RESEARCH ARTICLE

Unburnt areas in subtropical woodlands contain distinct reptile communities after extensive wildfire

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Abstract

Extensive wildfires can have profound impacts on fauna communities by altering the vegetation structure and resource availability. However, unburnt areas within a fire mosaic may be important habitat for wildlife while the surrounding area recovers after fire. To understand the importance of unburnt vegetation for reptiles, we studied community assemblages at 15 burnt and 15 unburnt sites in a subtropical woodland 12 months after a 25 000 ha wildfire. We tested the relative importance of unburnt areas and structural attributes on reptile abundance, richness, and community composition across this landscape. Unburnt areas had higher species richness and diversity, but not overall abundance. Reptile community composition differed significantly between burnt and unburnt areas. Woody debris, which was retained in unburnt areas but depleted in burnt areas, was positively associated with increased reptile diversity and richness. Our results suggest that unburnt areas are vital for maintaining reptile diversity and richness within a woodland landscape after wildfire. These findings demonstrate the importance of ensuring fire management programs retain unburnt patches of vegetation in fire-prone landscapes to sustain reptile communities.

KEYWORDS
conservation, fire management, reptile, unburnt areas, wildfire

INTRODUCTION

Wildfire is a natural and frequent event that has a profound impact on plant and animal communities (Clarke et al., 2010; Davis et al., 2016; Gill et al., 2003; Lindenmayer et al., 2008). Wildfire differs significantly from planned and managed burns in that it is usually more severe and extensive, and it often burns fire-sensitive ecosystems (Avitabile et al., 2013; Collins et al., 2023). Global fire regimes have been altered from historical conditions due to the suppression of Indigenous fire practices (Mariani et al., 2022) and anthropogenic-induced climate change leading to longer

and more intense fire seasons (Abram et al., 2021; Halofsky et al., 2020). These changes are evident in events like the megafires of 2019–20 in Australia (Legge et al., 2022), and across Canada and southern Europe in 2022–23 (Burton, 2023; Rodrigues et al., 2023). Frequent and severe fire can cause significant, and often detrimental, changes to ecosystems (Clarke et al., 2010) including shifts in ecosystem state (Steel et al., 2021), declines in biodiversity and species abundance (Kelly et al., 2020), and an increase risk of species extinction (Wintle et al., 2020).

Fires typically burn heterogeneously across landscapes, leaving mosaics of severely burnt, partially burnt, and unburnt, areas (Leonard et al., 2014; Robinson et al., 2013; Santos et al., 2016). The spatial arrangement of these areas is determined by variable factors such as windspeed and direction, air temperature, fuel load, soil moisture (Bradstock et al., 2005) and containment efforts, as well as fixed factors such as topography and natural barriers to fire (Mackey et al., 2021). The structure, composition, and size of partially burnt and unburnt areas determines if fauna can use them as refuges and persist within burnt landscapes over time (Puig-Gironès et al., 2018; Shaw et al., 2021).

Unburnt areas within an extensive wildfire boundary are typically small and provide limited refuge for fauna escaping the fire (Banks et al., 2011; Von Takach et al., 2022; Watson et al., 2012). However, they offer critical resources for individuals to persist; and may facilitate the recolonization of fire-sensitive species into the surrounding burnt area as it recovers (Diffendorfer et al., 2012; Hale et al., 2022; Pinto et al., 2018). Unburnt areas are not only critically important for maintaining fauna populations during a wildfire but also in the post-fire recovery and recolonization phase (Banks et al., 2011; Reynolds et al., 2022; Shaw et al., 2021).

Although unburnt areas can provide refuge habitats for birds and reptiles (Dixon et al., 2018; Reynolds et al., 2022; Robinson et al., 2014), the responses of reptiles to wildfire are complex and are influenced by ecosystem structure, physiology, behaviour, and trophic interactions (Nimmo Dale et al., 2012; Santos et al., 2016; Smith, 2018). The immediate effects of wildfire on fauna communities include mortality and forced emigration (Driscoll et al., 2012; Jolly et al., 2022). However, the most substantial impacts often occur in the weeks and months after the fire due to temporary habitat loss and degradation including a reduction in the availability of food, failure to disperse, reduced reproductive success and increased vulnerability to predation – particularly by invasive species (Andersen et al., 2012; Leahy et al., 2015; Pastro et al., 2011; Santos et al., 2022; Santos & Poquet, 2010).

Understanding the ability of fauna populations to survive and recolonize after wildfire is crucial for developing effective fire management strategies in fire-prone landscapes (Banks et al., 2011). As wildfires become more frequent and intense, unburnt areas are expected to become increasingly rare and valuable (Banks et al., 2011; Meddens et al., 2018; Shaw et al., 2021). Thus, it is important to understand the role of unburnt areas in maintaining and sustaining biodiversity within landscapes (McKenzie et al., 2004; Robinson et al., 2014; Von Takach et al., 2022).

To contribute to understanding the importance of unburnt areas for fauna communities after wildfire, we surveyed reptiles in burnt and unburnt areas within and around the boundary of a large wildfire in subtropical woodlands in eastern Australia. We compared the abundance, richness, and diversity of reptile communities, and the abundance of several common species, between burnt and unburnt areas 1 year after the wildfire. We also examined the relative importance of structural attributes that are relevant to reptiles in driving distribution patterns across this landscape. In the context of this study, we define an unburnt area, or refuge, as an area that remained unburnt within or directly adjacent to the 2012 wildfire scar. We hypothesized that reptile abundance, richness, and diversity would be higher in unburnt

areas due to the presence of key structural resources that are absent or reduced in burnt areas (Dixon et al., 2018).

MATERIALS AND METHODS

Study area and design

The study area is Chesterton Range National Park and adjacent Orkadilla State Forest, located approximately 40 km north of Morven in south-west Queensland, Australia (Figure 1). Together, these two estates conserve approximately 49 880 ha of woodland. The mean minimum and maximum temperatures are 2.6 and 19.7°C in winter and 20 and 34°C in summer (Bureau of Meteorology, 2014). Rainfall averages 570 mm per year and is summer-dominant (November to April), but heavy falls can occur at any time of the year.

