










Demographic change and loss of big trees in resprouting eucalypt forests exposed to megadisturbance

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Abstract

Aim: Increased tree mortality linked to droughts and fires is occurring across temperate regions globally. Vegetation recovery has been widely reported; however, less is known about how disturbance may alter forests structurally and functionally across environmental gradients. We examined whether dry forests growing on low-fertility soils were more resilient to coupled extreme drought and severe fire owing to lower tree mortality rates, higher resprouting success and persistence of juveniles relative to wetter forests on more fertile soils.

Location: Fire-tolerant eucalypt forests of temperate southeastern Australia.

Time period: 2020–2023.

Major taxa studied: *Eucalyptus*, *Corymbia*, *Angophora*.

Methods: Demographic surveys of tree mortality and regeneration in all combinations of dry/wet forest, fertile/less fertile substrates exposed to extreme drought and fire were conducted. We used Bayesian regression modelling to compare tree mortality, diameter, response traits, population structure and occurrence of fire scars between substrates/forest types.

Results: Overall mortality (20%–33%) and topkill (34%–41%) were within historically reported ranges for various forests and soil types. However, we observed an atypical trend of increased mortality and topkill in the largest trees, particularly when they had structural damage from past fires. Trees in wet forests on more fertile soils had the highest levels of mortality. Numbers of persistent resprouting juveniles were highest in dry forests on low-fertility soils. Dry forests growing on low-fertility soils appear more resilient to compound disturbances due to lower rates of mortality and higher rates of juvenile persistence. Wet forests on more fertile soils may experience greater demographic change due to higher mortality of small and large trees.

Main conclusions: Mesic forests on relatively fertile soils were found to be at relatively high risk of demographic change from compound disturbances. Combined, fire and drought are likely to reduce the number of large trees in affected areas, with consequences for forest carbon cycling and storage.

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KEYWORDS

Eucalyptus, fire scar, megadrought, megafire, mortality, resprouting, seedling recruitment, temperate forest, topkill, tree population

1 | INTRODUCTION

Exceptionally severe, persistent and widespread droughts (i.e. 'megadroughts', Cook et al., 2022) coupled with exceptionally large fires (i.e. >10,000 ha, 'megafires', Linley et al., 2022) are linked to climate change and now occur regularly in Earth's temperate regions (González et al., 2018; Trugman et al., 2018; Urrutia-Jalabert et al., 2023). Droughts have become hotter, resulting in increasing atmospheric water demand that drives increased drying of vegetation and soils. At the same time, more extreme heat days expose leaves to temperatures close to, or in excess of, their thermal limits (Arnold et al., 2021; Hammond et al., 2022; Hartmann et al., 2022). The combined effects of these compound 'megadisturbances' (i.e. herein defined as compound megadrought and megafire) have led to widespread devastation of forests, causing mass tree mortality and triggering forest reorganization that may alter ecosystem structure and composition across multiple time-scales (Gustafsson et al., 2019; Millar & Stephenson, 2015; Steel et al., 2023; Stephens et al., 2018). The sensitivity of forests to megadisturbances is likely related to resilience (i.e. traits promoting recovery) and resistance (i.e. traits promoting survival; Nolan, Collins, et al., 2021). For example, forests dominated by trees capable of epicormic resprouting from the stem and canopy are likely to regenerate overstorey foliage cover within a few years following fire, experiencing minimal changes to structure (Pausas & Keeley, 2017). In contrast, forests dominated by trees unable to resprout epicormically may lose much of their above ground biomass following severe fire and new overstorey trees must be recruited (Bowman, MacDermott, et al., 2014). The latter type of forests may shift towards a juvenile-dominated state that is fundamentally different in structure from the prior state (Bowman, MacDermott, et al., 2014; McColl-Gausden et al., 2021; Seidl & Turner, 2022). In the most extreme scenario, repeated severe disturbances at intervals shorter than the time it takes for species to reproduce could result in permanent changes to structure and composition, for example, replacement of forest with another vegetation type (Coop et al., 2020).

Widespread recovery of vegetation has now been reported across areas affected by megadisturbances (Gibson & Hislop, 2022; Qin et al., 2022). These studies primarily use relatively coarse-scale remotely sensed data and were unable to quantify stand-scale changes in population structure or accurately differentiate between regenerating shrubs and trees. For example, greenness indices derived from satellite data (e.g. Landsat) typically show rapid vegetation recovery (Hislop et al., 2018), but field-validated LiDAR data reveal a range of longer-term structural impacts (Karna et al., 2019), that is, 'spectral recovery' may not necessarily equate to successful resprouting of the overstorey. Spatial variability in forest recovery cannot be fully explained by fire effects alone, as other factors such

as pre-fire drought-stress level, ecosystem sensitivity to disturbance and variability in edaphic conditions (e.g. nutrient and moisture availability) are likely to influence forest recovery and shape post-disturbance forest structure (Callahan et al., 2022; Dong et al., 2023; Nolan et al., 2022; see Figure 1). Mesic forests may be more likely to experience reductions in hydrological functions and growth during drought than xeric forests (Bendall et al., 2022a; Helman et al., 2017). However, many species from both wet and dry environments may be equally vulnerable to drought effects because intrinsic vulnerability traits of woody species are strongly convergent with site water availability (Choat et al., 2012, 2018). There is currently a limited understanding of how forest responses to extremes of drought and fire are influenced by abiotic factors such as substrate composition, which mediates forest growth via nutrient and moisture supply (Callahan et al., 2022; Jump et al., 2017; Morford et al., 2011; Neff et al., 2006).

Nutrient limitation is a key factor affecting plant growth and thus ecosystem productivity (Morford et al., 2011; Neff et al., 2006). For example, woody species that grow on nutrient-poor soils typically allocate resources to tissue longevity and defensive structures used to survive disturbances (e.g. starch reserves, thick bark), at the expense of stem growth (Knox & Clarke, 2005, 2011; Orians & Milewski, 2007). Nutrient-poor soils may constrain forest productivity during wet periods, while nutrient-rich soils may experience relatively higher productivity, potentially leading to increased risk of dieback during drought due to structural overshoot (Callahan et al., 2022; Jump et al., 2017). For example, large, tall trees typical of productive old growth forests are broadly expected to be at elevated risk of mortality during hot drought due to the effect of increased vapour pressure deficit, which is predicted to increase plant water stress with tree height (Bennett et al., 2015; McDowell et al., 2022; McDowell & Allen, 2015). Thus, forest responses to disturbances may be mediated by soil conditions via the effects of nutrient availability on: (i) productivity, for example, 'boom and bust' dynamics driven by structural overshoot; and (ii) resource allocation, for example, investment in defensive structures versus stem growth.

There is evidence of mass tree dieback and mortality associated with severe, prolonged drought in southeastern Australia, although most surveys have been conducted in tablelands (e.g. upland and inland) on shallow soils in either dry forest or woodland (Cremer, 1966; Losso et al., 2022; Nolan, Gauthey, et al., 2021; Pook et al., 1966; Pook & Forrester, 1984). Fewer observations exist for coastal/sub-coastal or in wet vegetation types (but see Pook, 1986; Pook et al., 1997; Losso et al., 2022). Work to date in southeastern Australia has not explicitly compared drought responses across substrate types, yet work elsewhere has demonstrated that substrate plays a key role in moderating drought effects on vegetation (Callahan et al., 2022; Paz-Kagan et al., 2017). The worst drought

