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RESEARCH ARTICLE

Fire severity influences the post-fire habitat structure and abundance of a cool climate lizard

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Abstract

In the spring and summer of 2019–2020, the 'Black Summer' bushfires burned more than 97000 km^2 of predominantly *Eucalyptus* dominated forest habitat in eastern Australia. The Black Summer bushfires prompted great concern that many species had been imperilled by the fires. Here, we investigate the effects that fire severity had on the habitat and abundance of a cool climate lizard *Eulamprus tympanum* that was identified as a species of concern because 37% of its habitat was burnt in the Black Summer bushfires. We quantified habitat structure and the abundance of *E. tympanum* at sites which were unburnt, burnt at low severity and at high severity 10, 15 and 23 months after the fires. Our classification of fire severity based on scorch height and canopy status corresponded well with the Australian Government Google Earth Engine Burnt Area Map (AUS GEEBAM) fire severity layer. Ten months after the fires, sites burnt at high severity had less canopy cover, more bare ground and less fine fuel than sites burnt at low severity or unburnt sites. The abundance of *E. tympanum* varied with survey occasion and was greatest during the warmest sampling period and lowest during the coolest sampling period. The abundance of *E. tympanum* was consistently lower on sites burnt at high severity than sites burnt at low severity or unburnt sites. Our findings show that higher severity fires had a greater effect on *E. tympanum* than low severity fires. Our results suggest that *E. tympanum* were likely to have persisted in burnt sites, with populations in low severity and unburnt sites facilitating population recovery in areas burnt at high severity. Our results also suggest that wildfire impacts on *E. tympanum* populations will increase because the frequency and extent of severe fires are expected to increase due to climate change.

KEYWORDS
Black-summer bushfires, fire, fire severity, lizard, mega-fire, reptile

INTRODUCTION

Globally there is concern that climate change is driving shifts in fire regimes and in particular that the frequency, severity and extent of fires is increasing (Bowman et al., 2021; Canadell et al., 2021). For example, in the western United States, the onset of the annual fire season now occurs earlier in the calendar year due to the onset of warmer weather (Westerling et al., 2006). In Australia, extreme drought conditions precipitated the 'Black-summer bushfires of 2019-2020' which were the most extensive fires recorded since British colonization of Australia in 1788 (Abram et al., 2021; Collins et al., 2022). Overall, there is widespread concern that rising temperatures and more severe droughts associated with climate change will increase the frequency, extent and severity of wildfires in the future (Abram et al., 2021; Collins et al., 2022; Nolan et al., 2021).

Fire severity is widely appreciated to be a factor influencing the impacts of fires on wildlife and their habitats (Etchells et al., 2020; Jolly et al., 2022). For example, hazard reduction fires which are normally conducted during cool weather conditions are considered to be less severe and less harmful to wildlife than wildfires which typically consume more fuel and burn at higher temperatures (Jolly et al., 2022; Pastro et al., 2011; Price et al., 2022). However, there is less appreciation that the effects of fire on vegetation and wildlife within a single wildfire event may not be uniform owing to spatial variation in fire severity due to weather conditions, topography and fuel load (Bradstock et al., 2010; Etchells et al., 2020; Law, Gonsalves, Burgar, et al., 2022).

In the spring and summer of 2019–2020, a series of wildfires along the east coast of Australia burned more than 97 000 km^2 of predominantly *Eucalyptus* forest habitat (Collins et al., 2021). The Black Summer bushfires were remarkable not just for their extent but also for the vast area that was burnt at high severity (Bowman et al., 2021; Collins et al., 2021). Extremely low levels of humidity and moisture in the vegetation facilitated fires of extreme heat (Abram et al., 2021). However, there was considerable spatial variability in the severity of the fires due to topography, species composition of the forests and firefighting efforts (Gibson et al., 2020).

During the Black Summer fire event, the Australian Government commissioned a risk assessment of the impacts of the fires on vertebrates and plants (Legge et al., 2020). The desktop-based assessment process ranked fire impacts on individual species by considering the extent of known habitat burned, life-history traits and post-fire responses (Legge et al., 2020; Legge, Woinarski, et al., 2022). The southern-water skink, *Eulamprus tympanum* was identified as a species of concern in these desktop analyses because more than 37% of its distribution was estimated to have been burnt (Figure 1; Legge et al., 2020; Legge, Woinarski, et al., 2022). *Eulamprus tympanum* is a live-bearing cool-climate skink with a broad distribution in south-eastern Australia. *Eulamprus tympanum* is currently classified as least concern by the IUCN (Hutchinson et al., 2022). However, like many other cool-climate reptiles, very little is known about the post-fire response of *E.tympanum*, and hence, there was concern that the species could become threatened by the fires (Legge et al., 2020; Legge, Woinarski, et al., 2022).

