was considered a Bernoulli random variable, such that:

$$z_i \sim Bernoulli(\psi_i) \tag{1}$$

where ψ is the probability of species occupancy at site i and z_i denotes the true state of occurrence. We then assumed the observation of a species at site i is the outcome of another Bernoulli random variable, given by:

$$y_{ij}|z_i \sim Bernoulli(z_i p_{ij}) \tag{2}$$

where y_{ij} is the observed 'presence–absence' data and ρ_{ij} is the probability of detection. We modelled the influence of covariates using the logit link, given by:

$$\text{logit}(p_{ij}) = \alpha + \beta covariateA \tag{3}$$

where the probability of a species being detected at a site during a sampling occasion (p_{ij}) is a function of an overall intercept α and coefficients describing the effect of covariates.

A three-stage process was used to model the occupancy of each species. In stage one, we found the most parsimonious model for detection with a null model for occupancy. We used a dredge function in R to search through all combinations of detection covariates (temp, temp^2, rain, jul and jul^2) and found the detection model with the lowest Akaike Information Criterion (AIC) value. In stage two, another dredge was conducted on the 15 occupancy covariates with the best combination of detection covariates fixed. These covariates did not include any fire variables which were of primary interest for hypothesis testing. This resulted in comparing 2040 different models. The best combination of occupancy covariates identified with the dredge in stage two, while retaining the best detection covariates, became the 'base model'. Both dredges were performed with the dredge function from the MuIn R package, and occupancy models were constructed in a maximum likelihood framework using the 'unmarked' R package (Fiske and Chandler 2011; Kellner *et al.* 2023). A Pearson's correlation matrix was used to assess collinearity between covariates ($R = \geq 0.5$) where collinear covariate combinations were not considered in the dredge.

Stage three involved adding each fire covariate separately to the base model to create a set of competing models, each of which represented a different hypothesis about how the severity and scale of wildfire affected both species (Table 3). For example, Hypothesis 9 predicts that detections of both species are best explained by the amount of habitat burnt at high severity across large areas.

All hypothesis-base models were compared with AIC values, where <2 AIC values were considered a substantial improvement in model parsimony. Model goodness-of-fit was evaluated using three different tests with 10,000 bootstraps: sum of squared errors, Pearson's chi-squared and Freeman–Tukey chi-squared. We used an alpha value of 0.05 to determine

Table 2. Spatial covariates tested in the base model to predict glider occupancy.

Covariates	Description	Source	Grid size	Unit
carbon	Percentage of carbon contained in the topsoil (0–30 cm depth). https://esoil.io/TERNLandscapes/Public/Pages/SLGA/GetData-COGSDataStore_SLGA.html	Soils and Landscape Grid of Australia	30 m × 30 m	% carbon
elev	Elevation of the mid-points of the 200 m transect. Obtained in-field.	In-field	NA	m
forest_height	Height of the canopy at the study site.	Potapov *et al.* (2021)		m
fPAR_mean	Fraction of photosynthetically active radiation (400–700 nm of spectral range) intercepted by the sunlit vegetation canopy. Data aggregated for period 2000–2014.	Biodiversity and Climate Change Virtual Laboratory (BCCVL)1	500 m × 500 m	% of PAR
fPAR_var	Coefficient of variation of fraction of photosynthetically active radiation. Data aggregated for 2000–2014.	Biodiversity and Climate Change Virtual Laboratory (BCCVL)1	500 m × 500 m	% of PAR
GGP_var	Coefficient of variation of gross primary productivity (amount of carbon fixed during photosynthesis by all producers in an ecosystem). Data aggregated for 2000–2007.	Biodiversity and Climate Change Virtual Laboratory (BCCVL)1	500 m × 500 m	molCO$_2$ per m^2
soil_nitrogen	Proportion of nitrogen contained in the topsoil (0–30 cm depth) https://esoil.io/TERNLandscapes/Public/Pages/SLGA/GetData-COGSDataStore_SLGA.html	Soils and Landscape Grid of Australia	90 × 90 m	% nitrogen
mean_EDI	Average ecosystem disturbance index derived from MODIS Aqua Land Surface Temperature and Terra Enhanced Vegetation. Average of the yearly composites 2003–2013. Identifies time, location and magnitude of major disturbance events.	AusCover	500 m × 500 m	Disturbance index units
pp_annual	The sum of all 12 monthly precipitation estimates. Long-term climate data for 1976–2005.	Variables created using ANUCLIM ver. 6.1	500 m × 500 m	mm
pp_driest	Total precipitation calculated over the quarter of the year identified as the driest (to the nearest week). Long-term climate data for 1976–2005.	Variables created using ANUCLIM ver. 6.1	500 m × 500 m	mm
pp_season	Coefficient of variation of the weekly precipitation estimates, i.e. their standard deviation expressed as percentage of the mean of those estimates. Long-term climate data for 1976–2005.	Variables created using ANUCLIM ver. 6.1	500 m × 500 m	Dimensionless
soil_moisture	Root zone soil moisture. Soil moisture within the top 100 cm of the soil surface.	Bureau of Meteorology 2020	5 km × 5 km	% of water content/100 cm of soil
temp_season	Temperature variation across the year (coefficient of variation). Standard deviation of weekly temperature averages expressed as a percentage of the mean of those temperatures (i.e. annual mean). Long-term climate data for 1976–2005.	Variables created using ANUCLIM ver. 6.1	500 m × 500 m	Dimensionless
temp_warm	Mean temperature of the warmest three months of the year. Long-term climate data for 1976–2005.	Variables created using ANUCLIM ver. 6.1	500 m × 500 m	°C
Tsf	Time since fire. Years since the last fire event at the location of the site.	Generated from wildfires polygons	500 m × 500 m	Years