The study area borders the Brigalow Belt and Mulga Lands Bioregions. The major vegetation groups are open woodlands dominated by *Eucalyptus populnea* (poplar box), *Acacia harpophylla* (brigalow), and/or *Callitris glaucophylla* (white cypress pine). The topography includes large, rugged sandstone escarpments and undulating hills. Our study sites were all located in woodland dominated by poplar box, which is a fire-adapted ecosystem that has fire-stimulated germination and epicormic buds that are activated during fire events (Walker et al., 1981).

In October 2012, a large wildfire burned an estimated 25 000 ha across the study site over approximately 3 weeks (Figure 1). The wildfire was sparked by lightning strikes in Orkadilla State Forest. It burnt intensely due to high fuel loads from La Niña conditions (i.e., higher than average rainfall)
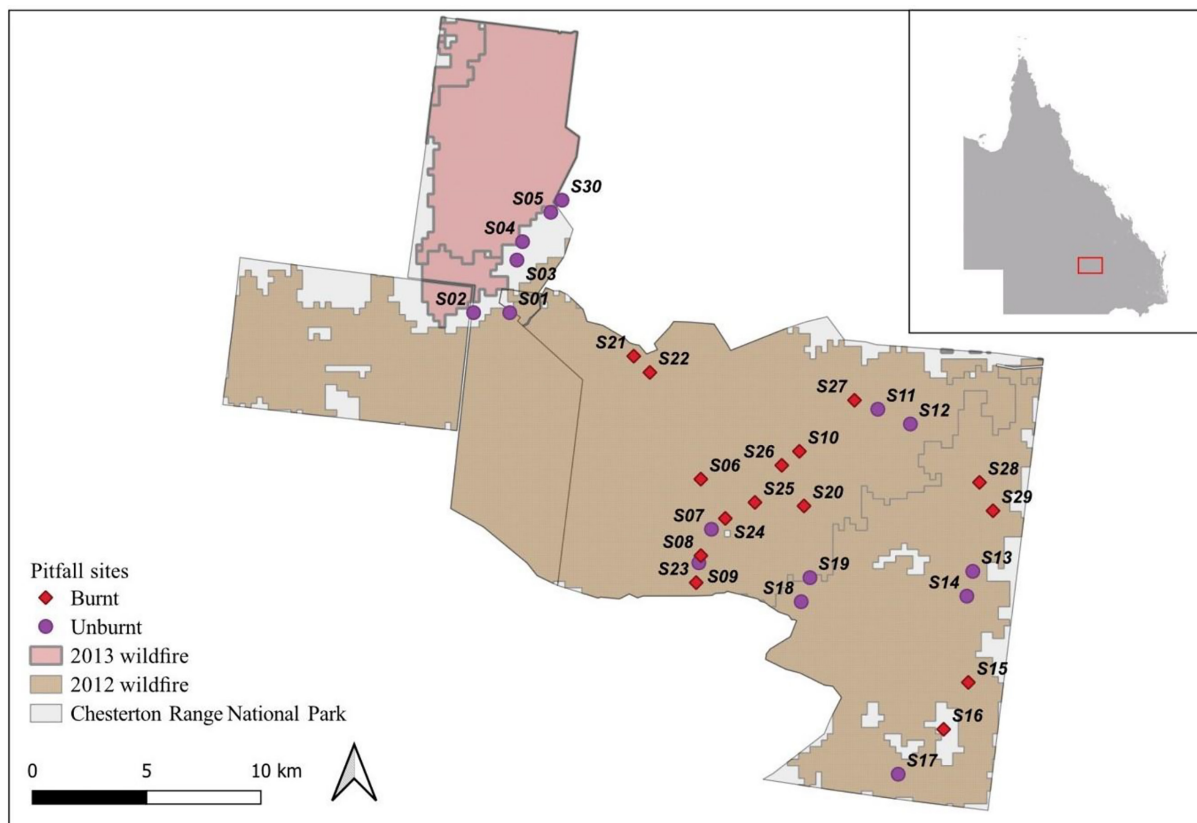

FIGURE 1 Location of burnt (yellow diamond) and unburnt (purple circle) sites in the study area. Red inset shows the location of the study area within Queensland, Australia.

over the previous 2 years, and strong winds at the time of the fire. However, the severity of the wildfire was patchy, with areas of crown scorch, areas with only the understory removed, and completely unburnt areas (SP pers obs.). A second large wildfire burnt a large section of Orkadilla State Forest a year later in October 2013 (Figure 1).

We surveyed 15 sites in burnt areas from the 2012 fire and 15 sites in unburnt areas (Figure 1). Burnt sites were primarily located where fire had burnt the understory and midstory, with areas of crown scorch avoided. Sites were chosen in these burn severities based on availability for selection. We believe this is likely due to our sites being in poplar box dominated woodlands which have a grassy understory and sparse shrub layer. Unburnt sites were in areas that had not been burnt for between 5 and 25 years and were positioned within, and adjacent to, the two wildfire extents. There is limited access across the survey area, so sites were restricted to areas with vehicle tracks. All survey sites were at least 600 m apart.

Reptile surveys

Reptiles were surveyed using passive pitfall traps and active searches. Reptiles were surveyed at each site during three sampling periods over the austral warm season within 1.5 years after both fires: (1) 13–20 November 2013, (2) 17–26 February 2014, and (3) 31 March to 8 April 2014. Each survey site consisted of 4×20 L pitfall traps and two drift fences (7 m long and 30 cm high) (Figure 2) and were surveyed for a minimum of 26 nights. All pitfall traps were installed at least 1 week prior to the first survey, to allow settling after disturbance. For consistency, all pitfall lines were located on a north–south axis. Pitfall traps were checked twice daily, between 6–10 am and 4–7 pm. Captured reptiles were identified to species level, measured [snout-vent length (SVL), weight, total length] and released immediately at the site. Each reptile was given a unique mark with permanent ink on the ventral surface to identify recaptures within a session.