Here, we report the results of field surveys conducted 10–23 months post fire to investigate the impacts that wildfires have had on the habitat structure and abundance of *E. tympanum* inhabiting the Boyd Plateau, near Sydney, Australia. Our study had two aims. First, because our analyses of the effects of fire severity on the habitat and abundance of *E. tympanum* were centred around a field-based classification of fire severity, we verified our classification of fire severity by comparing it with the fire severity classification of the Australian Government's Australian Government Google Earth Engine Burnt Area Map (AUS GEEBAM) fire severity layer derived from satellite imagery (Department of Environment and Water, 2020). Second, we compared the effect of fire severity on the habitat and abundance of *E. tympanum* by comparing habitat structure and the abundance of skinks in unburnt areas with areas subject to high and low severity fires. To determine if the effects of fire severity on *E. tympanum* were consistent over time, we conducted surveys for lizards on three survey occasions 10, 15 and 23 months post fire.

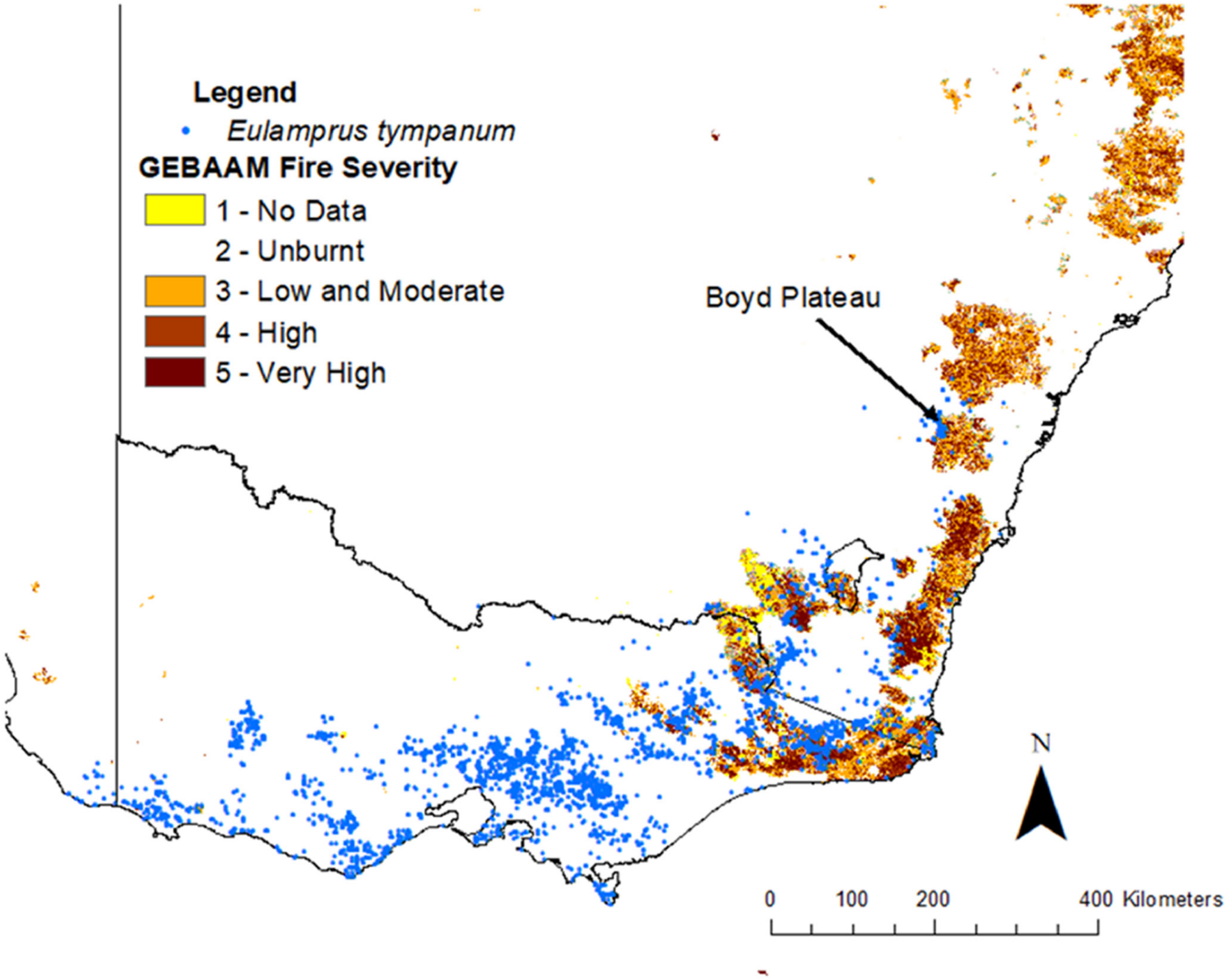

FIGURE 1 Map showing locality records for *Eulamprus tympanum* (blue dots) from the Atlas of Living Australia and the AUS GEEBAM fire severity index for areas burnt in the 2019–2020 fire season derived from analysis of Sentinel 2 satellite imagery in the Google Earth Engine. The arrow indicates the location of the Boyd Plateau where this study was undertaken.

