Fire Ecology

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The impact of a severe wildfire on canopy structure and composition in a lowland mixed-eucalypt forest in southeastern Australia

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Abstract

Background Forest fires of unprecedented scale and intensity have become a more frequent occurrence in many parts of the world. In southeastern Australia, the Black Summer fires of 2019–2020 impacted nearly 20 million hectares of forests. After more than a century of human impacts and other fires, there is a risk of shifts in species composition and forest structure. We studied lowland mixed-eucalypt forest in eastern Victoria to determine how variability in fire intensity influenced the structure and composition of the forest canopy.

Results We found that resistance to low-intensity fire, as measured by avoidance of crown loss, increased with increasing tree size and varied among species. Resistance to moderate- to high-intensity fire was low, but all species showed significant resilience, with 95% of trees able to recover all or a portion of their crowns through epicormic resprouting. Resilience increased with increasing tree size and varied among species. *Eucalyptus sieberi* was the least resilient and *E. baxteri* was the most highlighting an inverse relationship between resistance and resilience. Mortality (i.e., crown loss with no recovery) disproportionally impacted large *E. sieberi* trees subjected to high-intensity fire.

Conclusions As fire intensity increased, the relative proportions of the various species in the upper canopy shifted. Some species increased, while others decreased. Low-intensity fire however resulted in very little change to the structure and composition of the forest canopy. While areas of high-intensity fire may lead to shifts in relative abundance and dominance of eucalypt species, the general resilience of the eucalypt species to fire suggests a substantial inertia in the species composition in these forested landscapes. However, changes in canopy structure due to crown mortality in *E. sieberi* promoted increased openness which could promote this species regeneration and create a positive feedback loop which facilitates a shift in species composition in gaps created by crown and tree mortality.

Keywords *Eucalyptus*, Wildfire, Fire severity, Resprouting, Mortality, Resistance, Resilience

Resumen

Antecedentes Incendios forestales sin precedentes en escala e intensidad están ocurriendo más frecuentemente en muchas partes del mundo. En el sudeste de Australia, los incendios del verano negro de 2019-2020 impactaron cerca de 20 millones de ha de bosques. Luego de una centuria de impactos humanos y otros incendios, existe el riesgo de cambios en la composición de especies y en la estructura forestal. Estudiamos un bosque de eucaliptos ubicados en tierras bajas en el este de Victoria para determinar cómo la variabilidad en la intensidad del fuego influenció la estructura y composición del dosel forestal.

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Resultados Encontramos que la resistencia a fuegos de baja intensidad, medida en cómo evitar la pérdida de las coronas, se incrementaba con el tamaño de los árboles y variaba entre especies. La resistencia a fuegos de moderada a alta intensidad fue baja, aunque todas las especies mostraron una resiliencia significativa, con el 95% de los árboles capaces de recuperar toda o parte de de sus coronas mediante rebrotes epicórmicos. *Eucalyptus sieveri* fue la menos resiliente y *E. baxteri* la más resiliente, mostrando una relación inversa entre resistencia y resiliencia. La mortalidad (i.e. pérdida de corona sin recuperación) impactó desproporcionadamente los grandes árboles de *E. sieberi* sujetos a fuegos de alta intensidad.

Conclusiones A medida que la intensidad del fuego se incrementó, las proporciones relativas de varias especies iban cambiando en el dosel superior. En algunas especies éstas proporciones se iban incrementando, mientras que en otras decrecían. Desde luego, los fuegos de baja intensidad resultaron en muy pequeños cambios en la estructura y composición del dosel forestal. Mientras que áreas con fuegos de alta intensidad pueden derivar en cambios en la abundancia relativa y dominancia de especies de eucaliptus, la resiliencia general de las especies de eucaliptus al fuego sugiere una inercia substancial en la composición de especies de esos paisajes forestales. Desde luego, los cambios en la estructura del dosel debido a la mortalidad de las coronas en *E. sieberi* promueve la apertura de claros que puede promover la regeneración de esta especie, y crear una retroalimentación positiva que facilita un cambio en las especies en esos claros creados por la mortalidad de árboles y de coronas.

Introduction

Disturbances occur in all forested landscapes and play a significant role in shaping stand structure and species composition (Oliver and Larson 1996, Greenberg et al. 2016). Disturbances may vary from small, localized events that damage or kill a single tree to large-scale events that cause almost complete mortality of the forest. While disturbances are often considered destructive, they are a critical part of many forest ecosystems because they influence stand dynamics across a range of spatial and temporal scales (Sturtevant and Forten 2021). In recent decades, climate change has led to shifts in disturbance regimes. In many parts of the world, fire is the predominant disturbance type in forests (McLauchlan et al. 2020) and both fire extent and severity have increased significantly over the last half century in response to a drier and warmer climate (Kelly et al. 2013; Abatzoglou et al. 2021; Collins et al. 2022; Parisien et al. 2023). The effects of changing climate may have been compounded by changes in land management after the removal of Traditional Owners from the land (Guitterman et al. 2019; Laming et al. 2022; Mariani et al. 2022). In some cases, these changes may be outside the range of disturbance intensity or frequency that a forest type has experienced in recent centuries (Halofsky et al. 2020). Changes in disturbance regimes may precipitate shifts in forest structure and composition that threaten flora and fauna associated with the forests (Au et al. 2019). They may also promote stand structures and species mixtures that are more susceptible to moderate- to high-intensity disturbances, creating a positive feedback loop (Barker et al. 2018).

Growing concerns over the impact of climate change on forests has focused considerable effort on understanding how forests will respond to changing disturbance regimes. To understand the impacts of fire on forests, one should distinguish between fire severity, the impact of fire, from fire intensity, the energy of the fire. Fire severity is the result of interaction between fire intensity, the energy per unit of time and space, and the response of the trees at the site (Trouvé et al. 2020). Two fundamental categories of response are resistance, the ability of a forest to remain unchanged by a disturbance, and resilience, the ability to recover to a previous state after a disturbance (Lloret et al. 2011). In regions where fire is the dominant type of disturbance, previous studies have highlighted the difference in resilience mechanisms between forests dominated by obligate-seeder species and those dominated by resprouting species. In forests dominated by obligate-seeder species such as *Eucalyptus regnans* (Ashton 1981), *Eucalyptus delegatensis* (Fagg et al. 2013), *Pseudotsuga menziesii* (Franklin et al. 2002; Halofsky et al. 2020), and various *Pinus* spp. (Kolb et al. 2007, Halofsky et al. 2020), moderate- or high-intensity fire can kill most or all of the trees and the forest regenerates from seed released after the fire. If fire recurs before the new cohort of trees becomes reproductively mature, localized species loss may occur (Fairman et al. 2016, Duivenvoorden et al. 2024).

In forests dominated by resprouter species, such as the mixed-eucalypt forests of southeastern Australia (Fairman et al. 2017, 2019; Collins 2020) and oak (*Quercus* spp.) forests in the northern hemisphere (Falk 2017, Pausas and Keeley 2017), moderate- to high-intensity fire is likely to defoliate trees. However, many of the tree species in these forests are able to recover their crown area after the fire by resprouting from the stem and branches. These forests have a different post-fire canopy profile than undisturbed forests (Karna et al. 2020). If fire recurs before the trees have fully recovered their crowns, then there may be persistent changes to the foliage distribution and openness of the forest. The changes may be reinforced by a reduced ability of trees to recover, which may result in increased mortality if high-intensity fires recur at short intervals (Fairman et al. 2019).

Trees that are able to resprout may do so from the base of the tree (i.e., basal resprouting), along the stem and branches of the tree (i.e., epicormic sprouting), or both. Some species are exclusively basal resprouters (e.g., *Eucalyptus pauciflora* in southeastern Australia), whereas other species have the capacity for both types of response. Basal resprouting in the absence of epicormic sprouting has been referred to as "top kill" (Fairman et al. 2017, 2019). For most resprouter forests, top kill is the most extreme impact of fire and may result in long-term changes in forest structure and ecosystem function. The potential for top kill usually decreases with stem size (Trouvé et al. 2021); however, the probability of top kill increases for a given stem size in subsequent fires if they occur in quick succession (Fairman et al. 2019; Collins 2020).

Species' responses to fire vary across a spectrum of impacts in fire-prone ecosystems. Facultative seeder species that are common in such ecosystems (Prior and Bowman 2020; Underwood et al. 2023) have the ability to respond by sprouting or by seedling regeneration. The predominance of a particular type of response varies with fire intensity and the interaction of species response with fire intensity and frequency shapes the relative abundance of species. Changes in fire regime have the potential to alter the relative abundance of species through elimination of some species and increasing abundance of other species. For example, a shift to a regime with higher frequency and intensity could increase the relative abundance of species with a stronger reproductive response (Fairman et al. 2017) and decrease the diversity of species (Richter et al. 2019).