A 10-min timed search was completed at each site between 7 am and 10 am during the 3rd sampling period. Searches were confined to a 20×25 m area centred on the pitfall array (Figure 2). Active search methods included
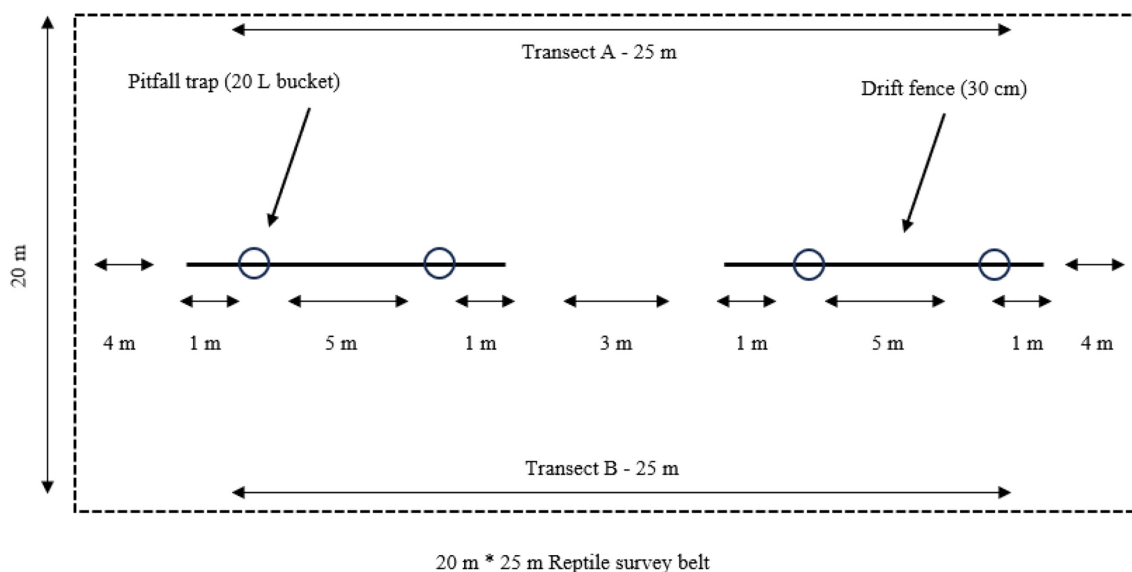

FIGURE 2 The configuration of each survey site. The 20×25 m reptile survey belt (dotted area) is the bounded area for systematic reptile searches and several microhabitats for reptiles described in Table 1. Transects A and B represent vegetation surveys as described in Table 1.

TABLE 1 Ecological attributes that were assessed at each site, method used for their measurement, and the literature used to identify each as likely to be important.

Ecological attribute	Unit	Description	References
Ground vegetation cover	% cover	Mean ground vegetation cover (across 10 samples). Estimating the % of vegetation cover in a 1 m² quadrat located every 5 m along two 25 m transects (Figure 2)	Bruton et al. (2016), Catling et al. (2001), Cogger (2018), Garden et al. (2007), and McElhinny et al. (2006)
Canopy cover	% cover of foliage >15 m	Mean canopy cover (across 10 samples) was visually estimated by using a 5 cm wide and 50 cm long PVC pipe every 5 m along two 25 m transects	Coops & Catling (2000) and McElhinny et al. (2006)
Number of logs	Count	Fallen timber >30 cm long and >5 cm diameter in a 20×25 m survey belt	Cogger (2018), Garden et al. (2007), and McElhinny et al. (2006)
Number of hollow logs	Count	Fallen timber with hollows of >3 cm diameter in a 20×25 m survey belt	Bruton et al. (2016), Cogger (2018), Garden et al. (2007), and McElhinny et al. (2006)
Standing dead trees	Count	Number of standing dead trees (DBH >25 cm) in a 20×25 m survey belt	Cogger (2018), Garden et al. (2007), and McElhinny et al. (2006)
Termite mounds	Count	Number of terrestrial termite mounds in a 20×25 m survey belt	Bruton et al. (2016) and Garden et al. (2007)
Ground burrows	Count	Number of burrows >3 cm diameter within a 20×25 m survey belt	Bruton et al. (2016) and Garden et al. (2007)
Shrub cover	%	Mean of 10 values, using a 1 m² canvas gridded into 2.5 cm×2.5 cm cells at 1 m above ground. Number of gridded cells covered by vegetation shadow every 5 m along two 25 m transects	Catling et al. (2001), Garden et al. (2007), and McElhinny et al. (2006)
Distance to burn perimeter	m	Distance to the nearest are burnt in 2012	Diffendorfer et al. (2012)
Structural complexity	Score (0–18)	Total structural complexity using a 0–3 scoring system for each of six structural elements	Bruton et al. (2016) and Coops & Catling (2000)
Burn status	Burnt/ unburnt	Burnt/unburnt in the 2012 wildfire	Banks et al. (2011)

visual scanning and turning over logs, rocks, and leaf litter. Individuals were not captured or marked during active searches.

Ecological attributes

Based on available literature, eight structural attributes and one site context attribute were identified as potentially important for local reptiles (Table 1). Structural attributes were measured at each site using a combination of line transects and plot counts. Termite mounds, standing dead trees, logs, hollow logs, hollow trees, and ground burrows were all counted within a 20×25 m quadrat centred on each site (Figure 2). The quadrat size was chosen based on Bruton et al. (2013) and Garden et al. (2007) (Table 1). The percentage of ground vegetation cover, shrub cover, sub-canopy cover, and canopy cover were measured every 5 m along two 25 m long transects at each site (Figure 2). Canopy and sub-canopy cover were estimated visually using a vertically-held 5 cm wide and 50 cm long PVC pipe (Cox et al., 2000). Percentage ground cover was measured in a 1 × 1 m quadrat every 5 m along the two 25 m transects and shrub cover was measured using a 1 m² canvas to count the number of gridded cells that were obscured by shrub cover (Garden et al., 2007). Structural attributes were measured during the second survey period.

The approximate distance to nearest burnt location was measured on site for each unburnt site.