METHODS

Study region

The study was conducted on the Boyd Plateau in Kanangra Boyd National Park which was extensively burned during the Black Summer Bushfires between December 2019 and January 2020 (Figure 2). The Boyd Plateau is approximately 11 000 ha in area and has an elevation of 1060–2000 m and is near the northern limit of the distribution of *E. tympanum* (Figure 1). The Boyd Plateau has a cool moist climate and has low average annual temperatures (mean annual temperature = 9°C) and relatively high annual rainfall (mean annual rainfall = 930 mm). Snow occurs regularly in the winter months, but quickly melts. The vegetation is predominantly eucalypt forest dominated by mountain gum (*Eucalyptus dalrympleana*) and snow gum (*Eucalyptus pauciflora*. The understorey is dominated by grasses, particularly, *Poa seiberana*, *Poa labillardierei* and *Poa tenera* (Black, 1982). The shrub layer is sparse and dominated by *Acacia obliquinervia*, *Acacia melanoxylon*, *Exocarpos cupressiformis* and *Lomatia myricoides* (Black, 1982).

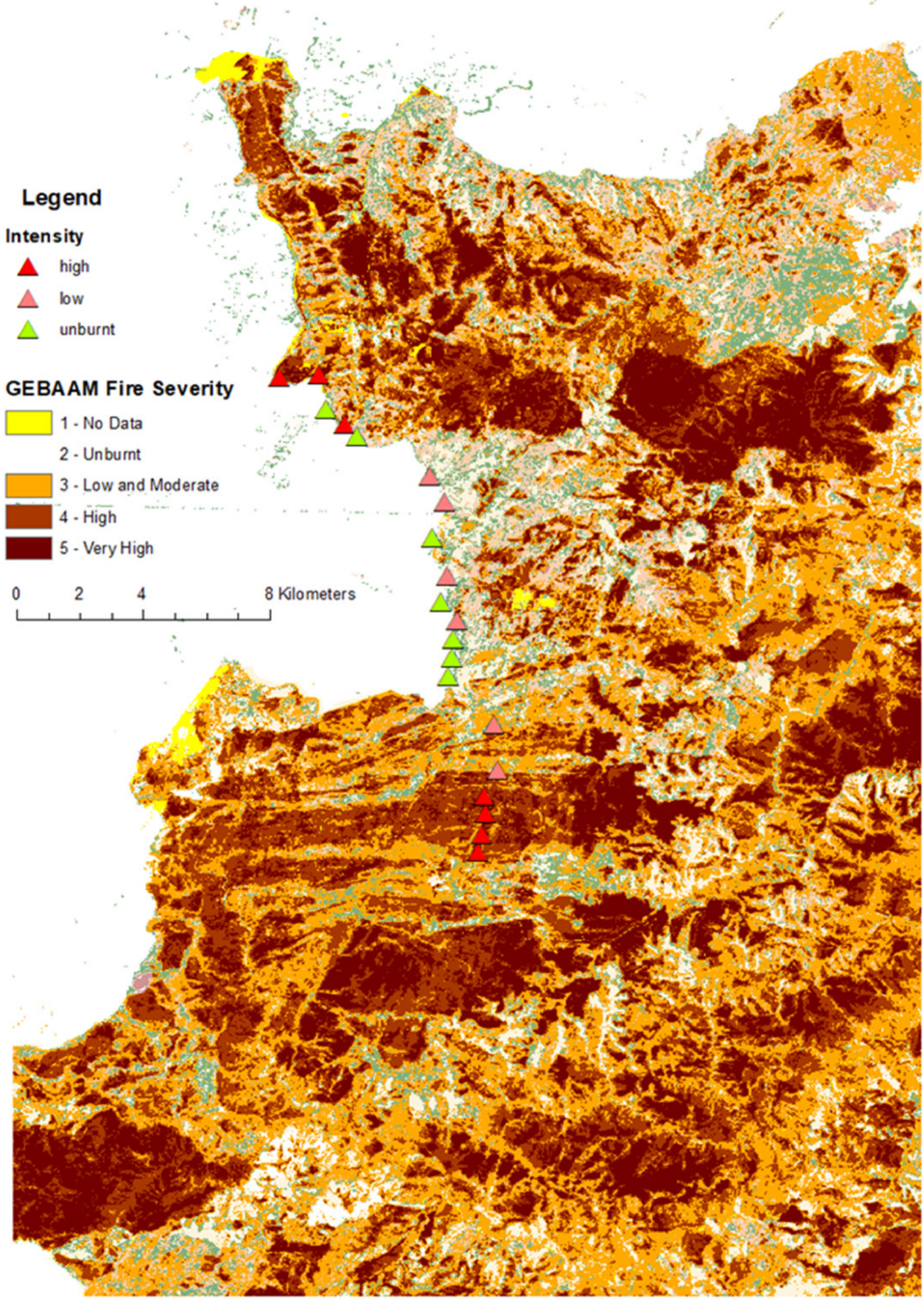

FIGURE 2 Location of the study sites where surveys for *Eulamprus tympanum* and habitat variables were measured on the Boyd Plateau. The study sites are categorized by a field-based measurement of fire severity and are overlaid on the AUS GEEBAM layer of fire severity.