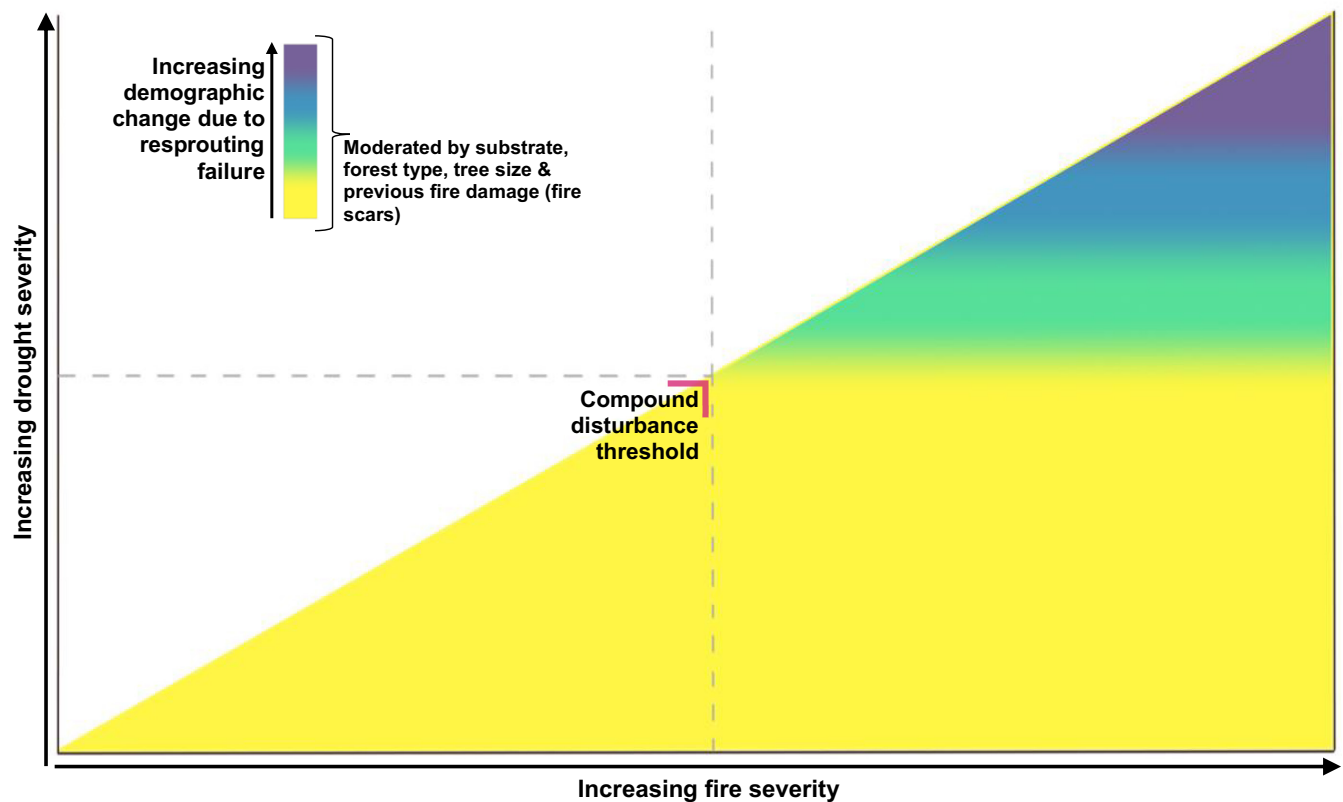


FIGURE 1 Conceptual diagram of the compound effects of fire severity (x-axis) and drought severity (y-axis) on the likely magnitude of demographic change due to resprouting failure (colour gradient). Pink arrow in centre represents hypothetical compound disturbance threshold.

on record (2017–2019), including the hottest year on record (2019), was then followed by massive, widespread wildfires that occurred across southeastern Australia during the so-called 'Black Summer of 2019/2020', leading to widespread canopy defoliation of forests spanning a range of substrates and climates (Bureau of Meteorology, 2020; Collins et al., 2021; Nolan, Boer, et al., 2020). Subsequent widespread vegetation recovery followed, driven by above-average rainfall (Fasullo et al., 2023; Qin et al., 2022). The scale of the Black Summer fires and prior hot drought highlighted an urgent need to conduct a large-scale field study of eucalypt responses to megadisturbance across a broad latitudinal gradient and across multiple forest types and substrates, while controlling for time-since fire, fire severity and drought severity. We hypothesized that the extreme, record-breaking nature of the compound severe drought and fires may have pushed forests beyond a compound disturbance threshold and that variability in demographic change could be detected due to the moderating effects of forest type (e.g. wet or dry) and substrate (e.g. higher or lower fertility, Figure 1). Specifically, we expected lower productivity dry forests, particularly those on nutrient-poor soils, to be better adapted to cope with extremes of drought and fire due to evolutionary selection for enhanced drought-avoidance and persistence strategies. We asked whether dry forests were better able to resist demographic change than wet forests, owing to lower tree mortality rates and higher persistence of juveniles, following combined

severe drought and fire. We also asked whether substrate (i.e. soil fertility) interacted with forest type to moderate responses to combined severe drought and fire via its effects on productivity.

2 | METHODS

2.1 | Study area

The study took place in southeastern Australia, spanning multiple bioclimatic regions across a broad latitudinal (-29.1° and -37.7°) and elevational range (near sea level to almost 1600m a.s.l.; Figure 2a). Surface geology is variable but large areas are dominated by sedimentary and igneous material such as sandstone and granite (NPWS, 2003). Sandstone-derived soils are generally of low fertility, while granite-derived soils are of moderate fertility (Clements et al., 2003; Eimil-Fraga et al., 2014; Turner, 2022). Soils in wet forests typically reach a higher level of structural development, with higher levels of organic matter and nutrients contributing to increased site productivity (Laffan et al., 1998). Dry sclerophyll forest (DSF) dominates elevated areas such as ridges, spurs and exposed aspects, while wet sclerophyll forest (WSF) dominates gullies, sheltered aspects and elevated areas with higher fertility soils and higher rainfall (Keith, 2004; McColl, 1969; Wardell-Johnson et al., 2017). Over the study region the minimum average monthly temperature