We generated a structural complexity score for each site using a 0–3 scoring system for each of six structural elements, where a score of 0 meant the element was not present, and scores of 1–3 represented increasing amounts of the element (Coops & Catling, 2000). The six structural elements that contributed to the structural complexity score were shrub cover, number of logs, number of hollow logs, ground cover, number of termite mounds, and the number of standing dead trees, all of which can influence reptile communities (Bruton et al., 2016; Fischer et al., 2004; Garden et al., 2007). Scores for each of the six structural elements were summed to derive the structural complexity score (Table 1).

Statistical analyses

We conducted three analyses to assess the importance of unburnt areas for reptiles. First, we used generalized linear models to test the effects of burn status on species richness, total abundance, diversity, and each of the three most common species. Second, we used multivariate techniques to determine whether there was a community shift in response to burn status, and to identify species driving this change. Third, we used generalized linear models to assess relationships between ecosystem variables and total abundance, richness, diversity, and the abundance of the three most common reptile species (>20 captures). Results for all three sampling periods were pooled for each site for analyses due to small sample sizes within each sampling period.

Burn status: Community abundance, richness and diversity

To assess the effect of burn status we fitted generalized linear models assuming a negative binomial distribution for total abundance and species richness, and a Gaussian distribution for species diversity. Species diversity was calculated using Simpson's Diversity Index, which considers the relative abundance of species at each site (Morris et al., 2014). We considered model terms statistically important if the 95% confidence intervals did not include zero. Due to the high number of rare species, we additionally used chao estimators to examine reptile richness and diversity.

Burn status: Community composition

We used both parametric and non-parametric multivariate methods in stage two to assess the effect of burn status on community composition. First, we fitted a parametric multivariate linear model in the R package mvabund (Davis et al., 2016; Wang et al., 2022) using a species × site abundance matrix. Multivariate p-values were calculated using parametric bootstrapping based on 1000 residual resamples, using a negative binomial error distribution to determine if there was an overall change in community composition. We then used univariate p-values to determine if individual species were driving any community response to burn status. We report unadjusted univariate p-values because there are many species and the power to detect differences is low (Davis et al., 2016). However, the results are interpreted with caution (Nakagawa & Schielzeth, 2013). For the multivariate analysis, we excluded six species that were recorded at only one site.

Secondly, we conducted a non-parametric permutational analysis of variance (PERMANOVA; anosim function in vegan) using a Bray–Curtis distance

matrix to compare community composition in burnt and unburnt areas. We used non-metric multidimensional scaling to visualize differences between burn treatments. We tested both transformed and untransformed data and found that the results were similar, so we report the results from the untransformed data. We also conducted a similarity percentage analysis (SIMPER) to identify the species that contributed the most to differences observed between treatments, and this was based on 1000 permutations. This analysis was undertaken in the vegan package for the statistical program R (R Core Team, 2023), in the functions 'metamds' and 'simper' (Orkansen & Simpson, 2017).

Ecological attributes

For the final stage of analysis, we fitted a series of generalized linear models to assess relationships between ecological attributes and reptile abundance, richness, diversity and the three most common reptile species: *Lygisaurus foliorum* (tree-base litter-skink), *Morethia boulengeri* (Boulenger's snake-eyed skink), and *Carlia munda* (shaded-litter rainbow-skink). Prior to analyses, we tested for correlations among predictor variables using Spearman's rank correlation. For highly correlated pairs of these predictor variables ($R > 0.6$), we excluded the least influential variable from the analysis for each response variable. Predictor variables included burn status, structural complexity, number of logs, ground cover, shrub cover, and distance to the nearest part of the burn perimeter. To allow direct comparisons between the parameter estimates, the predictor values were scaled and centred prior to analysis (Gelman, 2008). Interactions among predictor variables were not anticipated or tested. We used Akaike's information criterion (AIC) corrected for small sample size to rank all models, with the lowest AICc considered the best model. We considered all models within $\Delta AICc < 2$ of the best model to be of equal weight and performance used model averaging to determine the strength and direction of the effects. Finally, we considered variables with parameters whose 95% confidence intervals did not intersect zero to be statistically important (Burnham & Anderson, 2010). Models of reptile species abundance and richness were fitted using the negative binomial distribution, and models of reptile diversity assumed a Gaussian distribution using the glm.nb and glm functions respectively in the package lme4 (Bates et al., 2015). All analysis was undertaken in the statistical program R (R Core Team, 2023).

RESULTS

Overall, 241 individuals from 36 species were captured or detected. We captured 193 individual reptiles from 35 species over 3120 trap nights for a total trap rate of 6.2%. An additional 48 individuals from 12 species were detected during 5h of active searching. One species, *Varanus varius* (lace monitor) was only detected by active searching (see Table S1 in Supplementary Appendix for further information). Abundance and richness at each site ranged from 2 to 20 individuals, and 2–11 species, respectively.