In southeastern Australia, lowland mixed-eucalypt forests typically consist of an uneven-aged canopy dominated by a mix of eucalypt species that are considered to be vigorous resprouters (Murphy et al. 2013). Prior to European colonization, the disturbance regime in these forests was characterized by frequent, low-intensity fires associated with cultural burning (Bowman 1998; Adeleye et al. 2021; Mariani et al. 2022, 2024). Over the past 200 years, the removal of Traditional Owners combined with logging and increasingly frequent high-intensity fires (Collins et al. 2022) has resulted in changes to forest structure and tree species dominance (Mariani et al. 2022). In particular, the facultative seeder species, *Eucalyptus sieberi*, has become more abundant and dominant in these forests over the last century (Incoll 1940; Chesterfield 1978, 1983; Horrocks et al. 1987, Featherston 1985). The response has not been universal however because not all forest containing *E. sieberi* have shown significant shifts in relative abundance of species. The allogenic, biogenic, and autogenic factors necessary to bring about the observed changes have not been analyzed. As a result, mechanisms that shape the abundances of co-existing species in these forests have yet to be discovered. Observations that *E. sieberi* regenerates prolifically and grows well under open stand conditions suggests that disturbance severity, which leads to tree mortality, drives the response. The response may occur in a positive feedback loop in which changes to more open stand conditions occur over several disturbances (Barker et al. 2021). The response could also include a threshold in stand condition beyond which further disturbance leads to an abrupt increase in abundance of *E. sieberi*, an example of a tipping point in forest resilience (Reyer et al. 2015). In 2019–2020, the largest recorded fire event in temperate Australian history—the Black Summer fires—occurred across Victoria and New South Wales in southeastern Australia. The 2019–2020 Black Summer fires represented a large, infrequent disturbance (LID) event, which can have landscape-scale impacts on forest structure and ecosystem processes that shape forest dynamics for decades or more (Turner and Gardner 2015). It also provided a unique opportunity to study the impacts of fire over a wide geographical area and a broad spectrum of intensities. The overarching goal of this study was to better understand how fire of varying intensity impacted the regions species-rich eucalypt forests. In particular, we addressed the following questions:

- How do species, tree size, and fire intensity interact to determine tree responses to fire?
- How do stand structure and species composition change after the fire?
- What attributes might give individual species an advantage in the post-fire landscape?

Methods

The study area

The study was conducted in lowland mixed-eucalypt forest (lowland forest vegetation community of East Gippsland in Cheal et al. 2011) in eastern Victoria, Australia. The community has an open forest structure with an open understory, dense shrub cover, and tall field layer. The canopy is dominated by *Eucalyptus* species. The understory has a sparse cover of *Persoonia linearis* and *Allocasuarina littoralis* to 5 m height. The understory has a diverse assemblage of heathy species to 1.5 m height. The field layer is dominated by wiry grass and sedge species. Fire is the primary disturbance in these landscapes. It is considered an integral part of the environment and a fundamental ecosystem process across southern Australia. Cheal (2010) suggested that the tolerable fire intervals for these forests is 8 to 60 years, and that they require patchy, low-severity fire to maintain the more fire-sensitive species in the community. This forest type is routinely burnt at low intensity for fuel reduction and ecological purposes at intervals varying from 3 to 10 + years. Prior to European colonization, the Traditional Owners of these lands would have used cultural burning to manage the forest for food resources and more generally as the practice of Caring for Country (Bowman 1998; Adeleye et al. 2021; Mariani et al. 2022, 2024).

In 2019–2020, the Black Summer burned through approximately 10 million ha of forest in Victoria and New South Wales. In Victoria's East Gippsland region, approximately 200,000 ha or 65% of the total area of lowland mixed-eucalypt forest burned (Fig. 1). The fire impact was assessed by the land manager adopting the standard approach of mapping the fire extent into severity classes. The assessment showed that approximately 50% burnt with high severity (i.e., with full crown scorch or crown burn). High-severity fires were widespread; major fire runs occurred across the coastal and foothill forests between Bruthen and Mallacoota. The extent of the 2019–2020 fire in East Gippsland provided a unique opportunity to study the effects of fire intensity on fire impacts and forest recovery among the various eucalypt species that co-occur in these forests.

In the absence of a map of distribution of fire intensity, fire severity mapping was used to stratify the fire into classes for the sampling of the range of fire intensity. This was based on the assumption that there would be a high degree of correlation between severity and intensity within a restricted range of forest composition and structure. The severity of fire in the 2019–2020 fire area had been assessed and mapped into five severity classes using remotely sensed satellite imagery captured immediately after the fire in early 2020. A preliminary survey in late 2021 indicated that almost complete defoliation had occurred and epicormic re-sprouting was evident on the stems of most trees within the three highest severity class areas (i.e., crown burn, high and moderate crown scorch). In areas classified as light crown scorch or no crown scorch, there was evidence of some foliage loss. However, at the time of this survey many crowns had almost fully recovered, there was little evidence of epicormic sprouting, and the understory appeared to be in a condition consistent with recovery 2 years after fuel reduction burning.

Our study plots were located within the 2019–2020 Black Summer bushfire complex footprint and were stratified to sample across the full range of observed fire severities. To do this, we reclassified the five severity classes from the assessment into three broader classes:

- Crown burn: severity class 1 (*90–100% of eucalypt and non-eucalypt crowns are burnt with widespread crown loss and a high-intensity understory burn*)

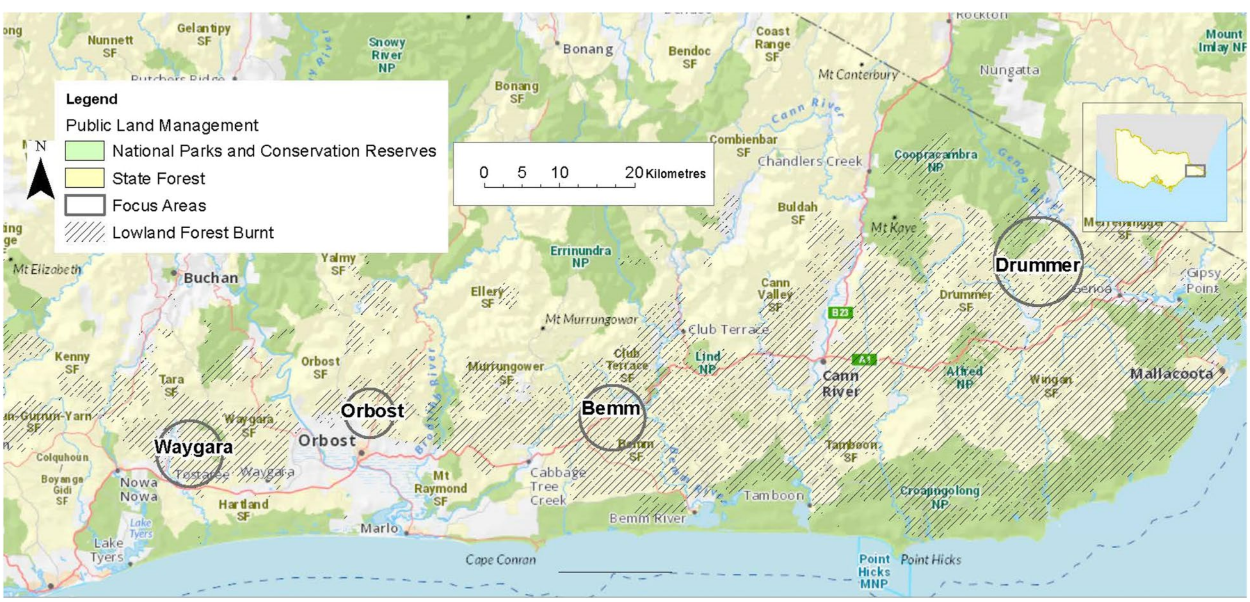

Fig. 1 The extent of lowland mixed-eucalypt forest burnt by the 2019–2020 fires in eastern Victoria and the location of the four focus areas (Waygara, Orbost, Bemm, and Drummer) selected for the study of fire impacts

- High and moderate crown scorch: severity classes 2 and 3 (*35–100% of eucalypt and non-eucalypt crowns are scorched, some crowns are burnt, with a low- to moderate-intensity understory burn with no crown scorch to intense understory burn with complete crown scorch of most eucalypt and non-eucalypts*)
- Light and no crown scorch: severity classes 4 and 5 (*less than 35% of eucalypt and non-eucalypt crowns are scorched with a low-intensity understory burn with isolated patches of moderate- to high-intensity understory burn and some crown scorch*)

The light and no crown scorch stratum was adopted as the control for the study, because it closely resembled areas subject to planned burning and is representative of normal land management practices in the lowland mixed-eucalypt forest across the region.