Experimental design

Following the 2019–2020 wildfires, we compared abundance of *E.tympanum* derived from active searches of 1 ha (100 × 100 m) sites which we classified as being unburnt ($n = 7$) or subject to high ($n = 7$) or low severity ($n = 6$) fires (Figure 2). The location of sites was determined by the availability of suitable forest habitat in the fire severity categories described above along access roads. Sites were located at least 50 m from roads and were spaced at least 500 m apart. Because of safety concerns due to falling timber in post-fire environments, sites were established within 200 m of roads to minimize the time that workers had to spend under the canopy. Surveys were conducted on three occasions, November 2020, April 2021 and November 2021.

Field-based classification of fire severity

During the first round of surveys conducted in November 2020, sites were classified as being unburnt or burnt at high or low severity. Sites were classified as being burnt at low severity if their understorey showed evidence of recent burning (scorch marks on tree, burnt stumps and burnt shrubs) but the canopy of *Eucalyptus* trees remained intact. Sites were classified as being burnt at high severity if the understorey showed evidence of being recently burnt and the canopy also showed evidence of having been burnt (i.e. leaves in the canopy were either absent or evident as epicormic buds).

Concordance with AUS GEEBAM

Following the field surveys, we verified our field-based classification of fire severity with the classification in the fire severity layer produced by AUS GEEBAM which was derived from Sentinel Satellite Imagery (Department of Environment and Water, 2020). AUS GEEBAM indexed fire severity using an index of vegetation (Relativized Normalized Burn Ratio) calculated from the difference in vegetation condition before and after the Black Summer wildfires from Sentinel 2A satellite imagery at a 20 m resolution (Department of Environment and Water, 2020). AUS GEBAAM has five classes; (1) no data, (2) Unburnt: Little or no change observed between pre-fire and post-fire imagery, (3) Some change or moderate change in the vegetation index when compared to reference unburnt areas, (4) High: Vegetation is mostly scorched and (5) Very high: Vegetation was clearly consumed. To do this, the coordinates for each survey site were entered into a geographic information system and intersected with the AUS GEEBAM layer for fire severity. We then tested for correspondence between our field-based burn classifications and AUS GEBAAM values by converting the AUS GEBAAM to a 3-level scale whereby high = very high/high, low = low and unburnt = unburnt and comparing the result to our 3-scale field-based classifications.

Habitat assessments

Vegetation and ground cover

Habitat assessments were undertaken at each survey site in November 2020, approximately 10 months after the fires, to quantify differences in habitat structure related to fire severity. Four 50 m^2 quadrats were randomly selected within the 1 ha survey sites. In each quadrat, a 50 cm × 20 cm chequered coverboard with ten 10 × 10 cm squares (Letnic & Fox, 1997) was used to quantify understorey vegetation density at five levels of strata (0–20 cm, 20–50 cm, 50–100 cm, 100–150 cm and 150–200 cm). Measures were repeated five times per quadrat (at 1 m intervals) with an observer at a 10 m distance scoring vegetation density at each strata by counting the number of visible coverboard squares. This resulted in five measurements per quadrat and 20 measurements per site for each level of strata. For analyses, we calculated understorey vegetation density as the sum of the number of 10 × 10 cm squares obscured for all strata.

Ground cover within each quadrat was measured using the step-point method (Letnic & Fox, 1997) at 10 haphazardly chosen 1 m intervals, with the type of cover beneath the observer's big toe being recorded at each interval. Cover type was classified as: bare ground, fine fuel (leaves and sticks) and live (green) cover.

All coarse woody debris (CWD) within the 50 m^2 quadrat was measured for maximum width, minimum width, total length and level of decay. Each piece of CWD > 50 cm long with a minimum width of >5 cm and more than 50% of its length within the plot was surveyed. For each piece, we recorded the large and small end diameter (cm), length (cm) and decay class (1–3; where 1 was 'fresh' and 3 was 'heavily decayed'). The volume of CWD on each site was calculated as the sum of the volumes of fallen large CWD which were estimated using Smalian's formula (volume of a frustum of paraboloid; equation 2) as given in Woldendorp et al. (2002) where V is volume of the log (m^3), L is piece length (m), Ab is the cross-sectional area at the largest end of piece and As is the cross-sectional area at the smallest end of piece.

$$V = L \times (\mathrm{Ab} + \mathrm{As}) / 2$$

Canopy cover was sampled along 25 m transects that traversed each of the four 50 m^2 quadrats where understorey habitat structure was assessed on the survey sites. Along each transect at 0, 12 and 25 m intervals, a canopy cover estimate was recorded using the smartphone applications *Percentage Cover* (iOS) or *HabitApp* (Android). Images were taken 1.5 m above-ground using a device's front facing camera oriented towards the canopy. The applications determine percentage cover by converting canopy within the raw image into black pixels and calculating the percentage of black pixels against total image pixels.