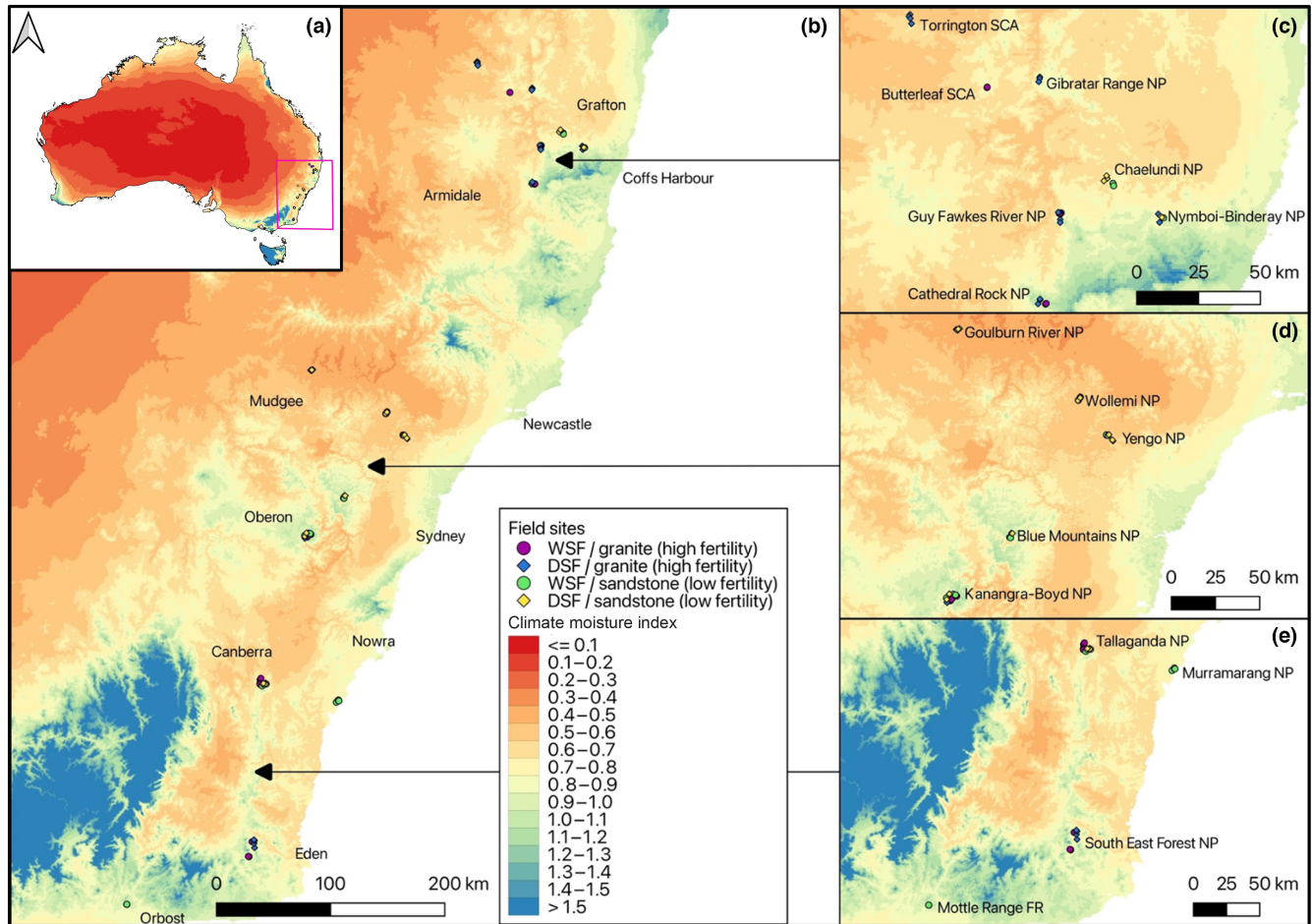


FIGURE 2 Composite image of the study region showing site locations (WSF/granite=purple circles; DSF/granite=blue diamonds; WSF/sandstone=green circles; DSF/sandstone=yellow diamonds) in relation to a climate moisture index (colour gradient). Panel (a) shows location of study region (pink rectangle) in relation to Australia. Panel (b) shows study region in relation to major towns. Panels (c–e) show zoomed in views of northern, central and southern parts of study area respectively and National Parks where sites were located. DSF, dry sclerophyll forest; FR, Flora Reserve; NP, National Park; SCA, State Conservation Area; WSF, wet sclerophyll forest. Climate moisture index=mean annual value of monthly ratio of precipitation to potential evapotranspiration (CSIRO, 2014).

ranges between -3.8 – 8.4°C and maximum average monthly temperature ranges between 18 and 31.9°C , while mean annual rainfall ranges between 460 and 2395mm (NPWS, 2003). Forests are dominated by tree species from the genera *Eucalyptus*, *Corymbia*, and *Angophora* (collectively referred to as ‘eucalypts’), with composition varying in response to climate (i.e. climatic moisture), geology and topography. See Supporting Information 1 for further details on climate and details on vegetation types and dominant species.

Fire regimes in forests of the study region typically consist of mixed severity wildfires and low to moderate severity prescribed burns (Bradstock et al., 2010; Collins et al., 2021). Fire intervals are typically between 5 and 20 years in DSF and 20 – 100 years in WSF (Murphy et al., 2013). Minimum ecological fire thresholds, for example, the minimum fire interval required to maintain ecological functions, vegetation composition and structure, have been described as 5 – 7 years in DSF and 25 years in WSF, although longer intervals are recommended for some variants of these forest types (Kenny et al., 2004).

2.2 | Fire and drought datasets

Drought severity was quantified using the Standardized Precipitation-Evapotranspiration Index (SPEI, Vicente-Serrano et al., 2010). SPEI is a derived index of climatic water balance (precipitation minus evapotranspiration) obtained from gridded time series of monthly precipitation and potential evapotranspiration with a minimum reference period of 30 years; positive (surplus water) and negative (water deficit) values of SPEI represent standard deviations from mean values based on the reference period. SPEI was calculated at 12-monthly time scale, which is adequate for detecting drought stress in temperate eucalypt forests (Ma et al., 2015; Pook et al., 1997). Data used to calculate SPEI was obtained from the SILO database (SILO, 2022). SPEI was calculated using the ‘SPEI’ package (Beguería & Vicente-Serrano, 2023) in R version 4.2.1 (Bürkner, 2017; R Core Team, 2023).

Fire history data was obtained from the New South Wales State Government (DPE, 2023; NSW Government & DPE, 2023). Fire severity

mapping for the 2019/20 fires was obtained from the Fire Extent and Severity Mapping (FESM) database (DPE, 2023). Fire severity maps are generated using both Sentinel 2 and Landsat 8 sensors, with a minimum resolution of 30m. Five fire severity classes were identified for forests, based on the degree of overstorey canopy scorch and consumption. Fire severity was defined as follows: unburnt; low (burnt understorey only; >90% green canopy), moderate (partial canopy scorch; 20%–90% canopy scorch), high (complete canopy scorch/partial canopy consumption; >90% canopy scorched; <50% canopy biomass consumed) and extreme (complete canopy consumption; >50% canopy biomass consumed; DPE, 2023). Fire severity was verified upon arrival at field sites, via visual assessment across the largest plot (see *Field methods* for plot sizes). We verified that all sites were last burnt in 2019/20 at high or extreme severity, with the exception of three sites that were classified by FESM as high severity but upon inspection had actually burned at moderate severity. The three moderate severity sites were combined with the high severity sites for analyses.

2.3 | Study design

The study design incorporated forest type (DSF, WSF) and substrate (sandstone=lower fertility soil, granite=higher fertility soil). Within each combination of forest type and substrate, sites were placed along a climatic gradient as defined by a climate moisture index (CSIRO, 2014) to obtain a comprehensive representation of tree species across these forests. The climate moisture index was defined as the monthly ratio of precipitation to potential evapotranspiration. We constrained our potential sampling to areas of severe drought (SPEI ≤ -1.5) and high or extreme fire severity (i.e. complete canopy scorch or consumption; identified from fire severity mapping) to target areas of megadisturbance. We only considered areas that had not burnt within their minimum ecological fire threshold (e.g. 10 years for DSF, 25 years for WSF) immediately prior to 2019/20 to minimize the effect of previous fire history on tree responses. Within areas meeting the criteria above we sampled 89 sites (one plot and two smaller sub-plots per site, see *Field methods* for further information) that were distributed between the four substrate/forest type combinations and across the climatic gradient (20–24 sites per combination).

2.4 | Field methods

All data were collected between May 2022 and February 2023. All trees >20 cm diameter at breast height over bark (DBH) were individually measured within a 50m \times 20m plot. Trees 10–20 cm DBH were measured in a 50m \times 10m sub-plot, located on the downslope side of the main plot to increase the chances of recruits being derived from mature trees within the plot. Trees <10 cm DBH were measured in a 50m \times 5m sub-plot within the 50m \times 10m sub-plot. This plot design ensures representative sample sizes were collected across tree size-classes (McElhinny et al., 2006). When trees were multi-stemmed, the largest stem was used to determine the

maximum DBH. When there was uncertainty whether a juvenile tree was a new post-fire seedling or a juvenile resprout that had survived the fire (i.e. 'juvenile resprout', resprouter with extant/dead main stem <10 cm DBH), the litter and/or soil around the base of the stem was gently excavated to search for small burnt stems. Trees <2.5 cm DBH were tallied. All post-fire seedlings and juvenile resprouts were manually counted within 50m \times 10m sub-plot. Juvenile resprouts \geq 2.5 cm DBH were also included in mortality, topkill and resprout position analyses (see Section 2.5).