Burn status: Community abundance, richness and diversity

Reptile richness ($\beta = 0.32$, 95% CI: 0.01, 0.64) and diversity ($\beta = 0.07$, 95% CI: 0.01, 0.15) were higher in unburnt compared to burnt sites (Figure 3). Mean total abundance may have been greater at unburnt sites with more survey effort given the confidence intervals only marginally overlapped zero
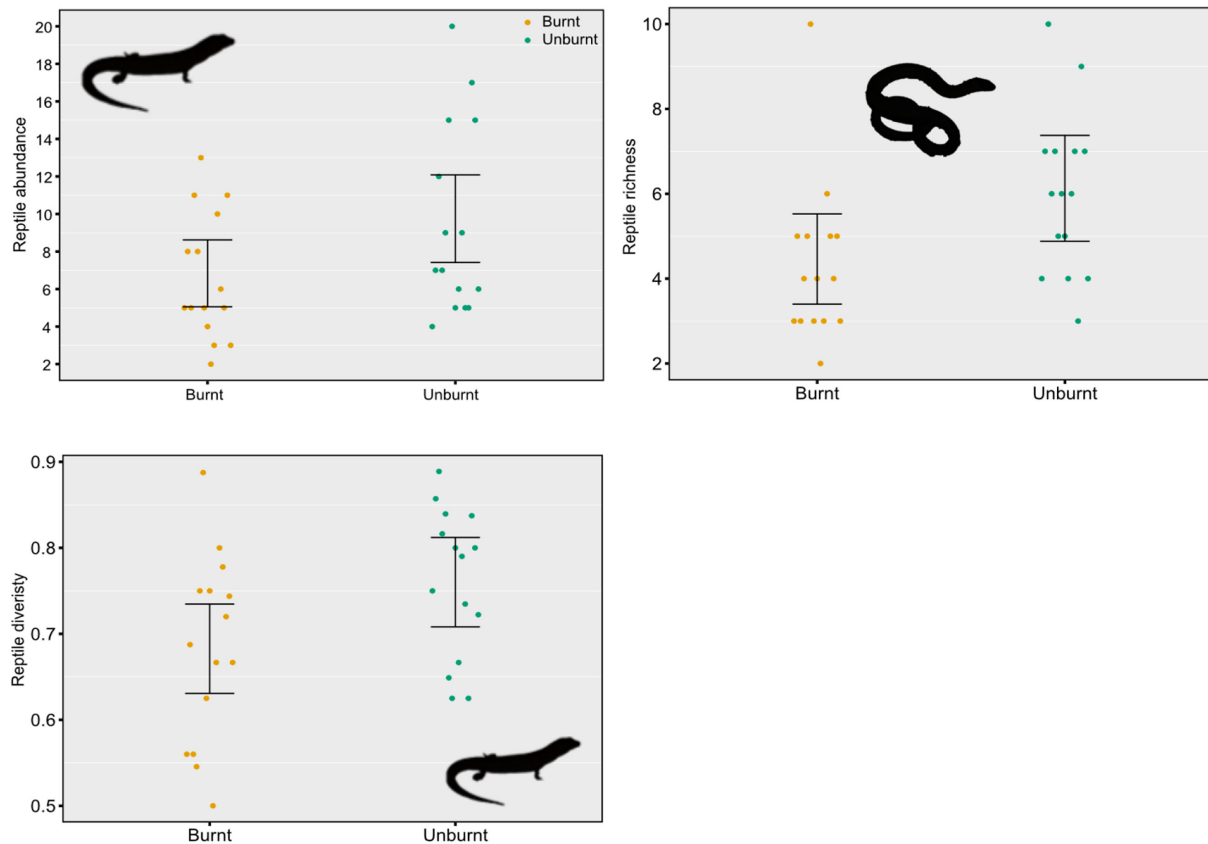
FIGURE 3 The predicted mean abundance, richness, and diversity of reptiles at burnt and unburnt sites. The error bars represent the 95% confidence intervals for the predicted counts and the dots represent the observed data.

($\beta = 0.36$, 95% CI: −0.0002, 0.72; Figure 3). Chao1 estimators were considerably higher for burnt and unburnt sites than pure counts (mean = 6.61, 95% CI: 4.5–8.28 and mean = 9.33, 95% CI: 7.67–10.98) (Figure S1 in Supplementary Appendix). Rarefaction curves suggest that burnt and unburnt areas were approaching an asymptote (Figure S2 in Supplementary Appendix). There were significantly more *L. foliorum* detected in unburnt areas ($\beta = 1.79$, 95% CI: 0.93, 2.86), whereas there were no differences in the abundance of *M. boulengeri* and *C. munda* between burnt and unburnt areas ($\beta = -0.52$, 95% CI: −1.24, 0.17 and $\beta = 0.40$, 95% CI: −1.32, 2.11), respectively.

Burn status: Community composition

Reptile communities differed significantly between burnt and unburnt sites (NP: $F = 57.11$, $p = 0.0$) and (P: Stress 0.2, Global $R = 0.173$, $p = 0.003$, Figure 4). In the parametric analysis, *L. foliorum* ($p = 0.002$) and *Diporiphora nobbi* ($p = 0.008$) were both more common in unburnt sites, whereas *Ctenotus allotropis* ($p = 0.023$) was more common in burnt areas. In the non-parametric analysis, *L. foliorum*, *M. boulengeri*, *C. munda*, *Heteronotia binoei* (Bynoe's gecko) and *D. nobbi* were the primary contributors to differences between the two ecosystem states, collectively contributing 50.3% of the difference. Only 5 out of 35 detections of *L. foliorum* were in burnt sites, *D. nobbi* was never recorded in burnt sites ($n = 7$), and *C. allotropis* was only found in burnt sites ($n = 4$). Twelve other species, with too few captures for individual analysis, were only found in unburnt areas. See Tables S2 and S3 in Supplementary Appendix for SIMPER and mvabund results.

Influence of ecological attributes

Number of logs was the most important explanatory variable for variation in reptile richness and diversity, having a positive influence on these variables (Table 2 and Figure 5). Reptile abundance may also be positively influenced by the number of logs, but there were two other well supported models for this response variable, namely the null model and ground cover complexity. Yet ground cover complexity was not an influential variable, with the confidence interval intersecting zero (Table 2).
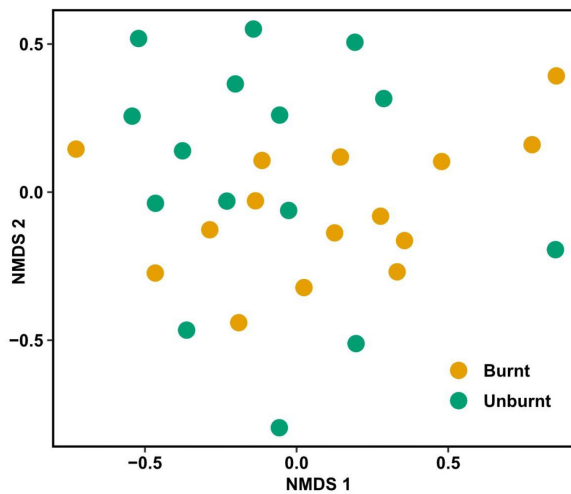

FIGURE 4 NMDS ordination of reptile species composition of 15 burnt and 15 unburnt sites (Stress 0.2).