Site-based covariates used were from Brizuela-Torres *et al.* (2024), unless otherwise stated.

whether there was a lack of fit. This was performed on the base models for each glider species, and both passed all goodness-of-fit tests (Supplementary materials Table S1, Fig. S1).

Results

We surveyed 223 sites on 610 occasions, with greater gliders detected more commonly and at more sites (144 detections across 66 sites) than yellow-bellied gliders (54 detections across 31 sites), (Fig. 2). Across all 223 sites, both species were detected least frequently in sites where high-severity fires had occurred at the site scale (local FESM) (greater glider n sites = 13, and yellow-bellied glider n sites = 4). The greater glider was detected at an almost equal number of sites where low-moderate severity fires (26) and no fires occurred (27). The yellow-bellied glider was detected in more sites with low-moderate severity burns compared to unburnt sites ($n = 16$ and 11, respectively). The estimated mean occupancy of the greater glider in the top performing model was 0.21 [95% confidence interval (CI): 0.15–0.30], which was higher than for the yellow-bellied glider of 0.07 (95% CI: 0.03–0.15). The respective detection probabilities for each species were 0.75 (95% CI: 0.67–0.81) and 0.48 (95% CI: 0.36–0.60) for one survey occasion.

The top-performing base model for the greater glider included two detection covariates (temp and temp^2) and six

Table 3. Summary of fire covariates and hypotheses.

Hypothesis	Description	Equation
Hypothesis 1	Base model, no fire covariate is predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + Base\ model$
Hypothesis 2	fesm_local, local fire effects are most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_local}\beta_2 + Base\ model$
Hypothesis 3	unburnt, distance to the nearest unburnt patch is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{unburnt}\beta_2 + Base\ model$
Hypothesis 4	fesm_med300, proportion of low-moderate severity fire within 300 m radius is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_med300}\beta_2 + Base\ model$
Hypothesis 5	fesm_med500, proportion of low-moderate severity fire within 500 m radius is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_med500}\beta_2 + Base\ model$
Hypothesis 6	fesm_med1000, proportion of low-moderate severity fire within 1000 m radius is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_med1000}\beta_2 + Base\ model$
Hypothesis 7	fesm_high300, proportion of high-severity fire within 300 m radius is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_high300}\beta_2 + Base\ model$
Hypothesis 8	fesm_high_500, proportion of high-severity fire within 500 m radius is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_high500}\beta_2 + Base\ model$
Hypothesis 9	fesm_high_1000, proportion of high-severity fire within 1000 m radius is most predictive of glider occupancy.	$logit(\psi) = \alpha\beta_1 + \text{fesm\_high1000}\beta_2 + Base\ model$