We selected four focus areas that had accessible forest across the fire impacted area of lowland mixed-eucalypt forest between Nowa Nowa and Mallacoota (Fig. 1 and Table 1). Within each focus area, four replicate plots within each of the three fire severity classes were established for a total of 48 plots (4 focus areas ×3 severity classes ×4 replicates). One additional plot was measured in the high and moderate crown scorch class in the Orbost focus area to give a total of 49 plots. All plots were measured between January and June 2022, approximately 2.0 to 2.5 years after the bushfire.

Plot establishment and measurement

Within each focus area, we identified stands greater than 5 ha representing each of the three fire severity classes and then established plots at least 50 m from roads, tracks, or major forest discontinuities. We selected stands that contained *E. sieberi* and at least two other eucalypt species, to maximize the opportunity to quantify post-fire changes in relative abundance of *E. sieberi*. A plot of 30-m radius was established within a representative part of the selected stand with at least 50% of the stand basal area in trees of the mature age class.

Within each plot, we measured a suite of attributes to describe the plot-level forest structure and composition. At the plot level, we measured canopy cover, the top height of one dominant or codominant tree of each eucalypt species, the top height of one subdominant and one suppressed tree of any species, and the char height on all trees that were measured for height. Canopy cover was estimated by visual assessment of crown projection by two independent observers. In addition, within each plot we systematically established 10 1-m radius plots within which the number of living trees less than 10 cm DBHOB was recorded. At the tree level, we measured several attributes for each tree >10 cm DBHOB that was assessed to be alive at the time of the fire. These included diameter at breast height over bark (DBHOB), dominance class and crown form (based on estimated pre-fire condition and tree height relative to neighboring trees), percent crown loss due to fire impact, the amount of recovery due to epicormic growth based on position and quantity of epicormic sprouts, and seed crop density using a visual guide developed for assessing seed for regeneration of harvested coupes (Bassett et al. 2006).

Table 1 Stocking, basal area, mean dominant height, and seed crop of trees > 10 cm DBHOB by focus area. Mean dominant height is the mean of one dominant/codominant tree of each species in each plot (N= 12 plots per focus area, 13 plots in Orbost). Letters indicate significant difference by Tukey test ($p <$ 0.05) in basal area and mean dominant height

Focus area	Stocking (no. trees ha^{-1})	Basal area (m^2 ha^{-1})	Mean dominant height (m)	Seed crop (M. seeds ha^{-1})
Orbost	167	27 a	31.1 ab	1.8
Waygara	254	28 a	28.3 a	1.0
Drummer	297	37 b	29.5 ab	1.3
Bemm	378	40 b	33.0 b	2.5

Pre-fire stand description

The measurement of plots 2.5 years after fire was used to estimate pre-fire stand condition. In many plots, the fire had removed foliage and branches; however, most of the stems and branches had remained intact after the fire. Basal area was significantly greater in Drummer and Bemm than in Orbost and Waygara (Table 1). In addition to the stocking of trees >10 cm DBHOB, there was an estimated mean density of 306 trees per ha <10 cm DBHOB in the plots prior to the fire.

Fourteen tree species in the genus *Eucalyptus* were recorded in across the 49 plots; however, three species (*E. sieberi*, *E. globoidea*, and *E. consideniana*) accounted for over 80% of the basal area and stocking. Species composition varied with focus area (Table 2).

Diameter of trees in the plots showed a negative exponential distribution commonly associated with uneven-aged stands (Fig. 2a). The proportion of *E. sieberi* increased with diameter class and *E. sieberi* trees tended to be larger and more dominant. Height increased with increasing DBHOB, and most of the tallest individuals were *E. sieberi* (Fig. 2b).

Data analysis

We categorized the tree-level measurements of crown loss and epicormic resprouting into mortality status and presence/absence classes of crown loss and crown death

Table 2 Overall species composition in lowland mixed-eucalypt forest plots by number of trees and basal area. The focus areas in which each species occurred are also shown

Species	Focus areas occurrence	% abundance	% basal area
E. sieberi	Bemm, Drummer, Orbost, Waygara	40.7%	48.2%
E. globoidea	Bemm, Drummer, Orbost, Waygara	30.6%	21.1%
E. consideniana	Bemm, Drummer, Orbost, Waygara	10.7%	14.6%
E. baxteri	Bemm	7.3%	5.0%
E. botryoides	Bemm, Orbost, Waygara	4.0%	4.2%
E. mackintii	Orbost, Waygara	3.9%	3.9%
E. muelleriana	Bemm, Drummer, Orbost	0.7%	0.6%
E. obliqua	Bemm, Orbost, Waygara	0.6%	0.7%
E. agglomerata	Drummer	0.4%	0.7%
E. tricarpa	Orbost, Waygara	0.3%	0.3%
E. polyanthemos	Orbost, Waygara	0.3%	0.1%
E. cypellocarpa	Drummer, Waygara	0.2%	0.5%
E. angophoroides	Orbost	0.1%	0.0%
E. croajingalensis	Bemm	0.1%	0.0%

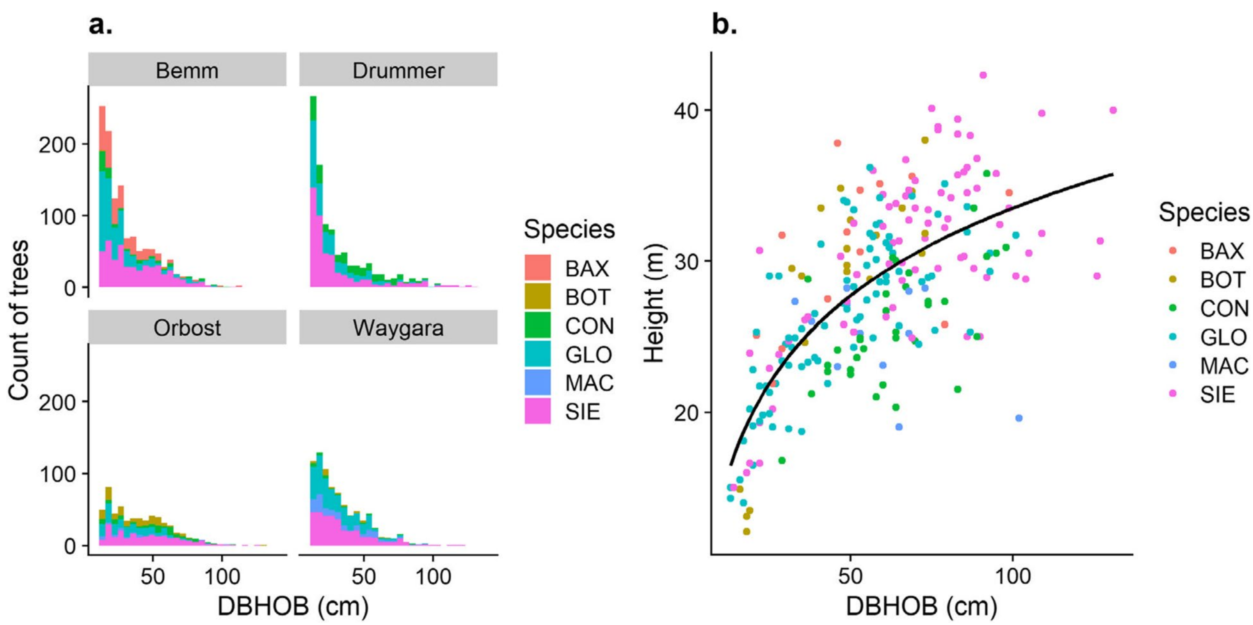

Fig. 2 **a** Total number of trees (count) by species vs DBHOB (cm) per focus areas and (**b**) height (m) vs DBHOB (cm) of trees selected for height measurement. The black solid line is a log transformed smoother fit to the data for visualization purposes. Species are identified by the first three letters in the species name (i.e., BAX = *E. baxteri*, BOT = *E. botryoides*, CON = *E. consideniana*, GL O = *E. globoidea*, MAC =*E. mackintii*, SIE = *E. sieberi*)

(Fig. 3, Table 3). We modeled the effect of species, tree size (DBHOB), and fire intensity on crown loss status, crown death status, and mortality status.