TABLE 2 Influence of structural attributes on reptile communities and species abundances from model-averaging of the top-ranked models for each response variable.

Response	Variable	Estimate	95% CIs
Abundance	Number of logs	0.18	−0.00, 0.37
	Ground cover complexity	0.12	−0.06, 0.30
Richness	Number of logs	0.20	**0.04, 0.34**
Diversity	Number of logs	0.05	**0.02, 0.09**
Lygisaurus foliorum	Ground cover complexity	0.65	**0.14, 1.15**
	Distance to fire scar	0.02	**0.01, 0.04**
	Number of termite mounds	−0.53	−1.11, 0.05
	Number of logs	0.56	**0.10, 1.02**
Morethia boulengeri	Ground cover	−0.54	**−0.88, −0.19**
	Number of logs	0.36	−0.12, 0.83
	Distance to fire scar	−0.01	−0.04, 0.01
	Ground cover complexity	0.18	−0.17, 0.53
	Number of termite mounds	0.15	−0.15, 0.45
	Shrub cover	−0.23	−0.65, 0.19
Carlia munda	Canopy cover	0.70	**0.35, 1.05**
	Number of logs	−0.61	**−1.20, −0.01**
	Number of termite mounds	−0.37	−0.78, 0.04
	Shrub cover	−0.71	−1.53, 0.11

Note: Cells highlighted in bold indicate confidence intervals that did not intersect zero.
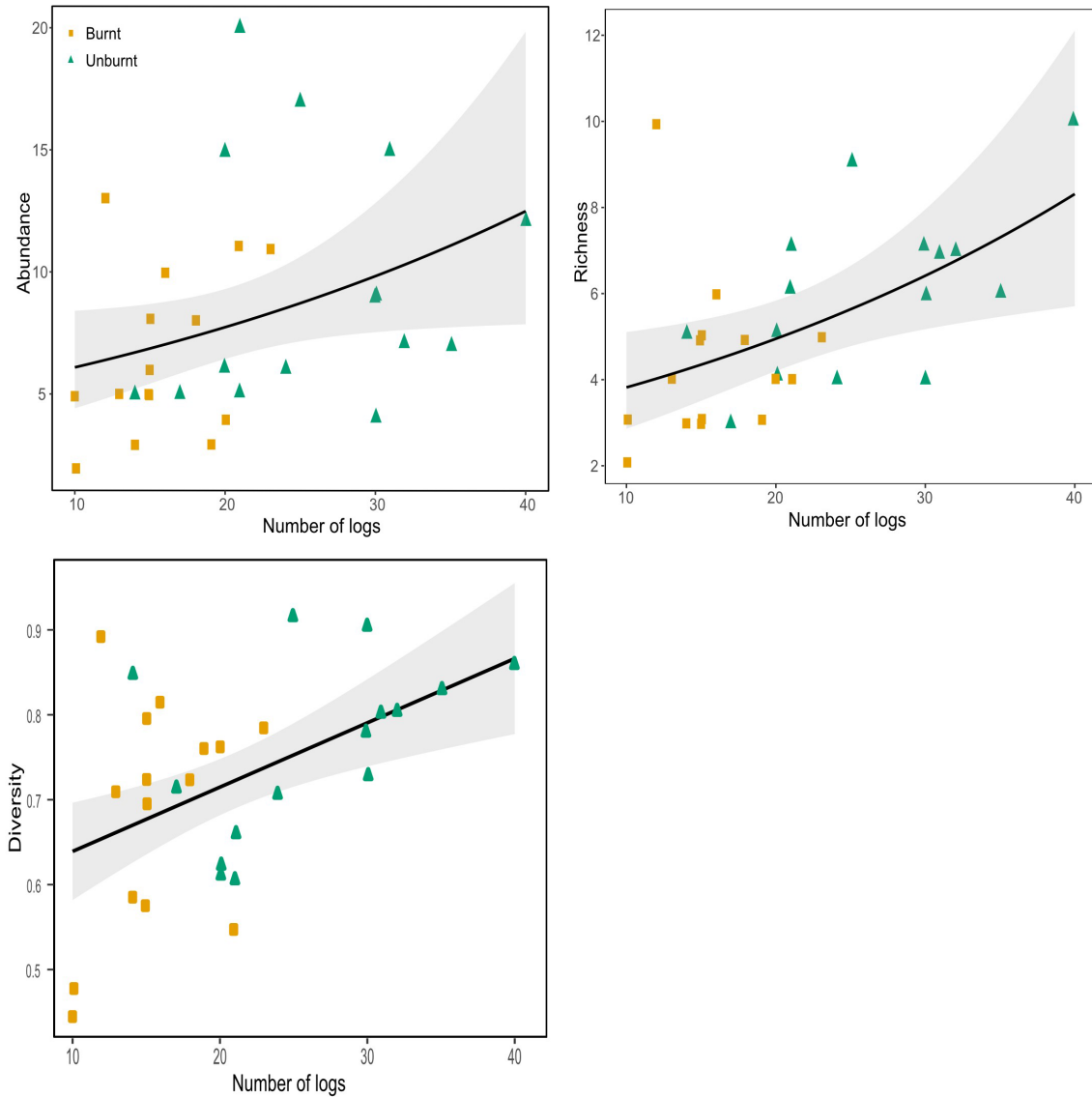
FIGURE 5 The responses of reptile abundance, richness, and diversity to the number of logs. The number of logs was the most important variable of all three models. The data points are the observed data, the solid lines are the model estimates and grey shading is the 95% confidence intervals.

For a full list of models, see Table S4 in Supplementary Appendix. See Figure S3 in Supplementary Appendix for the raw data of each habitat attribute measured.