For each stem we measured DBH, whether alive or dead, resprouting position and fire scar presence. DBH was measured over bark at 1.3 m above the ground on the uphill side of the tree. Whole-tree mortality (i.e. genet) was defined as a dead standing tree or fallen tree with or without an associated stump representing an individual that had died as a result of the most recent fire and associated drought. Dead standing trees were included if they still had small terminal branches, that is, stags/long dead trees with only primary/secondary branches remaining were not included. Stumps and fallen trees were only included in analyses if they were assessed to be damaged by the most recent fire, that is, bark present and little decay. The identity of dead stems <2.5 cm DBH was generally unable to be determined due to similarities with other burnt non-tree genera, thus mortality was not recorded for that size class. Trees were classified as 'dead' if they had no living leaves. Resprouting position was recorded as the highest position (canopy, stem or base) on a tree at which resprouting was observed (Bendall et al., 2022b). Trees that were resprouting from the base of the stem and showed no other evidence of live foliage were classified as 'topkilled'. Basal fire scars form following heat-induced cambium necrosis, which kills the outer bark and conductive tissues, exposing the heartwood to subsequent fires, termites and fungi (Gill, 1974; Gutsell & Johnson, 1996; Whitford & Williams, 2001). If the structural wood is reduced below a critical threshold, then stem collapse becomes likely (Mattheck et al., 1994). Therefore, we recorded all fire scars present before and/or created by the 2019/20 fires. We defined a fire scar as the presence of an injury at the tree base where bark and vascular tissue had been killed and either the heartwood and/or internal hollowing was clearly visible. Fire scars can be distinguished from other mechanical damage as they originate at the tree base and get narrower up the stem due to reduced heat exposure (Gill, 1974).

2.5 | Data analysis

Mortality, topkill and resprouting position were analysed at the tree-level. We used generalized additive modelling (Wood, 2017) to derive bounded estimates of response probabilities and differences for trees with and without fire scars sampled in each combination of substrate and forest type. Trees with DBH <2.5 cm were excluded from the mortality and topkill analyses (see above). For the resprouting analysis we included live trees with DBH <2.5 cm. DBH was included as a smooth term to account for known non-linear relationships between tree size and resprouting response (Bendall

TABLE 1 Summary of overall stand demographics and tree density.

Variable	DBH category	Sandstone/DSF mean \pm SE	Sandstone/WSF mean \pm SE	Granite/DSF mean \pm SE	Granite/WSF mean \pm SE
Live tree density (stems ha ⁻¹)	≥ 20 cm	180 \pm 16.6	224.8 \pm 14.1	195.9 \pm 11.3	242 \pm 15.8
	10–20 cm	75.5 \pm 11	60.4 \pm 12.7	53.2 \pm 15.9	54.5 \pm 11.1
	<10 cm	70.9 \pm 12.1	49.2 \pm 14.7	40.9 \pm 10	33 \pm 12.9
Dead standing tree density (stems ha ⁻¹)	≥ 20 cm	42.7 \pm 6.7	47.2 \pm 7.3	60.5 \pm 9.6	81 \pm 11.1
	10–20 cm	15.9 \pm 6.4	28.8 \pm 7.4	17.7 \pm 6.2	54 \pm 16.4
	<10 cm	24.5 \pm 12.8	14.8 \pm 6.9	15.9 \pm 5.9	37 \pm 13.5
Fallen tree density (stems/stumps ha ⁻¹)	≥ 20 cm	27.7 \pm 3.8	27.6 \pm 4.4	30 \pm 5.1	42.5 \pm 5.4
	10–20 cm	7.7 \pm 2.9	16.4 \pm 4.3	5.6 \pm 1.4	14.5 \pm 3.6
	<10 cm	11.8 \pm 4.6	11.2 \pm 5.6	10 \pm 4.4	14 \pm 3.5
Basal area live trees (m ² ha ⁻¹)		22.85 \pm 2.3	42.2 \pm 3.3	34.9 \pm 3.1	43.8 \pm 3.7
Basal area dead standing/fallen trees (m ² ha ⁻¹)		5.7 \pm 1	11.4 \pm 2.7	10.7 \pm 1.6	20.2 \pm 3.2
Number of seedlings (stems ha ⁻¹)		4592.7 \pm 1393	7156.8 \pm 1683.1	11085.5 \pm 4632.7	12,002 \pm 2790.6
Number of juvenile resprouts (stems ha ⁻¹)		965.5 \pm 144.8	377.6 \pm 109	409.1 \pm 87.6	262 \pm 114.1

Abbreviations: DSF, dry sclerophyll forest; WSF, wet sclerophyll forest; SE, standard error.

et al., 2022b; Fairman et al., 2019). Individual smooth terms were fit for each combination of substrate and forest type. A site-level random effect term was included to account for the nested sampling of trees within a site. Fire severity and the climate moisture index were included as covariates due to their potential influence on tree responses. Separate models were fitted for three response variables (mortality, topkill, resprouting position) using the equation:

$$\text{response} \sim s(\text{DBH}) + \text{substrate}^* \text{forest type} + \text{fire scar} + \text{severity} + \text{climate} + (1|\text{site}) \quad (1)$$

Mortality and topkill were modelled as Bernoulli-distributed variables and resprouting position was modelled as an ordinal variable. The number of post-fire seedlings and juvenile resprouts per site was analysed using a negative binomial distribution using the equation:

$$\text{response} \sim \text{substrate}^* \text{forest type} + \text{severity} + \text{climate} \quad (2)$$

Markov chains obtained from model fits were combined into a matrix of samples from the joint posterior distribution of model parameters, which we used to derive predictions of probabilities among the substrate/forest type combinations (Kruschke, 2015; Suzuki, 2019). We then used the matrix to calculate posterior difference distributions between contrasts of interest (e.g. DSF vs. WSF). Differences were summarized by calculating the mean (i.e. 'calculated mean difference'). Fundamental ecological differences existed between the forest types in our study, for example, trees typically grow larger in wet forests versus dry forests. Therefore, when calculating size-based differences among substrate/forest type combinations we only included predictions that were within the DBH range for each substrate/forest type combination. For example, we calculated the mean difference in the probability of mortality for the largest trees in one substrate/forest type versus the largest trees in another. Credible intervals ('CIs') were calculated as highest posterior density intervals (HPDI), in order to display the highest density 50% of model predictions ('CI⁵⁰') and lower/upper 95% bounds of model predictions. Where possible, overlap of CI⁵⁰ was visually assessed to support statements relating to the magnitude of difference between selected contrasts (i.e. differences were 'slight' = 5%–15%; 'moderate' = 15%–30%; 'substantial' =>30%). The data and R scripts used to generate the results are provided online in a data repository (see *Data availability statement*) and secondary results summaries can be found in [Supporting Information 2](#). All models were fitted using the 'brms' package for R version 4.2.1 (Bürkner, 2017; R Core Team, 2023).

3 | RESULTS

3.1 | Site-level data summary

We measured 4144 individual standing trees and 509 fallen trees/stumps that had existed prior to the most recent fire. We recorded 19,097 post-fire seedlings. Tree density was highest for post-fire

seedlings ($\sim 8600\text{ha}^{-1}$) and juveniles resprouts ($\sim 300\text{ha}^{-1}$) and slightly lower for established trees in other size-classes (e.g. $80\text{--}270\text{ha}^{-1}$; Table 1). Generally, around 23% of basal area per hectare was dead and 30% had been topkilled (Table 1).