The sampling design was stratified on fire severity. However, severity is the outcome of intensity interacting with trees of different species and sizes. In the absence of any means to directly measure fire intensity, the method of Trouvé et al. (2020, 2021), based on Canham et al. (2001, 2010), was used to jointly estimate the effect of species, tree size (based on DBHOB), and relative fire intensity on species-specific fire responses. Relative fire intensity was included as a latent (i.e., unobserved) variable that is estimated for each plot from the data. The fire response variable used in this analysis is the occurrence of crown death (i.e., the loss of foliage from the top portion of the tree above crown break without subsequent epicormic recovery

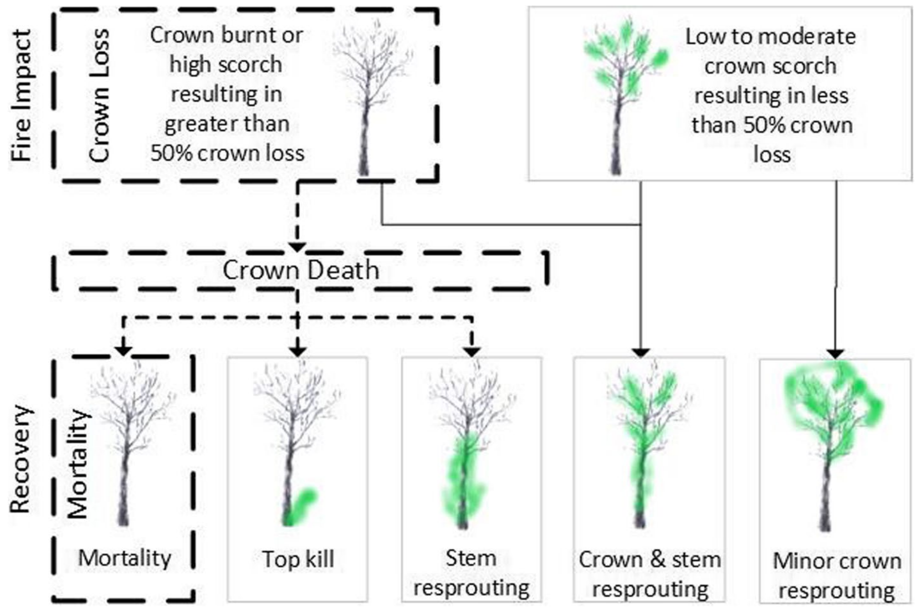

Fig. 3 Crown loss, crown death, and mortality classification. The immediate effect of fire, fire impact, is classified by the degree of crown loss. Recovery at 2.5 years after fire is classified by the presence/absence, position, and quantity of resprouting. The modeled responses, crown loss, crown death, and mortality are highlighted by boxes bordered by broken lines

Table 3 The mean, standard deviation, coefficient of variation (CV), maximum and minimum relative fire intensity estimates derived from the crown death model ($n = 49$) in focus areas

Focus area	Mean (Std Dev)	CV	*n*	Maximum	Minimum
Bemm	0.30 (0.19)	0.63	12	0.65	0.05
Orbost	0.40 (0.23)	0.58	13	0.77	0.14
Drummer	0.42 (0.29)	0.69	12	0.94	0.03
Waygara	0.46 (0.29)	0.63	12	0.96	0.10

in that portion of the tree). Crown death shows greater sensitivity to fire than other potential response variables such as crown loss (i.e., leaf loss without consideration of recovery) or top kill (i.e., the death of the above ground portion of the tree with subsequent basal resprouting).

Our model took the following form:

$$Y_{[ijk]} = Bernoulli\ \left(p[ijk]\right)$$

$$P_{[ijk]} = \frac{1}{1 + \exp(-\text{logit}_{[ijk]})}$$

$$\text{Logit}_{[ijk]} = \log\left(\frac{p_{[ijk]}}{1 - p_{[ijk]}}\right) = \alpha_{[j]} + \beta_{[j]} \times I_{[i]} \times D_{[ijk]}^{\gamma[j]}$$

where:

$$\alpha_{[j]} \sim N(\alpha_0, \sigma_\alpha)$$

$$\beta_{[j]} \sim N\left(\beta_0, \sigma_\beta\right)$$

$$\gamma_{[j]} \sim N\left(\gamma_0, \sigma_\gamma\right)$$

where y_{ijk} is the observed crown death status (0 = crown alive, 1 = crown dead) of the kth individual of species j in plot i and is assumed to be sampled from a Bernoulli distribution with probability of crown death p_{ijk}. The probability of crown death per individual p_{ijk} is modeled on the logit scale and was dependent on the relative fire intensity, tree diameter, and species. I_i is the relative fire intensity for plot i (on a scale of 0 to 1, with 0 being unburnt and 1 being the most intensely burnt plot), modeled as a latent random variable with a uniform prior distribution. D_{ijk} is the DBHOB (in cm) of the kth individual of species j in plot i, and α_j, β_j, and γ_j are species-specific parameters to be estimated.

The fire intensity estimate was verified by univariate analysis of the relationship between the plot-level estimates of fire intensity and measured plot level indicators of fire intensity (i.e., mean char height and the total canopy cover at 2.5 years after the fire). Separate linear regression models were fit for mean char height and crown cover percent at 2.5 years after fire (on a natural log scale) as a function of relative fire intensity.

The same method of analysis used for the crown death model was applied to crown loss; that is, the loss of crown due to scorching and subsequent leaf fall or through the direct effect of canopy fire. In the field, this response variable was assessed as the amount of defoliation due to fire, independent of subsequent growth and crown recovery. Crown loss status (0 = less than 50% of crown lost through fire impact, 1 = greater than 50% of crown lost through fire impact) was modeled as the response variable with species, tree size, and relative fire intensity as predictors. In this analysis, we used the relative fire intensity estimates for each plot from the crown death model rather than re-estimation as a latent variable. It was not possible to fit the same type of model to mortality status (0 = alive, 1 = dead), because mortality increased with tree size. Instead, we used a multi-level model relating mortality status to tree size (DBHOB) and relative fire intensity, with species as a random effect. The analysis indicated that mortality was related to fire intensity in one species, *E. sieberi*. On the basis of the species and fire intensity effects, we further analyzed the data using a multi-level model relating mortality status to tree size (DBHOB), relative fire intensity, and crown form class for *E. sieberi*. Crown form classes were defined as regrowth, highly regular, moderately regular, and irregular, which roughly corresponded to growth stages of regrowth, early mature, mature, and senescent following the system of Woodgate et al. (1994) and SFRI (2000). The impact of crown form on tree mortality was modeled as a random effect to account for variability due to this factor identified through prior knowledge and pool the estimates toward a common mean. The form of the model and coefficients are shown in Table S2 of the Supplementary Material. The crown death, crown loss, and mortality models utilized data from 3662 trees out of a total of 3762 trees measured; 8 species were removed because they had fewer than 30 trees per species, which was insufficient to fit the model. Univariate and multivariate linear regressions were used to determine the association between relative fire intensity and forest stand attributes, as well as environmental variables such as aspect, slope class, slope position, and disturbance history. All analyses were conducted using the R statistical program (version 4.1.3) (R Core Team 2023). The crown death, crown loss, and mortality models were fitted using the Stan statistical software (STAN Development Team 2023), implemented through the *brms* package for R version 2.18.0 (Burkner 2017).

Table 4 Percentage of trees with crown loss, crown death, and mortality of the six most common species in the lowland mixed-eucalypt forest study

Species	% crown loss	% crown death	% mortality
E. sieberi	73%	45%	5%
E. globoidea	75%	30%	3%
E. consideniana	82%	31%	4%
E. mackintii	80%	43%	3%
E. baxteri	87%	26%	1%
E. botryoides	74%	42%	3%

Results

Relative fire intensity estimates

The estimates of relative fire intensity (I) were distributed across the possible range from 0 (least intense) to 1.0 (most intense), varying from 0.03 to 0.96. Relative fire intensity was slightly skewed toward the lower intensities with approximately 66% of plots having estimated intensities lower than 0.50 (Supplementary Fig. S1). The distribution of relative fire intensity among the focus areas was uneven. For example, Bemm had a lower mean and narrower range of relative fire intensity values than other areas. In contrast, Waygara had a higher mean and broader range than the other areas (Table 3), with four of the top eight plots in terms of relative fire intensity scores. The coefficient of variation (CV) for relative fire intensity was similar across the four focus areas.

There was a moderately strong relationship between relative fire intensity and the two field-based indicators of fire intensity, mean char height ($R^2 = 0.58$, $p < 0.001$, $\alpha = 0.05$) and log(canopy crown cover 2.5 years after fire) ($R^2 = 0.68$, $p < 0.001$, $\alpha = 0.05$) (Supplementary Fig. S2). These relationships indicated that the model-estimated relative fire intensity is consistent with field observations up to 2.5 years after a fire. Relative fire intensity varied in response to two stand attributes: mean dominant height and basal area pre-fire. However, the strength of these relationships was weak, as indicated by the regression statistics (mean dominant height: $R^2 = 0.22$, $p < 0.01$, $\alpha = 0.05$; basal area: $R^2 = 0.23$, $p < 0.01$, $\alpha = 0.05$) (Supplementary Fig. S3). There were no significant relationships between relative fire intensity and environmental factors.

