

Changes in the resilience of resprouting juvenile tree populations in temperate forests due to coupled severe drought and fire

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Abstract Elevated tree mortality and reduced recruitment of new trees linked to drought and fires has been reported across a range of forests over the last few decades. Forests that resprout new foliage epicormically from buds beneath the bark are considered highly resilient to disturbance, but are potentially at risk of elevated mortality, demographic shifts and changes to species composition due to synergistic effects of drought and fire. Despite this, the effects of drought-fire interactions on such forests remain largely unknown. We assessed the effects of drought severity and fire frequency on juvenile mortality, post-fire seedling recruitment and replacement of

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Department of Ecology, Environment & Evolution, La Trobe University, Bundoora, VIC 3086, Australia juvenile trees (balance of recruitment minus mortality) following fire. We compared dry ridgetops and wet gullies (i.e. two forest types that inhabit different topographic positions in the landscape) across a temperate forest in southern Australia. Both forest types experienced higher rates of fire-induced juvenile mortality in areas that had experienced severe drought compared to moderate drought, though mortality rates were generally low across all drought and fire combinations (e.g. < 15%). This result indicated that topographic position did little to reduce juvenile mortality when exposed to severe drought plus fire. In wet forest, severe drought also reduced recruitment and replacement of dead juveniles by post-fire seedlings compared to moderate drought. In dry forest net-negative replacement increased with the severity of drought. Across both forest types, the total pool of juveniles was reduced under severe drought

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A. Leigh School of Life Sciences, University of Technology Sydney, Broadway, NSW, Australia (by 16–79 in DSF; 5–11 in WSF). Future increases in the frequency of coupled severe drought and fire could potentially increase the susceptibility of resilient temperate forests to major changes in structure and function.

Keywords Drought effects \cdot *Eucalyptus* \cdot Fire effects \cdot Temperate forest \cdot Tree mortality \cdot Tree recruitment

Introduction

The structure and function of forests are dependent on factors affecting tree demography (Bowman et al. 2009; Allen et al. 2015; Cobb et al. 2017). Disturbances can negatively impact demographic processes such as mortality and recruitment of new trees from seedlings through to maturity, by reducing the capacity of forests to perform key ecosystem services, such as carbon sequestration and provision of water and timber (Van Nieuwstadt 2005; van Mantgem et al. 2009; Stevens-Rumann et al. 2018). Although most tree populations possess traits that allow them to survive during a disturbance (i.e. resistance) or recover lost biomass post-disturbance (i.e. resilience) (Clarke et al. 2013; Pausas et al. 2016), major shifts in disturbance regimes may destabilise populations (Allen et al. 2010; Bowman et al. 2014; Enright et al. 2015). Drought and fire are two key disturbances affecting tree demography (Michaelian et al. 2011; Brando et al. 2014; Fairman et al. 2017). Anthropogenic climate change is increasing the frequency and severity of drought and fire across forests worldwide (Wotton et al. 2010; Clark et al. 2016; Abram et al. 2021). Mass tree mortality and recruitment failure associated with extreme drought and frequent fire have been observed across many forests globally (Allen et al. 2010; Brando et al. 2014; Clark et al. 2016), resulting in structural and compositional changes and, in extreme cases, ecosystem conversion (Moser et al. 2010; Bowman et al. 2013; Allen et al. 2015).

Population persistence through fire is dependent on the demographic balance between mortality and recruitment. Recruitment of seedlings and recruitment of juvenile trees to the mature stage, must be sufficient to compensate for overall fire-related mortality if populations are to be maintained. The composition of resilience traits (e.g. vegetative resprouting, recruitment) and resistance traits (e.g. thick bark, tall canopies, deep rooting) (Bond and Midgley 2001; Burrows 2013; Clarke et al. 2013) within a population determines the demographic response to fire. In populations of obligate seeders, high rates of mortality and recruitment are observed following moderate to high severity fires (Vivian et al. 2008; Fairman et al. 2016). Conversely, low rates of mortality and variable rates of recruitment are observed in populations of epicormic resprouters (Vivian et al. 2008; Clarke et al. 2013; Fairman et al. 2016). Low mortality rates of mature trees and the rapid recovery of biomass in forests dominated by epicormic resprouters has led to the presumption that these forests are somewhat insensitive to changes in fire regimes (Bowman et al. 2013; Catry et al. 2013; Matusick et al. 2016), though their fire resilience may be reduced in the presence of other stressors (e.g. drought, Nolan et al. 2021a).

In contrast to mature trees, juvenile trees in populations of epicormic resprouters suffer high rates of topkill (death of the above ground component) and mortality in response to frequent fire, which may limit the number of recruits successfully completing the primary juvenile stage and reaching fire-tolerant size-classes (Prior et al. 2009, 2010; Fairman et al. 2019). The impact of frequent fire on juvenile mortality and topkill may be further elevated through exposure to high severity fires (Fairman et al. 2019; Collins 2020). If mortality of juvenile trees exceeds replacement by new recruits, transition from one forest type to another (or to a non-forest vegetation type) could eventually take place (Bowman et al. 2013). Mortality levels facilitating such a transition may require decades of frequent high severity fire in resprouting eucalypt forests and would likely require external pressures such as drought to increase mortality and reduce recruitment (Fensham et al. 2015, 2017; Collins 2020).