Three species were captured in sufficient numbers to assess the influence of ecological attributes: *L. foliorum*, *M. boulengeri* and *C. munda*. Eight structural and contextual variables were well supported across all models and five of these relationships were significant (Table 2). The abundance of *L. foliorum* was positively associated with number of logs, distance to wildfire scar and ground cover complexity (Table 2 and Figure 6). The abundance of *M. boulengeri* was negatively associated with ground cover, and the abundance of *C. munda* was positively associated with canopy cover but negatively associated with number of logs (Table 2 and Figure 6). For a full list of models, see Table S4 in Supplementary Appendix.
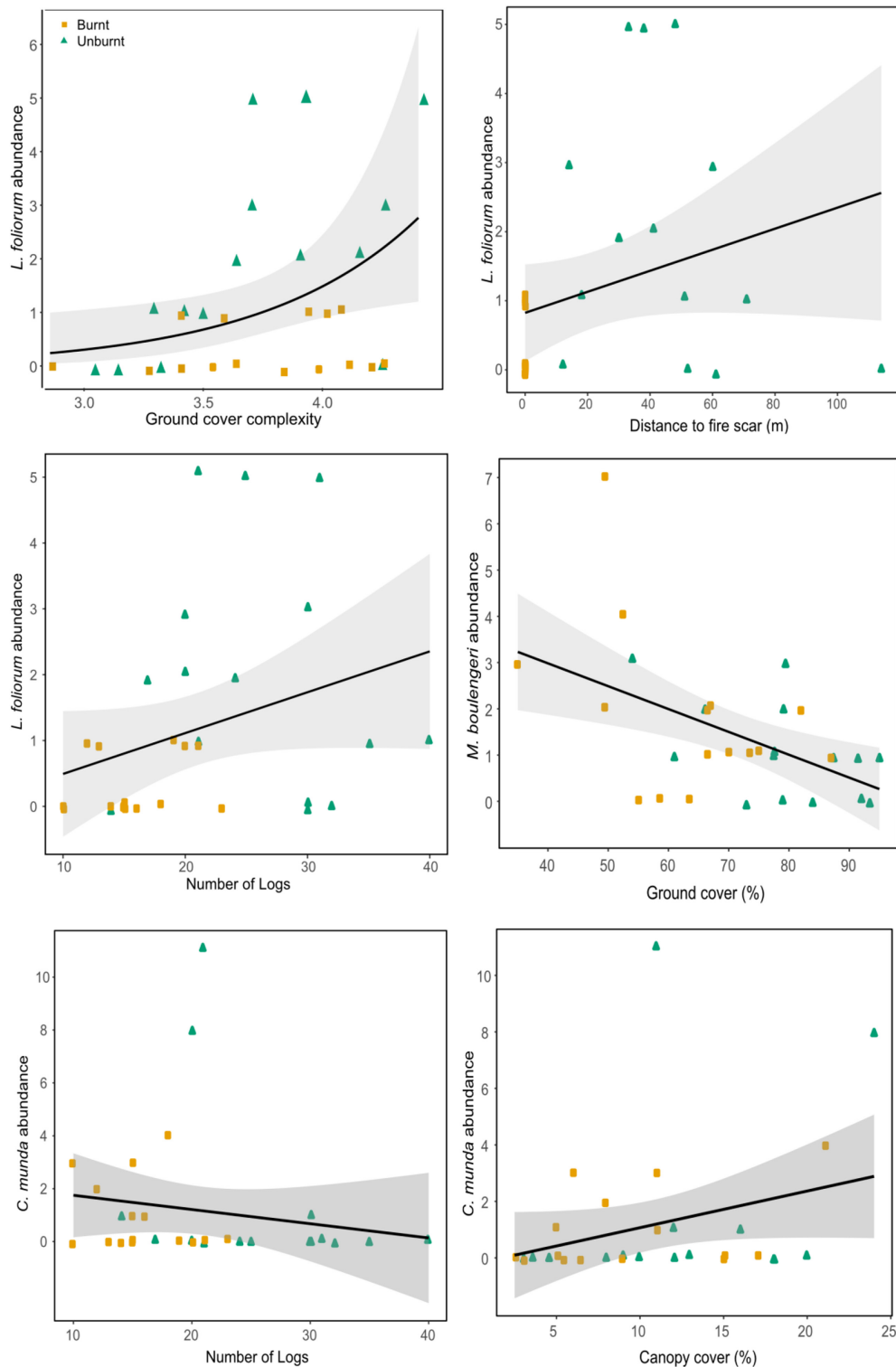
FIGURE 6 The response of abundance of three reptile species to variables in the GLMs whose model-averaged confidence intervals did not overlap zero. The data points are the observed data, the solid lines are the averaged model estimates and grey shading is the 95% confidence intervals.

DISCUSSION

Our study clearly demonstrates that unburnt areas are valuable for sustaining reptiles in a wildfire-prone landscape. One year after an extensive wildfire, unburnt areas contained a higher richness and diversity of

reptiles, and possibly higher abundance. We found that reptile communities inhabiting burnt and unburnt areas were distinct from each other. Our findings are consistent with research from temperate landscapes and subtropical woodlands, concluding that more reptiles species persist in longer unburnt areas (Dixon et al., 2018; Driscoll et al., 2012; Partridge et al., 2023). The amount of woody debris, a feature often depleted by fire, was the strongest driver of differences in reptile communities between burnt and unburnt patches. Overall, this study suggests that reptile communities in subtropical woodlands benefit from the retention of long unburnt vegetation, however, given species composition differed between long unburnt and burnt areas, maintaining a diverse reptile community across a fire-prone woodland landscape also requires recently burnt areas (Dixon et al., 2018; Driscoll & Henderson, 2008; Valentine et al., 2012).

Reptile community response to fire

We found that reptile communities differed considerably between unburnt and burnt areas in poplar box woodlands. Unburnt areas had a higher diversity of reptiles, and several species were found in these areas but not in burnt areas. Our results are consistent with previous findings from semi-arid grasslands, tropical savannas, and temperate and sub-alpine forests and banksia woodlands (Dixon et al., 2018; Hu et al., 2013; Masters, 1996; Valentine et al., 2012). The effects of wildfire on reptile communities are primarily due to the retention of structural attributes in unburnt areas that are depleted or lost in burnt areas (Valentine et al., 2012). Unburnt areas in this study were structurally complex with deep leaf litter, ample log cover, and extensive ground cover, all of which provide important shelter and thermoregulation resources for a diversity of reptile species. Thirteen species were only found in unburnt areas whereas only three of 36 (total) species were exclusively detected in burnt areas, suggesting that most species found in burnt areas also prosper in unburnt areas.