Species variation in crown loss, crown death, and mortality

The mean proportion of trees that experienced mortality (mean = 4%, range 1 to 5%), crown loss (mean = 76%, range = 73 to 87%), and crown death (mean = 37%, range 26 to 45%) varied among species (Table 4). The amount of interspecific variation varied among the different metrics, with very little variability in mortality and the greatest, although, still moderate, variability for crown death. The parameters (α, β, and γ) for the crown loss and crown death models varied with species, leading to different patterns based on species, DBHOB, and relative fire intensity (Table S1).

The fitted model for crown loss in response to species, DBHOB, and relative fire intensity had a very good fit at the species level with a high correlation between observed and predicted proportion of trees with crown loss. At the plot level, the fit was not as strong, as indicated by the greater dispersal of points around the 1:1 line (Fig. S4 Supplementary). The model predicted that crown loss increased with relative fire intensity and decreased with tree size (DBHOB), but the response also showed a low threshold of relative fire intensity ~0.25 above which all species experienced near complete crown loss (Fig. 4).

Below the threshold of relative fire intensity, the order of susceptibility of species to crown loss was *E. sieberi* < *E. botryoides* < *E. globoidea* < *E. mackintii* < *E. consideniana* < *E. baxteri*. At very low intensity ($I = 0.1$), the probability of crown loss was generally less than 25% for *E. sieberi* and *E. botryoides* and ranged from 25 to 50% in other species. At low intensity ($I = 0.2$), the probability of crown loss exceeded 50% for *E. baxteri*, *E. consideniana*, *E. globoidea*, and *E. mackintii* over their entire DBHOB range, whereas the probability of crown loss was less than 50% for trees greater than ~30 cm DBHOB for *E. botryoides* and *E. sieberi*.

The crown death model had a very good fit with high correlation between observed and predicted proportion of crown dead trees when summarized at both the plot and species levels (Supplementary Fig. S5). In contrast to the crown loss response, the modeled response of crown death to fire intensity was more linear and showed little evidence of a threshold effect. Crown death at three different levels of relative fire intensity (I: 0.2 = low, 0.5 = moderate, and 0.8 = high) increased with increasing relative fire intensity and decreased with DBHOB (Fig. 5). The order of susceptibility of species to crown death was reversed compared to the order of susceptibility to crown loss. The ranking of species in order of increasing susceptibility to crown death was *E. baxteri* < *E. consideniana* < *E. globoidea* < *E. mackintii* < *E. sieberi* < *E. botryoides.* This indicates that while *E. baxteri*, *E. consideniana*, and *E. globoidea* were more likely to suffer from crown loss than *E. sieberi* and *E. botryoides* (Fig. 4), if they did suffer from crown loss, *E. baxteri*, *E. consideniana*, and *E. globoidea* were much more likely to recover through crown and stem resprouting than *E. sieberi* and *E. botryoides* (Fig. 5).

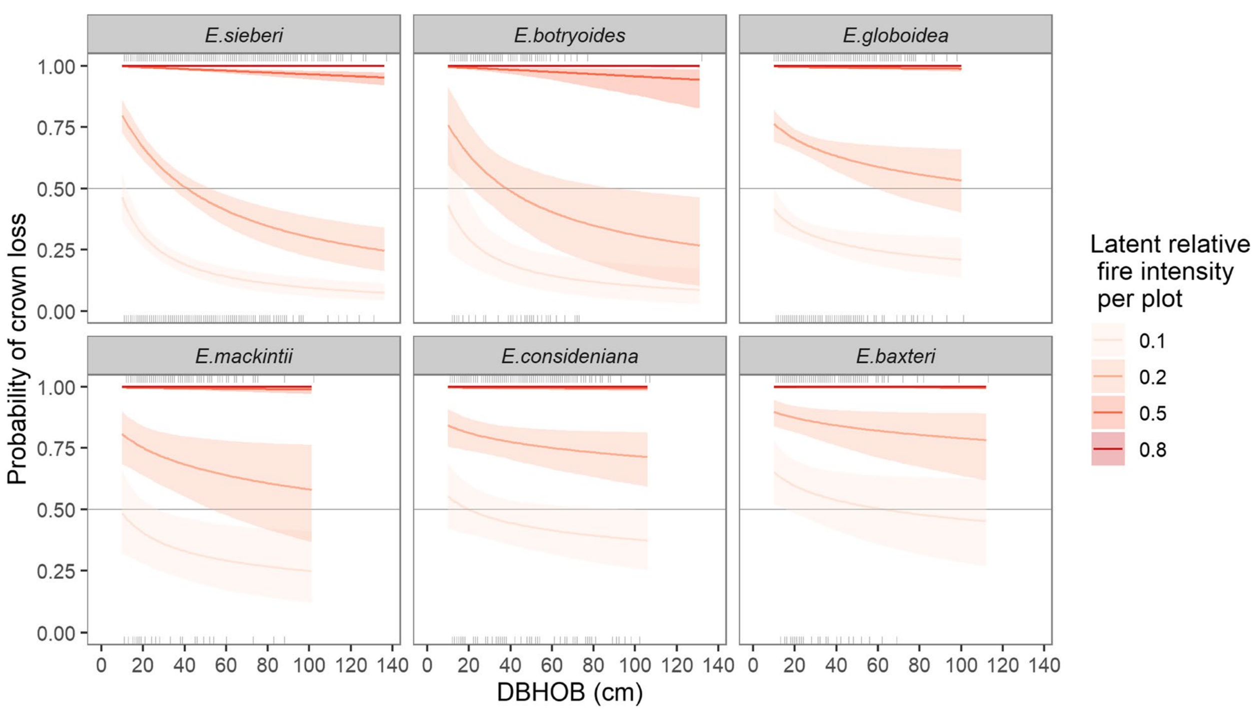

Fig. 4 Predicted proportion of trees with > 50% crown loss in response to species, DBHOB, and relative fire intensity for the six most common *Eucalyptus* species in lowland mixed-eucalypt forest areas in this study

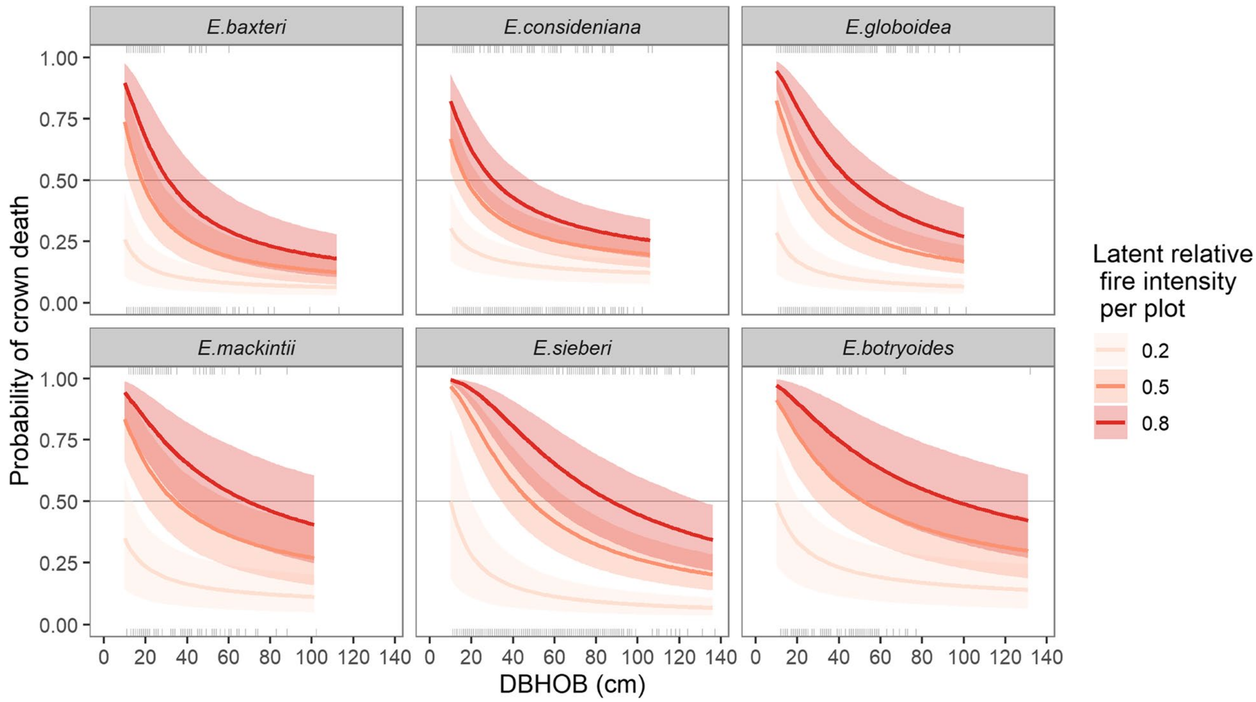

Fig. 5 Predicted proportion of trees with crown death in response to species, DBHOB, and relative fire intensity for the six most common *Eucalyptus* species in lowland mixed-eucalypt forest areas in this study