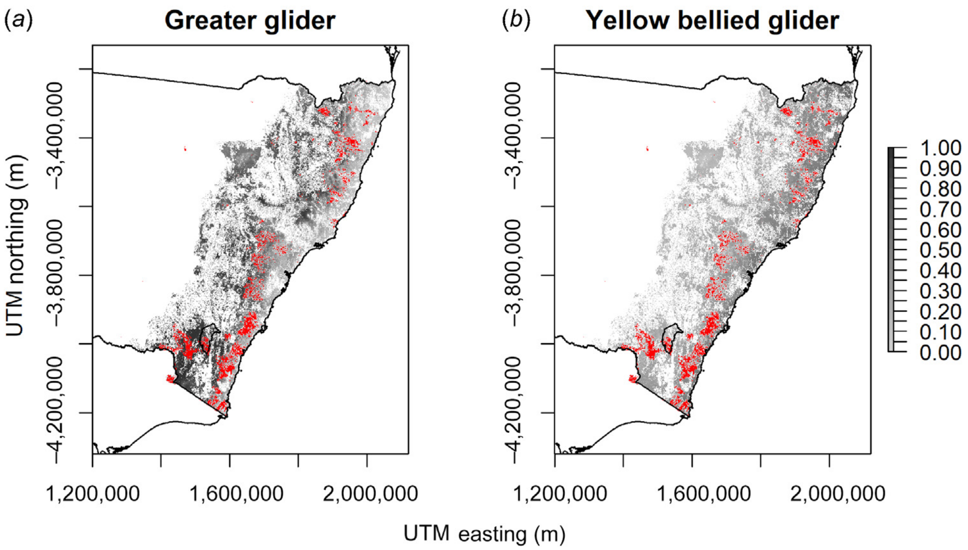

Fig. 2. Predicted occupancy of (*a*) greater glider and (*b*) yellow-bellied glider within vegetated areas of NSW, with the 2019–2020 fires shown in red.

occupancy covariates (forest_height, mean_EDI, soil_nitrogen, soil_moisture, temp_season and temp_warm; Table S1). The detection covariates included a negative correlation with temp (β = −0.48 ± 0.21 s.e.) and a negative concave correlation with temp^2 (β = −0.21 ± 0.11, Fig. S1). Out of the six occupancy covariates, three had negative correlations, which included mean_EDI (β = −0.75 ± 0.32 s.e.), soil_nitrogen (β = −0.46 ± 0.24) and temp_warm (β = −0.76 ± 0.22; Fig. 3). The other three had positive correlations with occupancy: forest_height (β = 0.51 ± 0.23), soil_moisture (β = 0.62 ± 0.27) and temp_season (β = 1.28 ± 0.42; Fig. 3).

A strong negative relationship between greater glider occupancy and high fire severity at the largest spatial scale (1000 m) was the most predictive fire covariate (Hypothesis 9, Table 3; and Table 4, Fig. 4). The second and third most predictive fire covariates were high fire severity within 500 and 300 m spatial scales, respectively (Hypotheses 8 and 7). All spatial scales of low-moderate severity fire proportions were less predictive compared to the base model containing no fire covariates. Distance to unburnt vegetation and local FESM scores were more predictive compared to the base model that contained no fire covariates but were less predictive than any of the spatial scales of high-severity fire.

Yellow-bellied glider

The top performing base model for the yellow-bellied glider (Table S1) included one detection covariate (temp; Fig. S3)