Reptile surveys

Two to three days prior to the commencement of surveys in November 2020, at each site, we deployed four ceramic roof tiles and two pieces of corrugated iron (100 × 70 cm), which were left permanently at the sites and used as artificial retreats. At each site on each survey occasion, we conducted an active search to the equivalent of one person hour and counted the number of *E. tympanum* that we observed. Active searches were conducted with the equivalent of one person-hour of search effort per hectare to standardize for a variable number of surveyors. During each active search, experienced herpetologists walked through the site scanning for lizards on basking sites and in leaf litter. During active searches, the herpetologists also searched for lizards by turning the artificial retreats, logs and rocks and by raking through litter. Temperature at the time of survey was recorded using a Kestrel temperature metre.

Data analyses

Kendall's coefficient of concordance (W) was used to evaluate the agreement between our field classification of fire severity (high, low and unburnt) with the AUS GEEBAM classification (very high/high, moderate/low and unburnt). Kendall's coefficient of concordance is a non-parametric rank-based test where a value of $W > 0.9$ provides an indication of concordance between the ranking of subjects between classifiers (Sokal & Rolf, 1981).

We used a generalized linear model with a Gaussian distribution to investigate the effect of fire severity (unburnt, low severity and high severity) on habitat structure. When main effects were significant ($p < 0.05$) we explored differences between treatment means using Fisher's least significant difference test. Analyses were conducted using SPSS V25.

We used generalized estimating equations to determine the effect of fire severity and sampling period on the abundance of *E. tympanum*. The main effects were fire severity (high, low and unburnt), survey period (November 2020, April 2021 and November 2021) and their interaction. Survey period was included as a fixed factor in the analyses as it was predicted that lizard abundance could vary through time due to factors such as time since fire and weather conditions at the time of survey (Letnic & Fox, 1997). Because the data were expressed as counts and there was a high frequency of zero counts, we used a negative binomial distribution. Because the data represented repeated counts of lizards at the same sites, a diagonal repeated measures error structure was used in models. When main effects were significant ($p < 0.05$), we explored differences between treatment means using Fisher's least significant difference test. Generalized estimating equations were conducted using SPSS V25.

RESULTS

Comparison of field and remote sensed fire severity classifications

There was moderate correspondence between our measure of fire severity and the AUS GEEBAM classification (Table 1; Kendall's Coefficient of Concordance $W = 0.930$, X^2 35.358, df = 19, 10, $p = 0.013$). All the sites that we classified as unburnt were mapped as unburnt by AUS GEEBAM (Table 1). Five of the seven sites which we classified as high severity were mapped as very high or high severity by AUS GEEBAM (Table 1). However, one site which we classified as high severity was mapped as low severity by AUS GEEBAM (Table 1). There were seven sites which had been burnt in the 2019/2020 fires which we classified as being burnt at low severity that were classified as unburnt by AUS GEEBAM (Table 1).

Habitat structure

Habitat structure was assessed during the November 2020 field trip, approximately 10 months after the fires. We found fire severity significantly increased the presence of bare ground (Figure 3c; Wald $X^2 = 35.529$,

TABLE 1 Correspondence between classification of field-based classification of fire severity and satellite-derived GEEBAM index of fire severity.

	Field-based classification of fire severity		
AUS GEEBAM severity	High	Low	Unburnt
Very high/high	6		
Low and moderate	1		
Unburnt		6	7