Mortality occurred at low levels (mean = 4%) in all species across the range of relative fire intensities. The probability of mortality increased with increasing DBHOB in two species, *E. sieberi* and *E. globoidea*, but was similar across the DBHOB range for the other four species. The probability of mortality of *E. sieberi* increased with increasing relative fire intensity and varied with crown form; trees of irregular crown form experienced higher mortality than trees of moderately regular crown form (Supplementary Fig. S6). Large trees with irregular crown forms in the region are generally old trees that contain hollows (Wagner et al. 2024) which makes them more susceptible to loss from fire (Parnaby et al. 2010). Mortality of species other than *E. sieberi* did not vary with relative fire intensity. It appears that across the low-elevation mixed species forests that we surveyed, there was mortality unrelated to fire. The most likely cause was environmental conditions before and after the bushfires. In the 2 years before the Black Summer bushfires, the region was impacted by intense droughts (Wang and Cai 2020), which led to widespread dieback and, to a lesser degree, mortality. In the 2 years after bushfires, the climate was much wetter and warmer than average (BOM 2021, 2022), which is known to increase the activity of pathogens, such as *Phytophthora cinnamomi*, which is known to cause mortality in eucalypt species of the low-elevation mixed species forests (Marks et al. 1975).

Changes in stand structure 2.5 years after fire

The crown loss and crown death patterns associated with tree size and species resulted in changes in the canopy structure of these forests 2.5 years after fire. The nature of these changes was directly associated with relative fire intensity and appears to exhibit a threshold response in which stands that experienced low-intensity fires ($I <$ 0.25) were largely unchanged and those with moderate- to high-intensity fires ($I >$ 0.25) experienced major changes. In areas subject to low-intensity fire, the change in stand structure after the 2019–2020 fires was minimal. While there was sufficient radiant heat to defoliate a large proportion of trees across all tree sizes and species, crown recovery from epicormic sprouting was rapid and widespread. Nearly all trees > 30 cm DBHOB showed substantial crown recovery, as did most smaller trees (> 80%). Two and half years after the fires, the stands that experienced low-intensity fires were approximately 25% more open than the mean pre-fire stand conditions. Plot level crown cover varied from 20 to 70% (mean = 47%) compared to typical crown cover values of 45–75% (mean = 65%). Some of the reduction in crown cover can be attributed to small trees that had experienced crown death. Recovery of the small trees is primarily through basal resprouts, which often have rapid shoot growth and can quickly develop into saplings. In larger trees that have experienced crown loss, recovery was incomplete, with branch elongation of epicormic shoots less than 50% of their pre-fire crown dimension. However, at the current rate of branch elongation and crown expansion these stands should fully recover their pre-fire canopy cover within the next 3 to 5 years.

In areas subjected to moderate- to high-intensity fire, almost all trees experienced >50% crown loss; however, there were distinct differences among species in epicormic recovery. Crown death (i.e., crown loss with no epicormic recovery on the branches and upper bole) was disproportionally more common in *E. sieberi*, the most abundant species in the study plots. Nearly all small trees and a small proportion of larger *E. sieberi* trees experienced crown death in plots with moderate fire intensity (I= 0.25–0.50). In plots with high fire intensity (I> 0.5), nearly all small trees and a large proportion of larger trees experienced crown death. *Eucalyptus globoidea*, the second most abundant species in this study, experienced significantly less crown death than *E. sieberi* in plots with moderate or high fire intensity, particularly among larger trees. In some plots, *E. consideniana* or *E. baxteri* was more abundant than *E. globoidea* and their different susceptibility to fire played a significant role in shaping post-fire stand structure. The probability of crown death for these species was marginally lower than that for *E. globoidea* and much lower than for *E. sieberi*.

The overall crown death response resulted in very low crown cover 2.5 years after fire in plots with moderate fire intensity (mean crown cover =25%) and high fire intensity (mean crown cover =8%) (Fig. 6). Crown recovery was generally poor with many epicormic shoots at <25% of the pre-fire branch length. This contributed to low crown cover and to open canopy conditions. Crown death also contributed to lowering of the canopy and changes in the relative cover by species of the various strata in recovering stands. As relative fire intensity increased, the relative proportions of the various species in the upper canopy shifted. Some species increased (e.g., *E. baxteri*, *E. consideniana*), while others decreased (e.g., *E. botryoides* and *E. sieberi*). The characteristics of a typical residual stand are summarized in Supplementary Table S3.

Discussion

Extreme fires are becoming more common around the world and have the potential to cause widespread changes in the composition and structure of a region's forests (e.g., Kelly et al. 2013; Abatzoglou et al. 2021; Collins et al. 2022; Parisien et al. 2023; Cunningham et al. 2024). Many ecological systems experience tipping points beyond which the system changes state (Reyer et al. 2015). An excess of disturbance can push ecological systems beyond tipping points and may lead to state change. In the lowland mixed-eucalypt forests of southeastern Australia, a shift toward more frequent and more intense fires may be pushing the system toward such a tipping point. In 2019–2020, the largest fires in southeastern Australia's recorded history swept through millions of

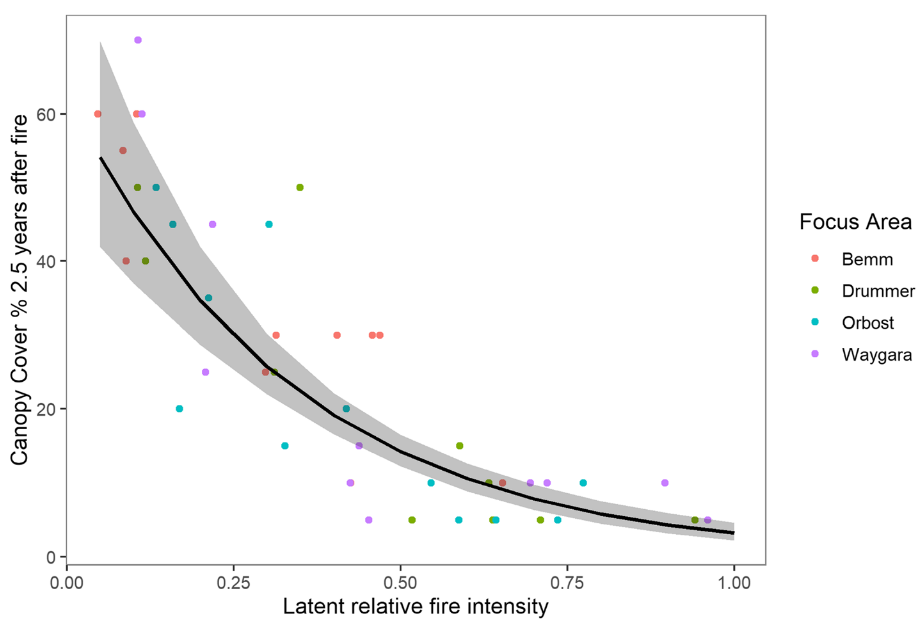

Fig. 6 Plot-level relative fire intensity vs canopy cover (%) 2.5 years after fire in the study of lowland mixed-eucalypt forest. Also shown are the fitted line and 95% confidence interval of the linear regression model of crown cover percent 2.5 years after fire (on a natural log scale) as a function of relative fire intensity

hectares of forests. While we found no evidence for the loss of any of the canopy eucalypt species in these forests, we observed distinct changes in canopy structure and species' relative abundance in areas impacted by moderate- to high-intensity fires due to species-specific differences in tree mortality, crown loss, and crown recovery. This may lead to a shift from a landscape dominated by relatively diverse mixed-species eucalypt forest to one dominated by *E. sieberi*. Observations of increased dominance of *E sieberi* in the region have been attributed to an increase in disturbance intensity in recent decades.

The 2019–2020 bushfires were the most severe in recorded history and therefore provide an opportunity to understand the impacts of fire on the response of *E. sieberi* and associated species. The study has highlighted some key differences between *E. sieberi* and the other common species of the lowland mixed-eucalypt forest, such as *E. baxteri*, *E. consideniana*, and *E. globoidea*. The immediate effect of a single large disturbance is the reduction in crown cover and height of *E. sieberi.* While this implies a decline in *E. sieberi* dominance in the forest canopy, the fires have provided an opportunity for the establishment of a new cohort in the more open post-fire forest. The open conditions may lead to a pulse of recruitment of *E. sieberi*, similar to the post-fire response of obligate seeder eucalypts such as *E. regnans* and *E. delegatensis* (Fairman et al. 2016). This pulse of recruitment, if successful, could lead to increased occurrence of *E. sieberi* in the canopy over time and create a positive feedback loop where the next high-severity fire leads to more crown mortality and more recruitment of *E. sieberi*. Several severe disturbance events in quick succession may reduce the capacity of established trees to resprout (Fairman et al. 2019) further exacerbating the positive feedback loop. Positive feedback could increase the dominance of *E. sieberi* and reduce the ability of multiple eucalypt species to functionally coexist in these forests.