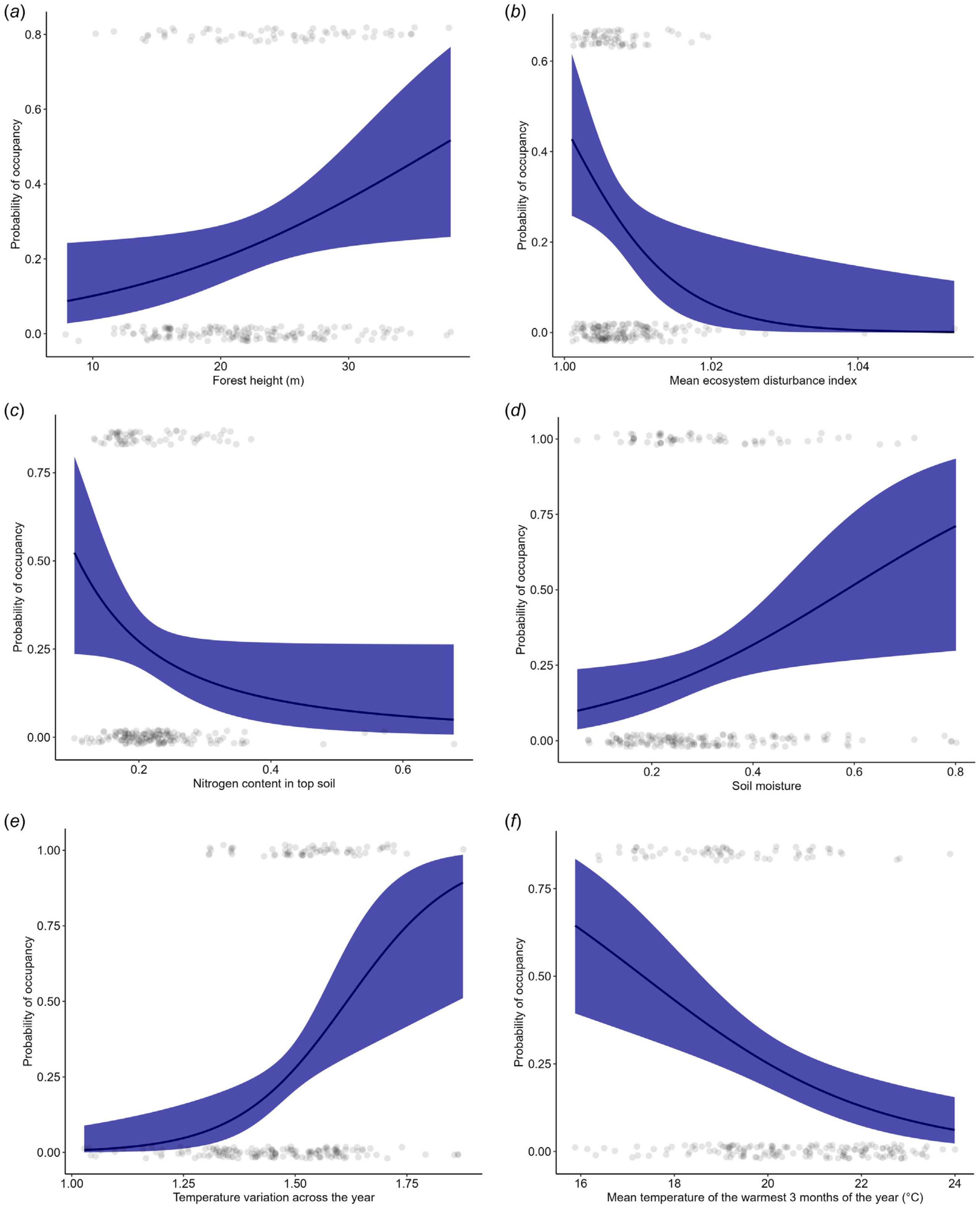

Fig. 3. Correlations from the base model between greater glider occupancy and covariates: (*a*) forest height, (*b*) ecosystem disturbance index, (*c*) soil nitrogen, (*d*) soil moisture, (*e*) temperature variation across the year and (*f*) temperature of the warmest three months of the year.

Table 4. Comparison of parsimony between all greater glider models containing fire covariates.

Model	β_1 (s.e.)	β_2 (s.e.)	*n*	ΔAIC	AIC weight
fesm_high1000	−0.92 (0.24)		11	0	0.67
fesm_high500	−0.80 (0.23)		11	3.15	0.14
fesm_high300	−0.78 (0.22)		11	3.55	0.11
fesm_local	L-U: −1.33 (0.38)	H + L-U: −0.13 (0.35)	12	4.74	0.06
dist_unburnt	−0.77 (0.28)		11	7.58	0.02
Base model			10	14.36	0
fesm_med500	0.12 (0.20)		11	15.99	0
fesm_med1000	0.10 (0.19)		11	16.01	0
fesm_med300	0.12 (0.19)		11	16.09	0

n = number of variables. Base model = p(temp + temp^2), ψ(forest_height + mean_EDI + soil_nitrogen + soil_moisture + temp_season + temp_warm). β_1 and β_2 are the fire covariate beta coefficients in the order they appear in the model column. L-U is the contrast beta value comparing low-medium severity to unburnt, and H + L-U is the beta value comparing high + low-medium severity to unburnt.