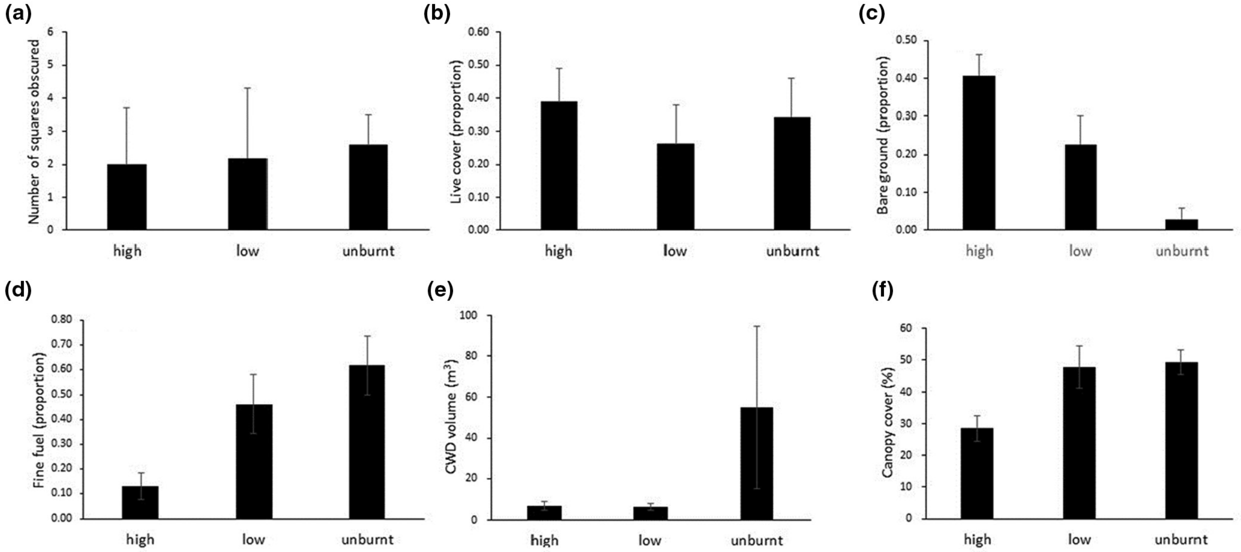

FIGURE 3 Effect of fire severity on (a) understory vegetation density, (b) Live ground cover, (c) bare ground, (d) Fine fuel, (e) Coarse woody debris (CWD) and (f) Canopy cover. Error bars represent ±1 standard error.

df = 2, $p < 0.001$), with both high severity (high vs. unburnt; $p < 0.001$), and low severity (low vs. unburnt; $p = 0.04$) fire sites having more bare ground than unburnt sites. Between burn intensities, bare ground was greater in areas of high severity burn than low severity burn (high vs. low; $p = 0.01$).

Similarly, fire severity decreased fine fuel cover (Figure 3d; Wald $X^2 = 16.985$, df = 2, $p < 0.001$). Fine fuel cover was less in high severity sites relative to unburnt (high vs. unburnt; $p < 0.001$) and low severity burn sites (high vs. low; $p = 0.012$). There was no difference in fine fuel cover between unburnt and low severity burn sites (unburnt vs. low; $p = 0.240$).

Canopy cover was significantly decreased by fire intensity (Figure 3f; Wald $X^2 = 17.438$, df = 2, $p < 0.001$), with cover greater at unburnt and low severity sites than at high severity burn sites (unburnt vs. high; $p < 0.001$, low vs. high; $p = 0.002$). However, canopy cover did not differ between unburnt and low severity burn sites (unburnt vs. low; $p = 0.827$).

No effect of fire on understorey vegetation density (Figure 3a; Wald $X^2 = 0.851$, df = 2, $p = 0.653$) or live ground cover (Figure 3b; Wald $X^2 = 0.708$, df = 2, $p = 0.702$) were found. Furthermore, fire severity did not influence the total volume of coarse woody debris (Figure 3e; Wald $X^2 = 3.560$, df = 2, $p = 0.169$). However, there was considerable variance in CWD on unburnt sites (Figure 3) which was due to one site having exceptionally high CWD cover.

Effect of fire severity on *Eulamprus tympanum* abundance

Over three survey periods, we conducted a total of 60 person hours of searching for *E. tympanum*. This search effort yielded 171 observations of *E. tympanum*. Other lizard species encountered during surveys were *Egernia cunninghami*, *Egernia saxatilis*, *Eulamprus heatwolei*, *Carinascincus coventryi*, *Hemiergis talbingoensis*, *Liopholis whitii*, *Pseudemoia entrecasteauxii*, *Pseudemoia spenceri* and *Saproscincus mustelinus*.

Across the three survey periods, *E. tympanum* were recorded at four out of seven high severity burn sites, five out of six low severity burn sites and six out of six unburnt sites. There were marked differences in air temperature at the time when lizard surveys were conducted between the three survey periods. The warmest survey period was November 2020, when the mean air temperature when surveys were conducted was 24.4°C (SD ±2.2°C). The mean air temperatures at the time when lizard surveys were conducted in April 2021 and November 2021 were 14.1 °C (SD ±3.77°C) and 10.7°C (SD ±1.6°C) respectively.

There were significant effects of fire severity (Figure 4; Wald $X^2=6.836$, df = 2, $p=0.033$) and survey period (Wald $X^2=59.016$, df = 2, $p<0.001$), on *E. tympanum* abundance, but there was no interaction between fire severity and survey period (Wald $X^2=1.154$, df = 3, $p=0.766$). *Eulamprus tympanum* abundance was greatest during searches conducted in November 2020 which coincided with a period of warm weather (Figure 4). Post hoc tests indicate that *E. tympanum* abundance was lower at high severity fire sites than it was at low severity ($p<0.001$) and unburnt sites ($p=0.007$). There was no difference in *E. tympanum* abundance between low severity and unburnt sites ($p=0.219$).