Interspecific variation in resistance and resilience to fire

Radiant heat from low-intensity fires can kill leaves in tree crowns, leading to partial or complete crown loss. All six of the eucalypt species in this study experienced crown loss when subjected to low-intensity fires. However, their ability to resist crown loss varied by species and increased with increasing tree size. This pattern is consistent with other studies that attribute increasing resistance to greater bark thickness in larger trees (Lawes et al 2021; Bennett et al. 2016) and higher position of foliage (Fernandes et al 2008). Interspecific differences in the ability to resist crown loss largely paralleled variation in bark characteristics. The species exhibited variations of the smooth and rough bark types commonly found in eucalypt species. Smooth-barked species shed their outer bark annually, which maintains a thin outer bark, whereas rough-barked species retain the outer bark for longer, resulting in thicker bark. The rough-barked species show a diversity of forms characterized by fiber type, length, and arrangement, of which common forms are stringy- and iron-bark (Jacobs 1955). The most common bark form among the species of the lowland mixed-eucalypt forest is stringy-bark, but the most abundant species, *E. sieberi*, is half-barked with the lower stem classified as iron-bark. This species has shown the greatest resistance to fire, which is probably related to the very dense, hard bark on the lower stem that resists ignition and insulates the stem from radiant heat. Additionally, its upper stem and branches have smooth bark, reducing the likelihood that it would burn in a low-intensity fire. The bark on the stem of *E. botryoides* is intermediate in hardness, but the upper stem and branches are also smooth and relatively fire-resistant. The stems of *E. baxteri*, *E. globoidea*, *E. consideniana*, and *E. mackintii* have loose, fibrous stringy-bark. Their bark is prone to ignition and is often partially consumed during a fire. This can result in greater heating of the underlying wood tissue compared to *E. sieberi* and *E. botryoides*.

The high resistance to low-intensity fire by *E. sieberi* and *E. botryoides* is likely to lead to some advantages, such as increased growth, maintenance of reproductive capacity including crown seed stores, and a greater ability to avoid crown loss from subsequent low-intensity disturbances at short intervals. The low resistance of other species to low-intensity fire leads to foliage redistribution within the crown, but the effect is of short duration and any disadvantage fades after a few years of growth and crown recovery. The crown loss results indicate that there is a relatively low threshold of relative fire intensity beyond which complete defoliation due to scorching is likely and that that threshold is similar among the study species.

As fire intensity increases, species' resistance to fire breaks down and substantial fire impact occurs. As fire intensity increases, differences in resilience, the ability of tree species to *recover* from fire, have a much greater influence on post-fire canopy composition and structure. The six eucalypt species in our study, which are among the most common eucalypt species in the region, were highly resilient to fire, with 95% of individuals resprouting after crown loss. Even after high-intensity fire ($I >$ 0.8), 92% of the trees were able to resprout. Resilience to fire also increased with tree size, with large trees less likely to experience crown death than small trees (Fig. 5). Resprouting frequency and position varied among species. *Eucalyptus sieberi* and *E. botryoides* were more likely to experience crown death post-fire (i.e., no resprouting) than the other species and when they did resprout, it was typically from the stem or the base of the stem rather than from the crown (Fig. 7). This variation in response can be explained by upper bark characteristics. The persistent, rough bark on small branches in the crowns of stringy-bark species better protects the epicormic buds, which are just below the bark surface (Jacobs 1955), from fire than the smooth bark on the upper stem and branches of *E. sieberi* and *E. botryoides*, which are therefore more likely to experience crown bud damage during intense fires. This result is consistent with the findings of Subasinghe Achchige et al. (2022) that after radiant heat exposure there was greater loss of cambium cell viability in smooth-bark compared to stringy-bark species. The high resilience of the eucalypt species in this study is consistent with several previous studies (Fairman et al. 2019; Trouvé et al. 2020, 2021). The lower resilience of *E. sieberi* is also consistent with a previous study that found that resprouting height was lower in *E. sieberi* than in stringy-barks (Collins et al. 2020).

The higher resistance to low-intensity fire and lower resilience to moderate- and high-intensity fire in *E. sieberi* and *E. botryoides* relative to other species suggests that there may be a trade-off between these traits. High investment in thick bark low in the stem provides protection from low-intensity fire, but low investment in bark in the upper stem and crown leaves the tree susceptible to more intense fires and limits their ability to recover crown leaf area rapidly after a fire. In contrast, the stringy-bark species, which have a more even distribution of bark along the stems and branches, receive less protection from low-intensity fire, but are less susceptible to moderate- and high-intensity fires.

Mortality

Mortality was greater in *E. sieberi* than the other species and increased with relative fire intensity. This is consistent with earlier observations (e.g., Incoll 1981; Chesterfield 1983) in similar forests. Mortality of *E. sieberi* also increased with tree size which is contrary to the general finding of mortality declining with increasing tree size (Trouvé et al. 2021). Collins (2020) found that top kill declined with increasing tree size in plots impacted by a crown fire in higher elevation forests with similar eucalypt species. Interestingly, they found slightly higher mortality in larger trees in plots that had experienced an understory fire. Their results may differ from ours due to differences in the diameter range modeled in their study (10–60 cm) compared to ours (10–140 cm). We found lower mortality in trees < 60 cm, particularly for low fire intensities. Our results may also differ due to different fire intensities experienced across our plots, but because Collins (2020) did not estimate latent fire intensity, it is not possible to compare the range of fire intensities between the two studies. The incidence of high mortality in large trees has been reported in previous studies. Wagner et al. (2024) noted a loss of large *E. sieberi* trees after the 2019–2020 Black Summer bushfires. Fairman et al. (2019) also found that mortality was marginally higher in larger diameter trees than in smaller diameter trees after a single fire event in dry eucalypt forest in south-eastern

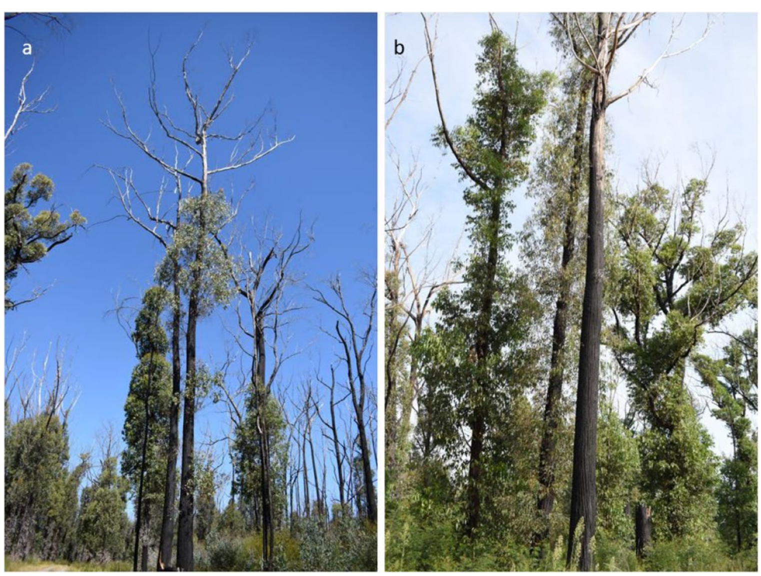

Fig. 7 Variation in resprouting response after high-intensity fire: **a** *E. sieberi*—epicormic resprouting is restricted to the stem and crown death is evident and **b** stringy-bark species—epicormic resprouting extends from bottom of the bole through to branches and crown death is not evident

Australia. In long unburnt *Pinus ponderosa* stands in the western US, where fire was re-introduced after a century of suppression, large trees also suffered high mortality rates (Hood 2010) possibly due to greater fuel accumulation and resultant localized increase in fire intensity under larger trees. Fagg et al. (1986) attributed mortality of mature *E. sieberi* trees in wildfire-impacted forest to the pathogen *Phytophthora cinnamomi*, to which *E. sieberi* is highly susceptible. Above average rainfall in East Gippsland in the 2 years following the Black Summer bushfires would have produced favorable conditions for infestation by *P. cinnamomi*.

Fire-induced mortality may alter the composition or relative species abundance of a forest, as well as altering its structure. The higher incidence of mortality in large *E. sieberi* trees compared to other species is likely to contribute to spatial and temporal heterogeneity of fire-impacted forest. While other tree species recover through epicormic sprouting, the gaps created by canopy mortality of *E. sieberi* or tree mortality of large *E. sieberi* provide opportunities for seedling and coppice regeneration to establish. The regeneration of the highly competitive *E. sieberi* could take advantage of these canopy gaps and maintain its occurrence in these stands. Interactions between tree mortality and crown death may increase gap sizes and light availability through reduced crown cover (Fig. 6), which could eventually lead to shifts in species dominance toward *E. sieberi*.