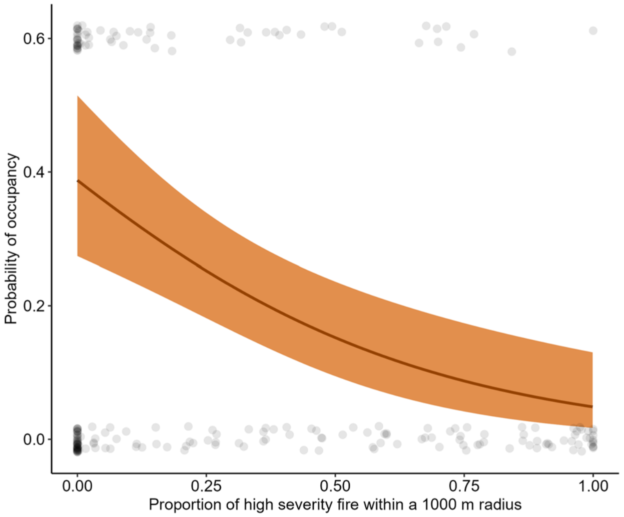

Fig. 4. The relationship between greater glider occupancy and proportion of severe fire within a 1000 m radius. Based on results from model 'fesm_high1000'.

and two occupancy covariates (mean_EDI and temp_season; Fig. 5). Both occupancy covariates had negative correlations (mean_EDI $\beta = -0.76 \pm 0.39$ s.e. and temp_season $\beta = -0.55 \pm 0.23$), whereas the detection covariate had a positive correlation (temp $\beta = 0.31 \pm 0.22$).

The local FESM score variable was the most predictive fire covariate for the occupancy of the yellow-bellied glider (Table 5, Fig. 6). Yellow-bellied gliders showed a 2.2 times higher likelihood of occupancy in unburnt sites, and sites with low-moderate severity local burns had a 2.5 times higher likelihood of occupancy compared to sites with high-severity burns. The second, third and fourth most predictive models sequentially decreased in spatial scale regarding the proportion of high-severity fire burnt within a buffer. Low-moderate severity fire buffers were less predictive at all spatial scales compared to the base model that contained no fire covariates. Distance to unburnt vegetation was slightly more predictive compared to the base model (a difference of 1.01 AIC values).

Discussion

We demonstrated different responses of two gliding marsupials with contrasting ecological traits to the extent and severity of wildfire. In line with predictions, three years after the 2019–2020 wildfires, the occupancy of both species of gliders had diminished at severely burnt sites, where the fire had consumed all canopy resources. Occupancy of the greater glider declined further with increasing severe fire at the largest spatial extent. In contrast, occupancy of the yellow-bellied glider was best explained by severity at the local site scale. For both species, increasing amounts of low-moderate severity fire in the landscape surrounding survey sites did not diminish glider occupancy, regardless of the size of the neighbourhood buffer. This accords with our expectations that both species are resilient to partial canopy scorch, where essential resources remain.

Greater gliders are vulnerable to severe, landscape-scale fire

Our study confirms that greater gliders are vulnerable to landscape-scale, high-severity fire. We posit primary factors that explain this decline are (1) their highly specialised diet, which is depleted following canopy fire, (2) dependency on tree hollows that can be diminished post severe fire and (3) their low dispersal capacity, which reduces post-fire recolonisation. In the complete absence of eucalypt foliage, greater gliders quickly succumb to starvation, due to their requirement for regular feeding (Foley *et al.* 1990). Gliders may survive the initial disturbance, but then perish *in situ*, losing weight, pouch young and being susceptible to predation (Tyndale-Biscoe and Smith 1969). In our study area, trees are not typically killed by fire. Instead, burnt trees respond with epicormic growth, allowing the canopy to regenerate (Keith 2004; Collins 2020). Greater gliders have been observed consuming epicormic regrowth, although are assumed to also require unburnt mature foliage to sustain them in the period between the fire and regrowth forming (Smith and Smith 2022). However, further research is required.