DISCUSSION

Our surveys on the Boyd Plateau showed that fire severity affected both habitat structure and the abundance of *E. tympanum*. Ten months after the fires, there was more bare ground, less fine fuel and lower canopy cover on sites burnt at high severity than sites burnt at low severity or unburnt sites. The abundance of *E. tympanum* was lower at sites burnt at high severity than it was at sites burnt at low severity or sites that were not burnt. Our findings parallel those of previous studies which have found that the effects of fire on terrestrial wildlife can vary depending on the severity at which it burns and that higher severity fires can have a greater effect than low severity fires (Law, Gonsalves, Burgar, et al., 2022; Law, Madani, Gonsalves, et al., 2022).

There was moderate correspondence between our measure of fire severity which used an assessment made on the basis of evidence of burning (scorch marks) and canopy cover (low severity = intact canopy, high severity = absent canopy) when we conducted our habitat assessments 10 months after the fire and the remotely sensed AUS GEEBAM fire severity layer. All the sites that we classified as unburnt were classified as unburnt by AUS GEEBAM. There was also good correspondence between our classification of sites as being burnt at high severity with the AUS GEEBAM classification of sites as being burnt at very high or high

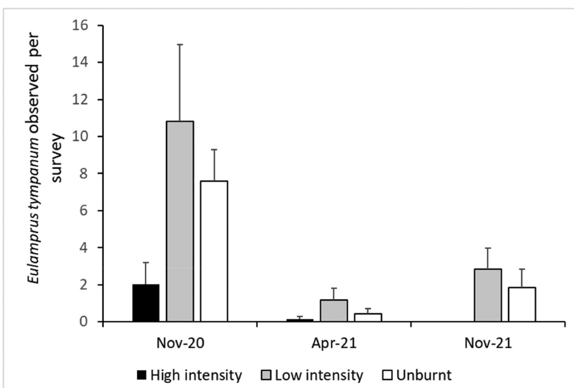

FIGURE 4 The mean number of *Eulamprus tympanum* sighted per survey at sites that were unburnt, burnt at low severity, and burnt at high severity during the Black Summer Bushfires. Surveys were conducted in November 2020, April 2021, and November 2021. Error bars represent ±1 standard error.

severity—with just one site that we classified as being burnt at high severity classified as being burnt at low severity by AUS GEEBAM. However, all the sites that we classified as being burnt at low severity were classified as being unburnt by AUS GEEBAM.

This discrepancy between our assessment of fire severity and the AUS GEEBAM index of fire severity is unlikely to have been due to misclassification of the sites as being burnt. This is because scorching, the presence of ash and charred vegetation clearly indicated that the sites had been recently burned. The discrepancy was also unlikely to be due to an error in the coordinates that we used for extracting the GEEBAM data because the survey-site coordinates were recorded in the middle of the sites and were situated at least 50 m away from the fire boundary which approximates to 2–3 pixels in AUS GEEBAM. It is more likely that the discrepancy between the classification systems stems from constraints on the remote sensing technique to classify areas as being burnt when the canopy remained relatively intact after the fire. This is because sites were classified as unburnt by AUS GEEBAM if there was little or no change in the pixel values for the vegetation index before and after the fire (Department of Environment and Water, 2020). Nonetheless, the correspondence between our classification as sites being burnt at high severity and sites mapped as being at very high or high severity by AUS GEEBAM indicates that there was good correspondence between our classification of sites being burnt at high severity with classification as very high or high severity by AUS GEEBAM.

The abundance of *E. tympanum* was consistently lower at high severity burnt sites compared to unburnt sites. However, the abundance of *E. tympanum* also varied markedly between sampling periods. Abundance of *E. tympanum* was greatest in November 2020 when warm weather conditions prevailed and was lower in the April 2021 and November 2021 sampling periods when weather conditions were substantially cooler. Air temperature is the most likely explanation for differences in abundance between sampling periods, as fluctuations in lizard activity between survey periods were consistent across fire severity categories (Figure 4) and previous studies have shown that the activity levels and hence detectability of lizards is temperature dependent (Heatwole & Taylor, 1987: Letnic & Fox, 1997). Nonetheless, because our sampling strategy did not involve following the fates of individuals and was carried out over an extended time frame, it remains a possibility that the decline of *E. tympanum* populations that we observed may not have been linked to the Black Summer fires but instead to another factor that we did not measure.

One explanation for the lower abundances of *E. tympanum* at high severity burnt sites is that lizards were directly killed by the fire and failed to recolonize post fire. However, previous studies, including on the closely related Blue-mountains water skink (*Eulamprus leuraensis*), have concluded that lizards are somewhat resilient to being directly killed by wildfires (Costa et al., 2013; Gorissen et al., 2015; Santos et al., 2022). Furthermore, our data show that many large logs remained after the fires on sites that were burnt at high severity, and that fire severity had no effect on the volume of coarse debris. Thus, we think it is likely that many lizards may have survived the fires because their shelter habitats remained (Langkilde et al., 2003; Schwarzkopf & Shine, 1991). This explanation is supported by our finding that *E. tympanum* were detected on sites burnt at high intensity and at low intensity.