3.2 | Modelling

3.2.1 | Tree-level mortality

Mortality at the tree-level had an overall mean probability of 25% but was higher in granite/WSF compared to the other substrate/forest types due to elevated mortality for small and large trees (granite/WSF = 32.9%; granite/DSF = 22.8%; sandstone/WSF = 22%; sandstone/DSF = 20.4%). The probability of mortality was highly dependent on fire scar presence or absence (mean probability of 38% vs. 8.8%, respectively) and also varied substantially with tree size (Figure 3a,b). Compared to trees with fire scars, most trees without fire scars were relatively less likely to die unless they were small (e.g. $<20\text{cm}$ DBH), an exception being small trees in granite forests, which had a mean probability of mortality of 25.4%–38% (Figure 3a). Across all substrate/forest types, trees with fire scars that were between 40 and 70 cm DBH had the lowest likelihood of mortality (22.6%–33.6%; Figure 3b). Mortality rates increased for trees with DBH of less than $\sim 40\text{cm}$, reaching a mean probability of 42.5% for sandstone/DSF, 49.5% for sandstone/WSF, 58.4% for granite/DSF

and 79.3% in granite/WSF (Figure 3b). Above 70 cm DBH, the likelihood of mortality rose sharply in granite forest types and sandstone/WSF, increasing by 12.3% in granite/DSF, 31.9% in granite/WSF and 23.3% in sandstone/WSF (Figure 3b). This was not the case for sandstone/DSF, where trees rarely exceeded 70 cm DBH and mortality decreased with tree size (Figure 3b).

Regardless of whether trees had a fire scar, mortality was more likely for small trees ($<20\text{cm}$ DBH) on granite compared to sandstone substrate in WSF, indicated by non-overlapping CI^{50} (20.1%–29.2% calculated mean difference at 10 cm DBH), and to a lesser extent in DSF (e.g. partially overlapping CI^{50} , 5.8%–13.4% calculated mean difference at 10 cm DBH, Figure 3a,b). There was little difference between the substrate/forest type combinations for intermediate size trees (e.g. overlapping CI^{50} , 1%–8% calculated mean difference at 50 cm DBH, Figure 3a,b). The largest trees with fire scars in sandstone/DSF (e.g. 75 cm DBH) were slightly less likely to die than the largest trees with fire scars in granite/DSF (i.e. 100 cm DBH; 16.5% calculated mean difference) but substantially less likely to die when compared to WSF forest type (27%–41.7% calculated mean difference, Figure 3b).

3.2.2 | Tree-level topkill

Topkill at the tree-level had an overall mean probability of 37.2% and this varied little among substrate/forest types (granite/WSF = 41%;

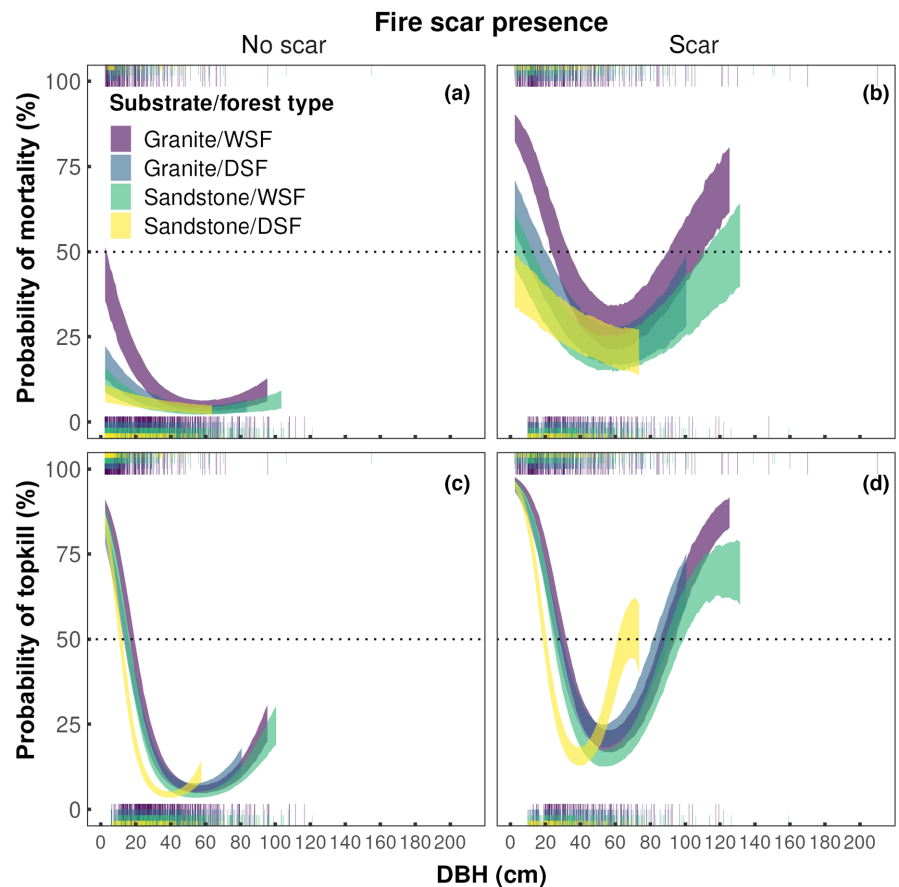


FIGURE 3 The effect of DBH (x-axis), substrate/forest type combination (coloured ribbons, left/right panels) and fire scar presence (left/right panels) on the probability of mortality (panels a and b) and topkill (panels c and d) for trees in forests of southeastern Australia exposed to megadisturbance. Coloured ribbons represent 50% credible intervals. The observed range of DBH values varied with substrate/forest type and fire scar category. Predictions for each substrate/forest type are constrained to within the 99th percentile of the observed DBH range for each plot window. Rug plots (narrow coloured vertical bars) at top (dead/topkilled trees) and bottom (live/not topkilled trees) of plot window represent the observation density across the complete range of DBH values used to inform the model. DSF, dry sclerophyll forest; WSF, wet sclerophyll forest.

granite/DSF = 36.6%; sandstone/WSF = 35.9%; sandstone/DSF = 33.9%; Figure 3c,d). However, the probability of topkill was twice as high for trees with fire scars compared to tree without fire scars (mean probability of 48.3% compared to 22.9% respectively) and varied substantially with tree size, although below 10 cm DBH the probability of topkill was very high irrespective of fire scar presence (e.g. >70%, Figure 3c,d). Trees without fire scars were generally unlikely to be topkilled unless they were small (e.g. mean probability >36% for trees <20 cm DBH), or to a lesser extent, larger than 50 cm DBH in sandstone/DSF (mean probability of 10.1%) or larger than 80–90 cm DBH in all other substrate/forest type combinations (mean probability of 14.6%–26.9%, Figure 3c). The stem DBH at which small trees became likely to be topkilled (e.g. >50% mean probability) was ~10–20 cm larger for fire scarred trees compared to unscarred trees (Figure 3c,d). Consequently, the probability of topkill for trees with fire scars and 20–30 cm DBH was comparatively much higher compared to trees of the same diameter without fire scars (mean probability of 33.4%–62.4% compared to 11.8%–30.9%, Figure 3c,d). Trees with fire scars experienced a dramatic increase in the probability of topkill (e.g. 50%–60% increase) as tree size increased from intermediate (e.g. 30–60 cm DBH) to the largest sizes within each substrate/forest type combination (Figure 3d, with the exception of sandstone/DSF, which peaked lower at a mean probability of 50.3% at 70–75 cm DBH, Figure 3d).

There was very little difference in topkill between trees with and without fire scars or between substrate/forest type combinations when trees were very small (e.g. <6% calculated mean difference for trees 10 cm DBH, Figure 3c,d). There was also a slight difference (e.g. 6–7% calculated mean difference) between granite/DSF, granite/WSF and sandstone/WSF across the range of DBH, although the granite forests had a higher chance of topkill at the largest trees sizes compared to sandstone/WSF (3.7%–19.1% calculated mean difference, Figure 3c,d). For sandstone/DSF, topkill was slightly less likely overall for average-sized trees (e.g. 30–35 cm DBH) compared to all other substrate/forest types (non-overlapping CI^{50} , calculated mean difference of 14.4%–24%, Figure 3c,d).