Previous studies have confirmed declines in greater gliders at sites of high fire severity, with post-fire persistence of greater gliders associated with amount of remaining habitat within the immediate and surrounding landscape (Lindenmayer *et al.* 2013; Chia *et al.* 2015; May-Stubbles *et al.* 2022; Smith and Smith 2022). However, this study and others confirm that greater gliders can persist where unburnt canopy resources remain. For example, Chia *et al.* (2015) found similar

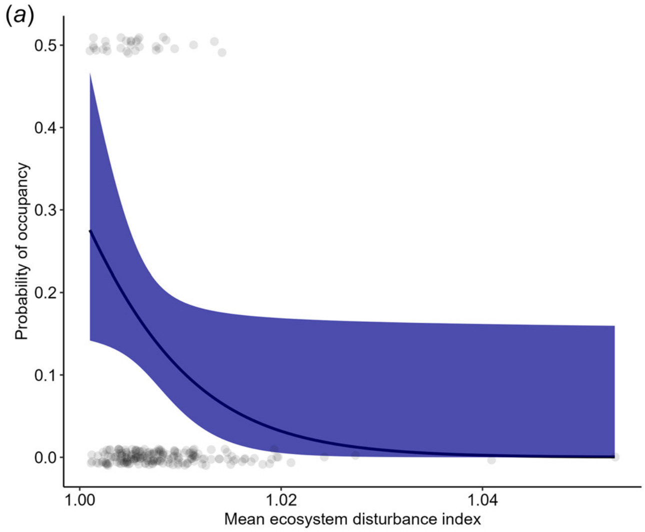

Fig. 5. Correlations from the base model between yellow-bellied glider occupancy and covariates: (*a*) ecosystem disturbance index and (*b*) temperature variation across the year.

Table 5. Comparison of parsimony between all yellow-bellied glider models containing fire covariates.

Model	β_1	β_2	*n*	ΔAIC	AIC weight
fesm_local	L-U: −1.01	H + L-U: −0.84	7	0	0.54
fesm_high_1000	−1.46		6	2.73	0.14
fesm_high_500	−1.27		6	3.39	0.10
fesm_high_300	−1.16		6	3.7	0.09
unburnt	−0.001		6	4.37	0.06
Base model			5	5.38	0.04
fesm_med_300	−0.34		6	7.18	0.02
fesm_med_500	−0.33		6	7.22	0.02
fesm_med_1000	−0.18		6	7.34	0.01

n = number of variables. Base model = p(temp), ψ(mean_EDI + temp_season). β_1 and β_2 are the fire covariate beta coefficients. L-U is the contrast beta value comparing low-medium severity to unburnt, and H + L-U is the beta value comparing high + low-medium severity to unburnt.

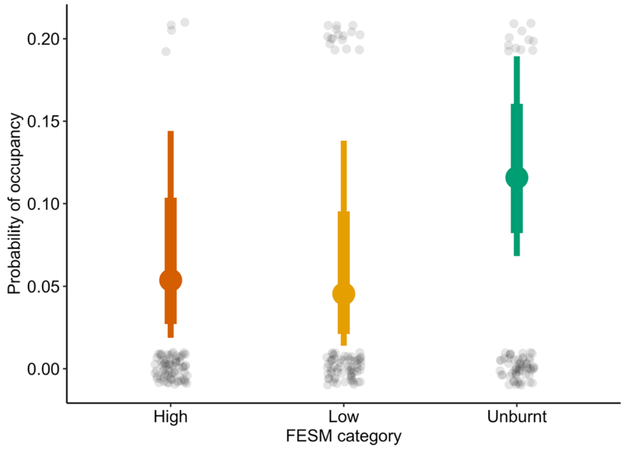

Fig. 6. The relationship between yellow-bellied glider occupancy and the local FESM ordinal score. Based on results from 'fesm_local'. Thick and thin bars indicate 80% and 95% confidence intervals, respectively.

abundance between sites completely unburnt and sites with only the understorey burnt. However, abundance declined with increasing amount of the canopy burnt within a site (May-Stubbles *et al.* 2022; Smith and Smith 2022) or in the surrounding landscape (Lindenmayer *et al.* 2013). Greater gliders have been found to occur in small unburnt patches ~1 ha (Berry *et al.* 2015), but patches that are too small are unlikely to sustain similar abundances to unburnt areas outside the fire (Green *et al.* 2024). Other factors may also contribute to post-fire declines. One to two years post fire, Smith and Smith (2022) observed a general decline in abundance of greater gliders across all areas previously occupied in the Blue Mountains, even in unburnt sites. Declines were attributed to a combination of fire severity, extreme heat during the 2019–2020 wildfire season and preceding drought (Smith and Smith 2022).