Changes to stand structure and implications for future stand development and management

In forests dominated by resprouting species, fire rarely leads to elimination of species. However, we observed differences in resprouting behavior that could affect the long-term species composition. The effect of differences in species-specific resilience to fires of varying intensity is likely to result in changes to both horizontal and vertical heterogeneity due to increases in the dominance of sub-canopy and understory trees (Fig. 8). For example, *E. sieberi*, the species most impacted by fire, has approximately 86%, 63%, and 18% of stems in the sub-canopy and understory after high-, medium-, and low-intensity fire, respectively. In contrast, *E. baxteri* has approximately 57%, 32%, and 16% of stems in the sub-canopy and understory after high-, medium-, and low-intensity fire, respectively (Fig. 8). Changes in stand structure

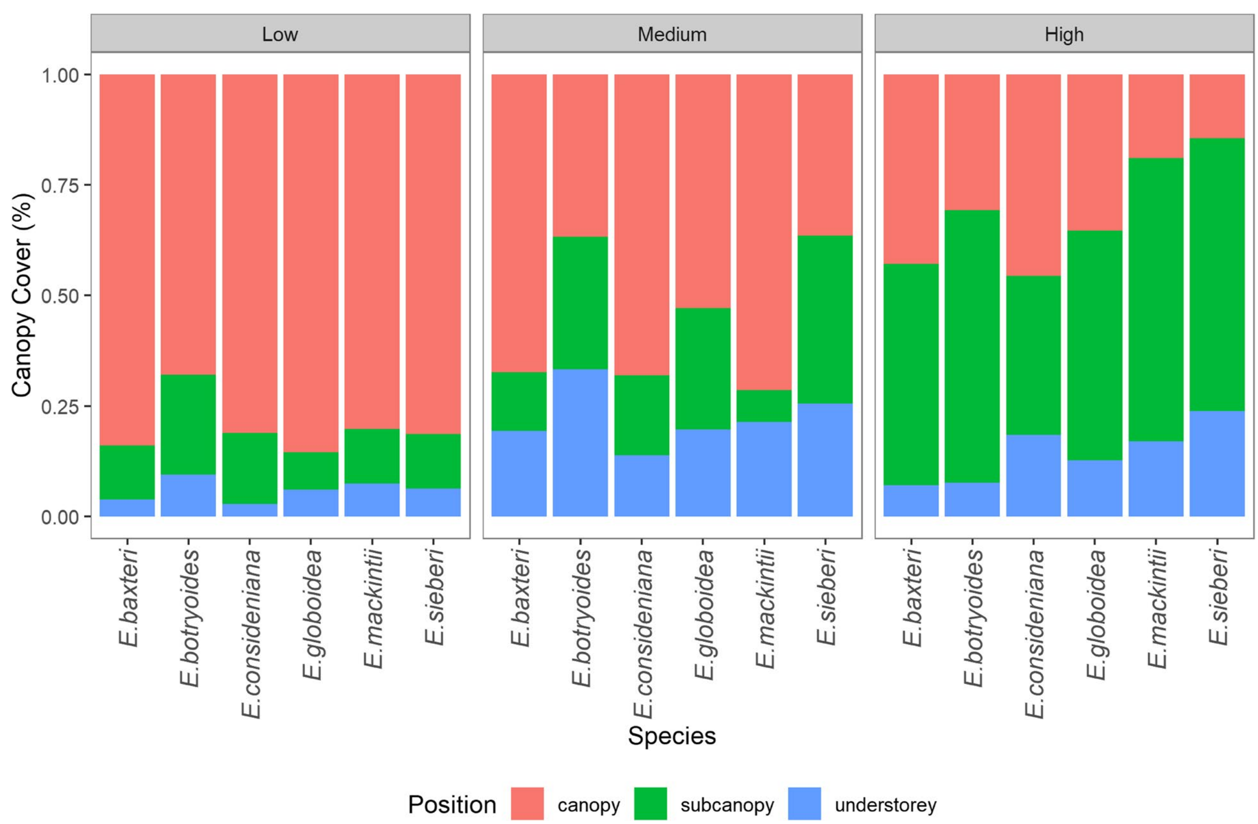

Fig. 8 Proportion of trees in different canopy positions after low-, medium-, and high-intensity fires for each species. The canopy position distribution is based on the tree size distribution in the sample plots, which results in some variation in ranking of canopy response from the ranking in species resilience in Fig. 5

and composition post-fire can have a significant effect on future stand development patterns. Studies of fire impacts in similar forest types in Australia indicate that changes to the structure may persist for a decade or more (Wardell-Johnson et al. 2017; Karna et al. 2020). The rate at which trees that experienced crown death can rebuild their crowns will determine the composition of the upper canopy for several decades. The mid-canopy, which was dominated by the crowns of early mature, suppressed mature, and larger regrowth trees, will also undergo changes after fire. Recovering mature trees may dominate the mid-canopy for a decade or more after fire as their crowns redevelop. Those species most affected by crown death will likely decline in the canopy and will require a long period to rebuild their crowns from sprouting lower in the stem before they are able to reclaim their position in the post-fire stand. This may give less dominant species a growth advantage that will allow them to increase their dominance within the stand.

The nature of the changes to a stand caused by a moderate- to high-intensity fire will be heavily influenced by the pre-fire composition. For example, stands with higher proportions of the less resilient species, *E. sieberi* and *E. botryoides*, may experience greater shifts in the relative cover by species and stand structure. *Eucalyptus sieberi* and *E. botryoides* are more likely to experience crown death and therefore experience canopy structural changes even under moderate-intensity fires (Fig. 8). The overall effect of decreased canopy height and crown cover over a large proportion of the stand is to create opportunities for a new cohort of trees to establish. The interaction between the density and rate of crown recovery of the surviving trees and the growth of trees establishing in the new post-fire cohort will drive future species composition and stand development pathways until the next major disturbance.

To counter this dynamic, forest management activities that aim to increase the relative abundance of the other, more resilient, eucalypt species may buffer against a shift toward *E. sieberi* dominated forests. The trend could also be reversed through other management techniques that reduce the frequency and extent of high-intensity fire such as fuel reduction burning at low intensity, cultural burning, and other management interventions that help suppress wildfires during periods of elevated fire behavior.

Conclusion

Disturbances shape communities by killing individuals, providing opportunities for regeneration, and altering the competitive hierarchy of species within the stand. Species-specific differences in the ability to withstand the impacts of a disturbance (i.e., resistance) and the ability to recover after the disturbance (i.e., resilience) mediate the impacts of any given disturbance. In the mixed-eucalypt forests of southeastern Australia, spatial variation in fire intensity across the footprint of the 2019–2020 Black Summer bushfires led to diverse outcomes of tree mortality and recovery. Resistance to low-intensity fire, as indicated by avoidance of crown loss, is demonstrated by many species in forest communities, particularly as trees grow and bark thickness increases. The eucalypt species in this study increased in resistance with tree size. Resilience is characteristic of many species in ecosystems that experience frequent, high-intensity disturbances. The eucalypt species in the lowland mixed-eucalypt forest showed high resilience with over 95% of trees recovering through epicormic resprouting after moderate to high-intensity fire. However, *E. sieberi*, which had the highest resistance, was the least resilient species in the community. Mortality disproportionately impacted large *E. sieberi* trees that experienced high-intensity fire. The high resilience of most of the eucalypt species in the forests we studied confers a high level of compositional inertia to these stands; that is, they only experience minor changes in composition after fires. However, the low resistance of most of the eucalypt species meant that the stands were generally more open 2.5 years after the fire.

Larger, more intense fires, driven by a changing climate, have the capacity to change the structure and composition of forests in many parts of the world. However, in southeastern Australia, most of the canopy eucalypts are resilient to fires due to their ability to resprout vigorously after a fire. This means that the composition of the forests may change little, although the relative abundance and structure of the canopy species may shift. The exception is in stands dominated by *E. sieberi*, which had low resilience and are therefore more prone to fire-induced mortality but can re-establish rapidly from seed. In these stands, moderate- and high-intensity wildfires may generate a positive feedback loop that promotes the establishment of the species over other species in the forest. The result would be a shift toward less diverse stands with fewer habitat values and less resilience to future disturbances.

Supplementary Information

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Supplementary Material 1.

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Authors'contributions
All four authors contributed to the study design, analysis, and writing of this paper. Mark Lutze supervised and participated in the field work to collect data.

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Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate.
Not applicable.

Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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