3.2.3 | Tree-level resprouting

Of the trees that showed resprouting, canopy resprouting was the most likely overall mechanism (mean probability of 72%), followed by basal resprouting (mean probability of 20%) and stem resprouting (mean probability of 15.5%). Overall, trees in wet forests were generally more likely to be successful canopy resprouters than trees in dry forests (mean probability of 74.7%–75.1% vs. 67.5%–68.5%) and trees in granite/WSF slightly less likely to be basal resprouters than the other substrate/forest types (mean probability of 15.9% vs. 20.9%–23.7%, Figure 4). Fire scar presence had little effect on the likelihood of stem resprouting (mean probability of 13.7 versus 17.3%) or canopy resprouting (71.2% vs. 72.9%, Figure 4a–d). Trees <10 cm DBH were highly likely to be basal resprouters (e.g. mean probability >80%) and trees slightly larger than this (e.g. 10–20 cm

DBH) had a moderate chance of being stem resprouters (mean probability of 30%–35%, Figure 4c–f). Trees with diameters larger than 20–30 cm DBH were likely to be canopy resprouters (e.g. >50% mean probability), with only a slight to moderate chance of being basal or stem resprouters (mean probability typically <25%). The DBH at which the transition from basal to stem to canopy resprouting occurred was larger for trees with basal scars than unscarred trees. The DBH range for this switch to basal or stem resprouting in medium-large trees varied between the substrate/forest type combination, peaking at conspicuously lower DBH for sandstone/DSF compared to the other substrate/forest type combinations (60 cm vs. 80–90 cm, Figure 4c–f). A lack of samples for some groups in the upper part of the DBH range meant that reliable inferences could not be drawn on the magnitude of the switch to stem or basal resprouting for medium-large trees (Figure 4c–f).

When trees were below about 20 cm DBH there was little difference between the substrate/forest type combinations in the probability of being in any resprouting position (mostly overlapping CI^{50} , calculated mean difference <5%–10%, Figure 4). Medium-large trees (e.g. 50–70 cm DBH) in sandstone/DSF were slightly more likely than trees in other substrate/forest type combinations to be stem resprouters (non-overlapping CI^{50} , calculated mean difference 4%–6%, Figure 4c,d). There was little difference in the likelihood of stem resprouting between the granite forests and sandstone/WSF, even at the largest trees sizes (mostly overlapping CI^{50} , calculated mean difference <9%).

3.2.4 | Recruitment

There was little difference in the density of post-fire seedlings across the substrate/forest type combinations, evidenced by strongly overlapping CI^{50} (Figure 5a). Higher seedling densities were primarily associated with higher values of the climate moisture index (i.e. cooler, wetter sites, see Supporting Information 2). There were substantially more juvenile resprouts in sandstone/DSF compared to the other substrate/forest types, evidenced by non-overlapping CI^{50} (calculated mean difference of 874 juvenile resprouts per ha, Figure 5b).

4 | DISCUSSION

The Black Summer exposed temperate eucalypt forests in south-eastern Australia to intense drought, recurrent heatwaves and massive firestorms (Abram et al., 2021; Collins et al., 2021; Squire et al., 2021) that may have been the most stressful conditions many extant trees had been exposed to during their lifetimes. We found that overall levels of tree mortality (25%) and topkill (37.2%) after the Black Summer megadisturbance were comparable to those reported in similar field studies of eucalypts exposed to high severity fire in southeastern Australia (e.g. <25% mortality, 20%–60% topkill, Collins, 2020; Nolan et al., 2022; Nolan, Boer, et al., 2020; Prior et al., 2016; Trouvé et al., 2021; Vivian et al., 2008). However, unlike

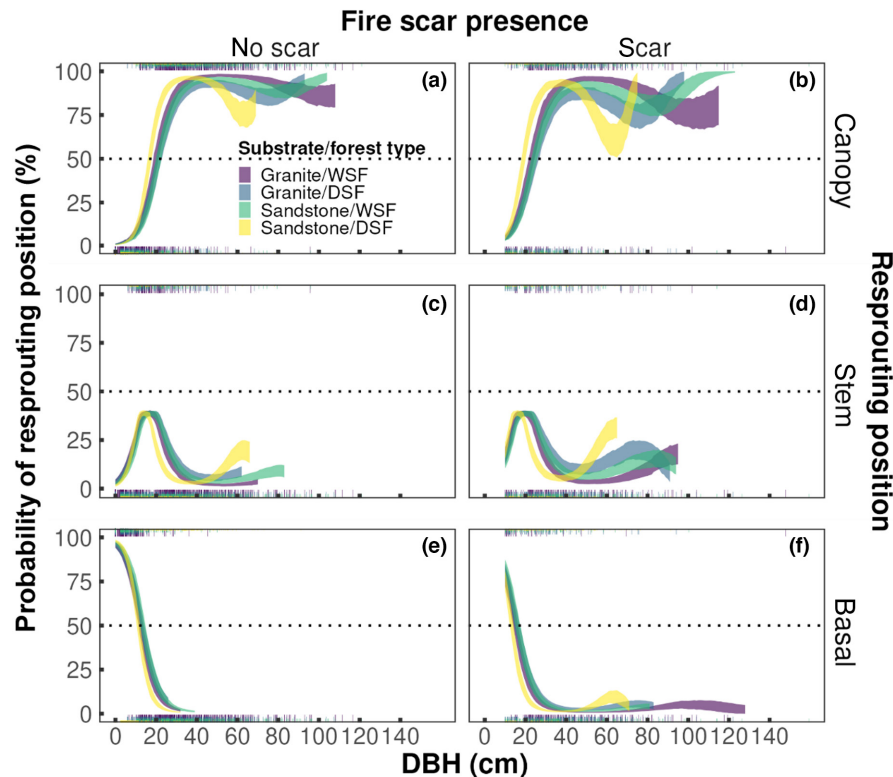


FIGURE 4 The effect of DBH (x-axis), substrate/forest type combination (coloured ribbons, left/right panels) and fire scar presence (left/right panels) on the probability of a live tree with evidence of resprouting being in each resprouting position (vertical panels; a and b = canopy resprouting, c and d = stem resprouting, e and f = basal resprouting) in forests of southeastern Australia exposed to megadisturbance. Coloured ribbons represent 50% credible intervals. The observed range of DBH values varied with substrate/forest type and fire scar category. Predictions for each substrate/forest type are constrained to within the 99th percentile of the observed DBH range for each plot window. Rug plots (narrow coloured vertical bars) at top (positive for corresponding resprouting position) and bottom (negative for corresponding resprouting position) plot window represent the observation density across the complete range of DBH values used to inform the model. DSF, dry sclerophyll forest; WSF, wet sclerophyll forest.

most previous studies in temperate eucalypt forests, we detected elevated rates of mortality and topkill for large diameter trees, suggesting reduced resistance to the 2019/20 megadisturbance. We found that the resistance of eucalypt communities varied across substrate and forest types, with greater mortality occurring in wet forests on higher fertility granite compared to dry granite forests or forests on lower fertility sandstone (Figure 3a,b). Both mortality and topkill rates varied strongly with stem diameter and were strongly amplified by basal fire scars, indicating that prior stem damage greatly impacts the ability of a tree to survive megadisturbance. Resprouting patterns of surviving trees and seedling recruitment were largely consistent across substrate/forest types, indicating a similar degree of resilience across the eucalypt forest communities. These results indicate that while megadisturbances are unlikely to lead to state conversion in these highly fire-tolerant eucalypt forests, important structural changes resulting from the loss of large diameter trees and partial canopy mortality will occur, and these changes will have important implications for biodiversity and ecosystem services. For example, the majority of above-ground carbon in eucalypt forests and other forests globally is stored in large trees (Collins et al., 2023; Gordon et al., 2018; Lutz et al., 2018; Nolan et al., 2022). If megadisturbance causes high mortality rates among

large trees, forests will become less effective at sequestering carbon, which will have global consequences.