Following local extinction, animals with low dispersal capacity take longer to recolonise patches (Ensbey *et al.* 2023). This is true of the greater glider, which can take decades to recover and recolonise (Andrew *et al.* 2014; Campbell-Jones *et al.* 2022). Severe wildfires in Royal National Park caused a complete collapse in the greater glider population (Maloney 2007), with no observations recorded for 18 years (Andrew *et al.* 2014). Similarly, 10 years after extensive wildfire in Victoria, greater gliders remained absent from sites burnt by high-severity fire (Campbell-Jones *et al.* 2022).

Yellow-bellied gliders decline at severely burnt sites

Yellow-bellied gliders were found to respond negatively to high-severity fire at the site scale. Our results indicate that 3 years post fire, the extent of severely burnt and regenerating eucalypt forest was not a barrier to yellow-bellied glider movement, and gliders were preferentially seeking out unburnt resources. In addition, spatial heterogeneity of the wildfire meant that unburnt sites were within typical nightly movements (590–2350 m, Goldingay 1989). Only a few studies have investigated yellow-bellied glider responses to fire, with responses varying from no discernible impact to local extinction. Goldingay and Kavanagh (1991) reported local extinction immediately following wildfire within a coastal population, whereas yellow-bellied gliders were found to persist in previously burnt inland landscapes 7 years after extensive wildfire (Kambouris *et al.* 2014). In tall wet forest, occupancy diminished with increasing amount of the landscape (within 400 m) that was both burnt by wildfire within the last 10 years and logged in the last 100 years (Lefoe *et al.* 2022). Two studies post 2019–2020 fires indicated declines associated with severe fire and loss of large trees. Goldingay *et al.* (2024) reported declines in occupancy of 13–66% across three landscapes of variable fire severity in southern NSW. In one of these landscapes, Bilney *et al.* (2022) specified a 26% decline in occupancy associated with extent of high-severity fire within 450 m, with no response associated with low severity. Both studies highlighted the importance of large hollow-bearing trees, especially in severely burnt or logged landscapes.

Our study demonstrates a preference by yellow-bellied gliders for unburnt sites, but that severely burnt forest is not a barrier for movement 3 years post-fire. In the short term, severe fire is expected to impact on habitat quality, immediately reduce the abundance of most food resources except for eucalypt sap and increase susceptibility to post-fire predation (Goldingay and Kavanagh 1991). With increasing time-since-fire, the recovery of forest resources would facilitate movement through severely burnt forest and provide more foraging options.

Environmental and climatic conditions influence species responses

Occupancy of both the greater glider and yellow-bellied glider declined with increasing environmental disturbance, in accordance with their habitat requirements (Gibbons and Lindenmayer 2002; Goldingay 2012). Both species require large, old growth hollow-bearing trees, which can be reduced in landscapes subjected to timber harvesting and severe fire (Gibbons and Lindenmayer 2002; Goldingay 2012; Goldingay 2021*b*). Timber harvesting can leave a legacy on the quality of habitat and associated forest fauna for many decades, with the impact depending on the intensity and prescriptions of harvest operations (Kavanagh 2000). In areas clear-felled, the recovery of large trees to a size that acquires suitable hollows can take more than 100 years (Gibbons and Lindenmayer 2002; Goldingay 2012). Our study aimed to minimise the influence of past logging disturbance by excluding sites known to be subjected to intense logging practices. However, not all past logging is accurately captured in historical map layers, hence the importance of consulting remotely sensed disturbance layers.

Temperature, moisture, forest height and productivity further influenced detection and occupancy of gliders. Detection of the yellow-bellied glider increased with increasing temperature, consistent with the species' association with coastal forest. Occupancy was also associated with less variation in annual temperature, indicative of coastal regions that do not experience extremes in high or low temperatures (BOM 2024). In contrast, detection of greater gliders increased with cooler temperatures, and occupancy increased with greater forest height, increasing soil moisture and variation in annual temperature. These latter variables are characteristic of cooler, high elevation, wet eucalypt forest (Keith 2004) and align with suitable greater glider habitat (Wagner *et al.* 2020).