Mean reptile abundance may be higher in unburnt areas, but we were unable to confirm this effect due to sampling limitations. Similar results have been found in Australia and other fire-prone environments (Santos et al., 2016; Smith et al., 2012). The abundance of reptiles in burnt areas is likely driven by the abundance of common generalist species that are well-adapted to open areas. They can exploit these open burnt areas and attain large population sizes due to the lack of competition with other species. This is consistent with previous studies where several burrowing and open area specialists increased substantially in post-fire environments (Doherty et al., 2015; Driscoll & Henderson, 2008; Smith et al., 2012). Our study was confined to poplar box woodlands, and it may be that fire adapted reptiles inhabiting this vegetation type can respond rapidly to increase their populations post-fire.

One of the three common species assessed for species-specific patterns (*L. foliorum*) was more abundant in unburnt sites. Our results are similar to the findings from Partridge et al. (2023) which also found this generalist species had a strong negative association with wildfire. This species inhabits a variety of ecosystem types (Wilson, 2022), and its distribution across landscapes is driven by the availability of structural attributes such as course woody debris and ground cover (Abom & Schwarzkopf, 2016; Singh et al., 2002). Both these attributes were depleted in burnt areas (see Figure S1 in Supplementary Appendix), which likely drove the response of *L. foliorum* to wildfire in this study.

Supporting this, Singh et al. (2002) found no difference between *L. foliorum* abundance before or after a planned burn where many of the structural attributes remained intact.

Influence of structural attributes

The availability of site-level structural attributes is an important consideration for understanding variation in reptile community responses (Doherty et al., 2015; Valentine et al., 2012). While the burn status was an important predictor of reptile community richness and diversity, and the abundance of *L. foliorum*, several structural variables were also highly correlated with reptile community richness and diversity, and the abundance of all three of the most common reptile species. Fire-induced structural changes have consistently been found to affect reptile communities (Dixon et al., 2018; Santos et al., 2016; Valentine et al., 2012). Our study is broadly consistent with previous findings – both in Australia and elsewhere – that reptile richness and diversity increase positively with the availability of coarse woody debris (Bruton et al., 2016; Manning et al., 2013; Santos & Poquet, 2010). Coarse woody debris provides reptiles with shelter, variability in thermal conditions to optimize thermoregulation, and habitats for invertebrate prey (Fischer et al., 2004; MacNally et al., 2001; Santos & Poquet, 2010). Our results show that the availability of coarse woody debris in the form of fallen logs is a critical resource for maintaining diverse reptile communities within woodland landscapes post-fire.

In this study, reptile species demonstrated highly individual responses to structural variables. The positive influence of number of logs, structural complexity, and distance to fire scar on the abundance of *L. foliorum* is comparable to other studies that have found this species to be positively associated with woody debris and ground cover, and negatively affected by wildfire (Abom & Schwarzkopf, 2016; Partridge et al., 2023; Singh et al., 2002). The lack of a strong relationship between *M. boulengeri* and woody debris, and a negative relationship of that species with ground cover, is interesting. Elsewhere, *M. boulengeri* is positively associated with woody debris and shrub cover (Bruton et al., 2016; Fischer et al., 2004; Michael et al., 2004). It has also been found to have a negative association with time since fire (i.e., not present in burnt areas immediately after fire) in mallee ecosystems (Nimmo Dale et al., 2012), whereas in this study it was more likely to be found in burnt areas. However, this is not so unusual given several other widely-distributed reptile species also vary in their response to fire across their range (Nimmo Dale et al., 2012). The skink *C. munda* was found to be positively associated with canopy cover and negatively associated with log cover, which is consistent with Trainor and Woinarski (1994).

Management implications

Fire management for biodiversity conservation typically involves creating a mosaic of different fire age classes in the landscape to cater for different responses to fire by different species, i.e. 'pyrodiversity' (Jones & Tingley, 2022; Taylor et al., 2012) and/or maximizing the extent and availability of old-growth vegetation with a long fire interval (Davis et al., 2016; Doherty et al., 2015). Our study highlights that unburnt areas play a role in supporting diverse reptile communities in subtropical woodlands, consistent with the latter objective. A key recommendation

from this study is that fire management programs in fire-prone woodland landscapes should aim to support the development and retention of long unburnt areas that provide refuge for reptiles and potentially source populations for dispersing individuals as surrounding areas recover their pre-fire attributes (Senior et al., 2023). Our findings also support implementing regular burns to ensure a mosaic of recently burnt areas continues to support species that are well-adapted to recent fire. This combination of advice is consistent with recommendations for conserving other fauna in fire-prone woodlands, including birds (Reynolds et al., 2022) and mammals (Leahy et al., 2015).

This study has further demonstrated that retaining key structural attributes, primarily an abundance of fallen logs, is critical for retaining diverse reptile communities and resilient reptile populations within fire-prone woodlands. Strategic management of fire is required in these landscapes to maximize the development and retention of these structural attributes. Ongoing research that examines the importance of time since fire and different fire intensities on reptile communities is required to facilitate the necessary use of prescribed burns to reduce overall fire risk while supporting ensuring fire management supports diverse and abundant reptile (and other ecological) communities. This includes the ability to identify to maintain a landscape that contains diverse fire age classes while still protecting longer unburnt vegetation.

AUTHOR CONTRIBUTIONS

Jon-Paul Emery: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); visualization (equal); writing – original draft (equal). **Tim S. Doherty:** Formal analysis (equal); writing – review and editing (equal). **Melissa J. Bruton:** Methodology (equal); supervision (equal); writing – review and editing (equal). **Stephen Peck:** Conceptualization (equal); investigation (equal); supervision (equal); writing – review and editing (equal). **Martine Maron:** Conceptualization (equal); methodology (equal); project administration (equal); supervision (equal); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT
The data and r scripts used in this study can be found on the online repository, figshare: https://doi.org/10.6084/m9.figshare.25903789.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.