In our study, many of the largest and likely oldest trees in the landscape had been killed or severely damaged (i.e. topkilled) following the compounding effects of extreme drought and fire. For example, with the exception of dry sandstone forests, all other forests experienced high losses of their largest trees (e.g. 37.7%–65.3%, Figure 3) and this loss was particularly evident in wet forests. Small tree mortality and topkill was also high but this was generally mirrored by increases in large tree mortality and topkill, resulting in atypical 'u'-shaped response curves.

Synthesis of global data suggests that drought-related mortality generally increases with tree size (Bennett et al., 2015). For example, large, tall conifers are predicted to be broadly more vulnerable to drought due to increasing constraints on canopy-scale water conductance as a function of increasing tree height and vapour pressure deficit (McDowell & Allen, 2015). High rates of mortality and topkill of large trees have also been reported for some fire-sensitive species exposed to severe fire (Barlow et al., 2003; Bowman, Murphy, et al., 2014; Trouvé et al., 2021) and compound disturbances from fire and insect outbreaks (McHugh & Kolb, 2003; van Mantgem et al., 2009). However, previous studies that monitored eucalypts

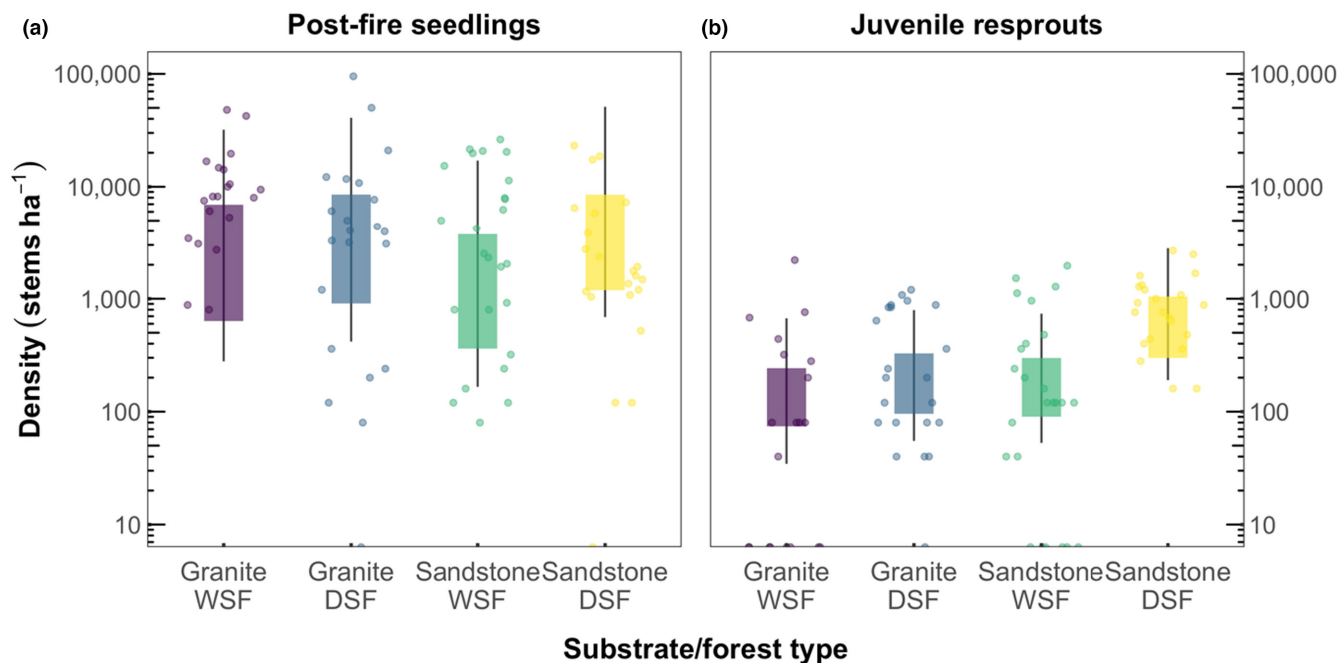


FIGURE 5 The effect of substrate and forest type (coloured boxplots and whiskers) on the predicted density of post-fire seedlings (panel a) and juvenile resprouts that had survived the fire (i.e. resprouter with extant/dead main stem <10 cm DBH, panel b) per hectare in forests of southeastern Australia exposed to megadisturbance. X-axis represents substrate/forest type combination and points represent raw data. Y-axis is log scale so that extremely high observations of seedling counts can be displayed. Coloured boxplots represent 50% credible intervals and black whiskers represent 95% credible intervals. DSF, dry sclerophyll forest; WSF, wet sclerophyll forest.

in forests and woodlands following extreme drought did not find that mortality increased with tree size (Losso et al., 2022; Nolan, Gauthey, et al., 2021). In fact, most studies of resprouting eucalypts have reported that both drought and fire-related mortality and topkill tend to decrease as trees become larger (Collins, 2020; Denham et al., 2016; Nolan, Gauthey, et al., 2021; Nolan, Rahmani, et al., 2020; Trouvé et al., 2021), likely due to larger trees having thicker bark protecting conductive tissues and greater capacity to access resources than small trees (Catry et al., 2010; Lawes, Adie, et al., 2011; Lawes, Richards, et al., 2011; Stephenson et al., 2014). Mortality in fire-sensitive eucalypts (e.g. obligate seeders) following severe disturbance is an exception, as mortality rates are similar across size classes, rather than 'u'-shaped due to inadequate protection of growth buds and lack of a lignotuber (Burrows, 2013; Clarke et al., 2013; Nicolle, 2006).

Bennett et al. (2016) also reported a 'u'-shaped mortality response curve comparable in magnitude to our result (e.g. 40%–50% mortality for trees >70 cm DBH) following the high severity 2009 Black Saturday fires in Victoria, Australia, which occurred under extreme drought and fire weather conditions in temperate eucalypt forest. Others have also reported 'u'-shaped mortality response curves but the mechanisms leading to mortality appear different to that detected in our study, for example, extremely high fire frequency (Watson et al., 2020) and interactions with termites (Williams et al., 2009).

Insect attack in eucalypts is typically related to defoliating psyllids (Hemiptera), wood-borers (e.g. Coleoptera) or termites (Isoptera).

Psyllid outbreaks are often confined to anthropogenically disturbed forests where natural processes that moderate psyllid populations have been disrupted by interactions between logging, weed invasion and over-abundance of a native bird species (bell miner, *Manorina melanophrys*; Lambert et al., 2022). Borers can damage structural and conductive tissues, potentially leading to branch shedding, die-back or structural failure (Lawson & Debus, 2016). White (2014a) suggested that some borer populations may increase during drought due to nutrient changes in the phloem and that outbreaks are typically more severe in senescent trees (also see Seaton et al., 2015; White, 2014b). Termites are also known contributors to structural failure in eucalypts (Whitford & Williams, 2001). We did not measure insect activity in our study or observe any anomalous levels of insect-related tree damage, but we cannot rule out that insect attack may have played a role in the mortality of trees at our field sites.

The evidence we have presented suggests that the 'u'-shaped response for mortality and topkill is likely to be a function of fire scar presence and tree size, with very small and very large trees being most likely to be killed or badly damaged. Fire scars reduce the functional area of conductive tissues required for transpiration and growth, causing impacts such as canopy dieback (Rundel, 1973; Shive et al., 2022; Sillett et al., 2015) to be compounded during drought (Bar et al., 2019; Dee et al., 2019; Losso et al., 2022). Fire-scar related impacts on tree function during drought may be further compounded by fire, as non-structural carbohydrates (NSCs) must be utilized to resprout (Clarke et al., 2013; Smith et al., 2018) and may become depleted, which can lead to post-fire mortality (Reed & Hood, 2023). Small diameter stems

require proportionally less cambial heating across their surface area than large diameter stems for fire scars to form that have a high arc length to DBH ratio (Stambaugh et al., 2017). Thus, small injuries (in an absolute sense) may have a relatively large effect on the health of small trees compared to small injuries in larger trees.