An alternative explanation for the lower *E.tympanum* abundance at sites burnt at high severity is that fires had indirect effects mediated by shifts in habitat characteristics (Gorissen et al., 2015). For example, it is likely that fire severity had a strong impact on both the thermal characteristics of sites and the exposure of lizards to predators (Costa et al., 2013; Doherty et al., 2022;

Gorissen et al., 2015; Roe et al., 2017). As evidence of this, sites burnt at high intensity had sparser canopy cover, less leaf litter cover and more bare ground in comparison to sites burnt at low intensity and unburnt sites. Consequently, the ground layer of sites burnt at high intensity would be more exposed to solar radiation and have fewer shady resting sites than sites burnt at low intensity or unburnt sites (Costa et al., 2013). Fire-driven changes in forest structure have been linked to increased microclimatic temperatures, and in turn shifts in thermoregulatory behaviour and temperature-dependent performance traits of reptiles (Roe et al., 2017; Wild & Gienger, 2018). Such shifts in habitat are likely to have influenced the suitability of the sites for *E. tympanum* which actively thermoregulates to maintain a relatively low preferred body temperature (~29°C–32°C; (Heatwole & Taylor, 1987; Neel & McBrayer, 2018; Schwarzkopf & Shine, 1991). Therefore, upshifts in microclimatic temperatures due to decreased canopy may render sites burnt at high severity unsuitable for *E.tympanum* until the canopy recovers.

In addition, previous studies on forest dwelling reptiles have found that although animals survived a high severity fire, their survival rates were significantly lower in the years following the fire, likely due to avian predation (Webb & Shine, 2008). In our study, lizards occupying sites burnt at high severity which had sparser canopy cover, less litter cover and more bare ground are likely to have been more exposed to predators, particularly avian predators (Blomberg & Shine, 2000; Schwarzkopf & Shine, 1992), than those at sites burnt at low severity or unburnt sites.

While they were burning, the Black Summer bushfires prompted much pessimism among ecologists and the general public who were concerned that an ecological catastrophe was unfolding due to the unprecedented extent and severity of the fires (Boer et al., 2020). Many feared that millions of animals were killed by the fires and that the fires would have disastrous impacts on the populations of many species (Dickman, 2021; Jolly et al., 2022). This was particularly the case for 'species of concern' that had a large proportion of their range burnt such as *E. tympanum* (Dickman et al., 2022; Legge, Rumpff, et al., 2022; Legge, Woinarski, et al., 2022). If the results of this study are extrapolated across the range of *E. tympanum*, they suggest that their populations are likely to have declined because there were extensive areas burnt at high severity during the Black Summer bushfires (Figure 1; Legge, Woinarski, et al., 2022). Indeed, Legge, Woinarski, et al. (2022) estimated that 19% of the range of *E. tympanum* was burned by high severity fires. However, our results also show that *E. tympanum* populations have persisted in areas burnt at high severity albeit in lower numbers than in nearby areas that were burnt at low severity or remained unburnt. Consequently, from an optimistic point of view, it appears likely that *E. tympanum* populations have persisted in areas burnt at high severity as well as in 'refuge' areas that were unburnt or burnt at low severity. The persistence of these populations in refuge areas should facilitate recovery of populations in areas burnt at high severity.

The findings of this study show that the effects of wildfire on vertebrate populations may not be uniform across burnt landscapes but instead vary with the severity of fire (Law, Gonsalves, Burgar, et al., 2022; Law, Madani, Gonsalves, et al., 2022; Law, Madani, Lloyd, et al., 2022). A sombre implication of this finding is that the impacts of wildfires on many vertebrate species will increase as the frequency, extent and severity of wildfires are expected to increase with climate change (Bowman et al., 2021; Canadell et al., 2021). However, another implication of our findings is that because fire severity varies across the landscape, there is likely to be areas burnt at low severity which may function as refuges from which populations can repopulate areas that were burnt at high severity.

AUTHOR CONTRIBUTIONS

Michael Letnic: Conceptualization (lead); data curation (equal); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (equal); resources (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Bridget Roberts:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Mitchell Hodgson:** Investigation (equal); methodology (equal); writing – review and editing (equal). **Alexandra Ross:** Investigation (equal); methodology (equal); project administration (equal); writing – review and editing (equal). **Santiago Cuartas:** Investigation (equal); methodology (equal); writing – review and editing (equal). **Yingyod Lapwong:** Investigation (equal); writing – review and editing (equal). **Owen F Price:** Investigation (equal); methodology (equal); supervision (equal); writing – review and editing (equal). **Nicola Sentinella:** Methodology (equal); project administration (equal); writing – review and editing (equal). **Jonathan K Webb:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data will be made available on reasonable request to the corresponding author

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