Greater gliders are particularly susceptible to warmer and drier conditions due to the species' narrow thermal and moisture tolerance (Rübsamen *et al.* 1984). Declines in greater gliders due to warming temperatures have been associated with low elevation sites with warmer temperatures in the Blue Mountains of NSW (Smith and Smith 2018). Declines in occupancy of greater gliders across Victoria have been attributed to areas experiencing increasingly warm nights above 20°C and less rainfall (Wagner *et al.* 2020). Similarly, Goldingay *et al.* (2022) detected drought-induced declines of the greater glider in northern NSW. Counterintuitively, we also detected declines in greater glider occupancy associated with higher concentrations of soil nitrogen. Interrogation of this result reveals that occupancy was lower in sites associated with rainforest, which has a high soil nitrogen content. Rainforest, however, does not provide a food source for greater gliders, as the species feeds almost exclusively on eucalypt leaves (Kavanagh and Lambert 1990; Comport *et al.* 1996).

Climate change and associated warmer and drier conditions threaten the persistence of both glider species. Climate modelling predicts major range contractions of both species due to a warming and drying climate (Handayani *et al.* 2019; Wagner *et al.* 2020). For the yellow-bellied glider, drought conditions and an increasingly drier climate contribute to a loss of canopy resources including reduced flower and nectar availability (Law *et al.* 2000; Law and Chidel 2008), with subsequent population declines (Goldingay *et al.* 2023). Climate change can lead to a reduction in nutritional value of eucalypt leaves (Lawler *et al.* 1996; Wujeska-Klause *et al.* 2019), and collapse and mortality of trees (Lindenmayer *et al.* 2012), endangering survival of both species. Increasing drought and fire associated with climate change is leading to greater mortality of large trees, particularly those with fire scars, and trees found in wet forests on more fertile soils (Bendall *et al.* 2024).

Conclusion

Our study reveals that similar species, in terms of morphology and habitat, can have differing responses to fire extent and severity due to variation in other biological traits. We show that both greater gliders and yellow-bellied gliders are highly vulnerable to severe canopy consuming fire, with the greater glider particularly vulnerable to the effects of severe fire across large areas, due to its relatively low mobility, narrow dietary niche and temperature tolerance, which result in a preference for cooler, high elevation, wet eucalypt forests across its range. In contrast, the yellow-bellied glider has greater resilience to landscape fire likely due to increased mobility and broader dietary requirements. These findings reiterate the importance of considering species specific traits and individual fire responses when assessing fire vulnerability, lest biodiversity responses be muted or negated (cf. Driscoll *et al.* 2024).

Based on our findings and ecology of both species, low-intensity fire that does not burn canopy resources (e.g. low-intensity prescribed burns and cultural burns) are unlikely to negatively impact either species. Such fires could be beneficial, when aligned with appropriate fire regimes for different forest types, to minimise the occurrence and intensity of future fires (Collins *et al.* 2023). Cultural burning has additional benefits beyond managing fuel loads, providing for diverse spiritual, social and ecological values (Pascoe *et al.* 2023).

Further research is needed to reveal what factors most determine the declines associated with high-severity fires, either instantaneous mortality from the fire itself or reduced survival in postfire landscapes (e.g. reduction in food or hollow resources). Determining this would reveal potential conservation management research targets to achieve persistence of these two glider species after severe fires. Similarly, our results demonstrate the relevance of considering species ecology in assessing their responses to fires, which is important for predicting impacts on other glider species to fire, including the threatened squirrel glider (*Petaurus norfolcensis*). Ongoing monitoring is also important to track species recovery. This would ideally be conducted as a Before After Control Impact (BACI) design, incorporating pre-fire data and regular widespread monitoring (Southwell *et al.* 2022). We recommend that to support current and future populations of greater gliders and yellow-bellied gliders, it will be essential to minimise the risk of landscape high-severity fire. In addition, maintaining essential habitat such as large, mature, hollow-bearing trees and feed trees will be critical for supporting ongoing persistence and recovery of these two large volant marsupials.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study are available in NSW BioNet at https://atlas.bionet.nsw.gov.au/UI_Modules/ATLAS_/AtlasSearch.aspx.

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Author affiliations

[A]Conservation and Restoration Science Branch, NSW Department of Climate Change, Energy, the Environment and Water, Parramatta, NSW 2150, Australia.

[B]School of Environmental and Life Sciences, University of Newcastle, University Drive, Callaghan, NSW 2308, Australia.