Larger, older trees have been exposed to more fires than younger trees and typically have a higher incidence of fire scars (Collins et al., 2012; Guyette & Stambaugh, 2004). Interactions between fire scars, associated stem hollowing and other agents of damage (e.g. termites, fungi) have been implicated as a primary contributor to collapse for large, old eucalypts (Whitford & Williams, 2001). It could be that under moderate drought and fire conditions, trees with fire scars retain enough resources to resist mortality or topkill but when a threshold is reached (e.g. compound disturbance threshold, Figure 1) resistance is overcome by external stressors. Thus, a possible explanation of why elevated mortality and topkill in large resprouting eucalypts has rarely been reported is that the disturbance threshold required to trigger this response is very high and also depends on the presence of underlying tree health issues associated with fire scarring and age.

An additional prerequisite for accurately detecting the responses of large trees is ensuring adequate sampling of large trees. For example, other studies examining tree mortality during the Black Summer fires by Nolan et al. (2022) and Volkova et al. (2022) did not detect a 'u'-shaped pattern in tree mortality in response to tree size across eucalypt forests similar to those examined in our study. One explanation for these differences could be the smaller sampling effort within forest types exposed to high severity fire, which limits the number of large trees in their datasets. For example, Nolan et al. (2022) only sampled 5–10 sites per forest type compared to 20–25 sites in our study. While Volkova et al. (2022) surveyed a high number of sites, their plot size was small (0.04 ha) and had been subjected to salvage harvesting, resulting in few trees >60 cm DBH. Even in our expansive dataset (89 sites, >4000 trees excluding seedlings) there were few trees greater in size than 60 cm DBH ($n=339$) and very few greater than 100 cm DBH ($n=41$). Undersampling of the largest trees in forests is an identified issue, as large trees are often rare in forested landscapes and therefore difficult to capture in field surveys using relatively small plots (Stovall et al., 2020). For example, using a very large dataset from a temperate conifer forest (1.8 million trees), Stovall et al. (2020) found less than 20 very large trees (e.g. >70 m tall) and estimated that 1100×0.1 ha plots would be required in order to capture at least 10 large trees taller than 60 m. This suggests that greater sampling effort and strategic planning is needed to capture the responses of large trees across landscapes.

4.1 | Demographic change varied with substrate and forest type

We found that dry forest on sandstone had no detectable increase in mortality for the largest trees in that forest type and had high numbers of juvenile resprouts along with average levels of seedling

recruitment, which is a common response pattern in dry eucalypt forests (Bendall et al., 2022b; Collins, 2020; Prior et al., 2016). This suggests that the population structure in dry sandstone forests has remained relatively stable despite megadisturbance, that is, low population turnover due to higher resistance of individuals. However, this may not guarantee future stability: if fire becomes too frequent, repeated physical damage may degrade the regenerative capacity of growth buds and place potential recruits at immaturity risk, for example, resistance traits do not develop fast enough to prevent mortality (Fairman et al., 2017, 2019). Additional population surveys of sites exposed to short fire intervals prior to the Black Summer drought and fires (see Le Breton et al., 2022 for identified areas) could shed light on the effects of temporally compounding disturbances on regeneration success.

Both single and multiple severe disturbances are expected to destabilize and reduce carbon stocks in fire-tolerant forests (Collins et al., 2023; Fairman et al., 2022), although the magnitude of change is likely to vary spatially, potentially owing to complex interactions between the severity of disturbance, climate, site productivity and forest type (Nolan et al., 2022). We found evidence that dry forests on sandstone experienced greater population stability compared to wet forests and to dry forests on more fertile soils (i.e. granite), suggesting that carbon losses were minimized in drier, nutrient-limited environments. In contrast, wet forests on granite had high losses of small and large trees, suggesting there were disproportionately higher carbon losses in wetter, more fertile areas.

In general, dry forests on granite responded more similarly to their dry sandstone counterpart compared to both wet forests, albeit with higher rates of small and large tree mortality and generally more extreme topkill. The responses of wet forests on sandstone were comparable to those of wet forests on granite but the response magnitude was moderated by substrate, leading to lower mortality and topkill. Our findings suggest that forests growing on higher fertility granite substrates have a greater tendency to shift states and experience population restructuring following megadisturbance compared to similar forests growing on lower fertility sandstone substrates, in which trees appear more resistant to change and capable of persisting with comparatively less population restructuring.

4.2 | Implications of megadisturbance in fire-tolerant eucalypt forests

The combined effects of extreme drought and severe wildfires resulted in overall tree mortality and topkill levels that were within historically reported ranges, although forests on higher fertility substrates experienced higher overall mortality than forests on lower fertility substrates due to elevated losses of small and large trees, particularly those with antecedent fire scars. The most extreme example of this is our result that the largest trees in wet forests on granite were up to 40% more likely than the largest trees in dry forests on sandstone to experience mortality (Figure 3b). Forests that are not severely constrained by nutrient availability or moisture (or

both) may be at relatively higher risk of demographic change, due to higher mortality of small and large trees, skewing demography towards small- to mid-sized trees. The tree size threshold at which disturbance-driven demographic change occurs is likely to shift down due to more frequent hot droughts and severe fires project under climate change. One consequence of this that may be already occurring is that forests could become depauperate of large trees, that is, collapse of old-growth forest elements and subsequently their associated fauna, which will have cascading negative impacts on carbon cycling, biodiversity and ecosystem function (Lindenmayer & Bowd, 2022; Lutz et al., 2018). Another consideration is that demographic change may manifest over different timescales among forest types. For example, in future, dry forests could experience higher frequency of severe fires than wet forests as a function of topographic position (e.g. exposed ridges), fuel availability and shorter tree heights, which could decrease epicormic resprouting success (Fairman et al., 2019) and increase rates of fire scar formation (Collins et al., 2012; McLean et al., 2015), leading to higher collapse rates of larger stems. Fire scars seem to be a major risk factor for large tree mortality and topkill (see Shive et al., 2022), likely due to imposing additional constraints on hydraulic function due to a reduction in conducting area (Dee et al., 2019; Rundel, 1973; Sillett et al., 2015) and increasing the likelihood of collapse due to structural failure (Gibbons et al., 2008; Mattheck et al., 1994; Whitford & Williams, 2001).

Our results suggest that southeastern Australian eucalypt forests exposed to similar megadisturbances in the future could experience further losses of large old trees, skewing demography towards smaller size classes, reducing the biomass and canopy height of forests. However, dry forests on lower fertility soils may have characteristics such as high individual tree resistance and fewer large trees that reduce their vulnerability to changes in population structure. Given the relatively high resilience of resprouting eucalypt forests to extreme disturbance (e.g. high rates of epicormic resprouting and low mortality), our results raise questions regarding the demographic stability of temperate forests globally, many of which are less resilient to drought and fire (Millar & Stephenson, 2015; Steel et al., 2023; Stephens et al., 2018). Our results provide a starting point for identifying forest susceptibility to demographic change, the threshold of which is likely to continue changing as new structural equilibria establish within tree populations during the new era of megadisturbance.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and associated code that support the findings of this study are openly available in figshare at https://figshare.com/articles/dataset/Forest_responses_to_megadisturbance/24540127.

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BIOSKETCH

The research team undertakes a wide range of research on terrestrial vegetation. Their research interests intersect in the study of ecosystem responses to compound stress events, in particular fire and drought and how they are being altered by climate change. They bring different expertise to bare on this research problem, including plant physiology, ecology, conservation planning and ecosystem modelling. More information on the researchers can be found here: <https://www.westernsydney.edu.au/hie/people/researchers>. Lead author Eli Bendall is an early career researcher interested in the effects of climate change and disturbances in forest ecosystems, eucalypt biology and species biogeography.

SUPPORTING INFORMATION

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

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