Resprouting plants respond to severe drought stress by utilising stored resources to sprout new leaves, maintain photosynthesis and survive (Zeppel et al. 2015). Severe drought may result in direct mortality or interact with fire to affect the pool of juveniles trees within a forest in a number of ways: (i) causing hydraulic failure and defoliation, leading to mortality pre-fire and increasing fuel loads that may further exacerbate fire impacts on surviving trees (Matusick et al. 2013; Ruthrof et al. 2016; Fensham et al. 2017; Nolan et al. 2021b); (ii) depleting carbohydrate stores pre-fire (e.g. via limiting the growth of storage organs) and potentially reducing post-fire resprouting success (Rosas et al. 2013; Bendall et al. 2022a); (iii) reducing the availability of canopy-stored seed by inhibiting reproduction or causing premature release of canopy-stored seed (Pook et al. 1997; Misson et al. 2010); (iv) constraining the potential recruitment niche, thereby limiting post-fire recruitment or elevating post-fire mortality (Moser et al. 2010; Savage et al. 2013). Thus, severe drought combined with frequent fire could potentially diminish the standing total pool of juveniles, leading to the development of a recruitment bottleneck.

Topography is a key driver of vegetation heterogeneity in temperate forests via its effects on resource gradients, such as soil nutrients and moisture (McColl 1969; Poulos & Camp 2010; Zellweger et al. 2015), and on fire behaviour (Bradstock et al. 2010; Collins et al. 2019a). Ridgetop environments are generally dry with low nutrient availability, whilst gully environments retain higher levels of moisture and soil nutrients (McColl 1969; Dyer 2009; Wang et al. 2009; Graham Milledge et al. 2013; Gou et al. 2021). Complex topography typically drives local-scale heterogeneity in fire regimes, with gullies usually experiencing patchier and less severe fires than ridgetops (Bradstock et al. 2010; Collins et al. 2019a). Gullies therefore may buffer more vegetation from the effects of drought and fire by providing refugia within topographically complex landscapes.

The temperate forests of southeastern Australia occur across climatically and topographically diverse landscapes that are periodically subjected to drought and fire (Bradstock et al. 2010; Abram et al. 2021). These forests are dominated by trees from the genera Angophora, Corymbia and Eucalyptus, which are collectively referred to as 'eucalypts' (Brooker & Kleinig 1999; Keith 2004; Boland et al. 2006). Eucalypts are resilient to fire, with most species possessing canopyheld seed stores and the capacity to resprout epicormically following canopy defoliating fires (Nicolle 2006; Burrows 2013). Eucalypts have diverse physiological responses to drought (Merchant et al. 2006, 2007), including well-developed storage organs used for post-disturbance resprouting (Burrows 2013), conferring resilience under extreme disturbance regimes (e.g. repeated high severity fires, Collins 2020). Dry sclerophyll forests (DSF), which dominate ridgetops on poorer soils are typically composed of small-medium sized trees (e.g. mature trees are typically 25–35 cm DBH and 10–15 m tall, Bendall et al. 2022b) and sclerophyllous shrubs (Keith and Benson 1988). Wet sclerophyll forests (WSF) grow in gullies or on ridges in higher rainfall areas with fertile soils and support relatively large, tall trees (e.g. mature trees are typically > 40 cm DBH and 25 m tall, Bendall et al. 2022b), usually with understories of soft-leaved plants and typically more fire- and drought-sensitive species compared to DSF.

In a related study we found that mortality and resprouting responses in larger trees (e.g.>10 cm DBH) were largely driven by tree characteristics such as previous fire damage, stems size and bark type, rather than increases in drought severity and fire frequency (e.g. > 10 cm DBH) (Bendall et al. 2022b). In particular, Bendall et al. (2022b) found that trees with small stem sizes, previous fire damage and thin, fibrous bark were more likely to experience mortality and changes in resprouting position (i.e. lowering of resprouting position). The present study investigated the effect of antecedent drought and fire frequency on mortality and recruitment responses of juvenile eucalypts to wildfire during 2013, across two contrasting forest types (DSF, WSF). We specifically focussed on small trees and asked whether the combined effect of severe drought and frequent fire is likely to lead to a bottleneck in juvenile recruitment. We asked whether: (i) juvenile survival and recruitment was lowest in areas exposed to severe drought and frequent fire; (ii) total juvenile abundance was lowest in areas exposed to severe drought and frequent fire; (iii) severe drought and frequent fire have synergistic effects on juvenile survival and recruitment. We also examined whether topographic heterogeneity influences spatial variation in the effects of drought and fire across these forests.

Methods

Study area

The methods herein largely follow that of Bendall et al. (2022b), although plot design, sampling protocol and data analysis differ from that study. The study region is located fully within (but does not represent in entirety) the Sydney Basin bioregion which covers approximately 45,000 km² along the eastern seaboard of southeastern Australia (Fig. 1). Soils are mainly sandstone- or shale-derived and of low fertility (DPI 2017). Elevation ranges from sea level to over 1200 m. Mean annual temperature and rainfall ranges between 11 °C-18 °C and 600 mm to 1500 mm, respectively, as a function of both altitude and distance from the coast (e.g. stations 068024, 063292, 066214, 067027, 061394, http://www.bom. gov.au/climate/data/, 08/07/2021). Exposed areas such as ridgetops are dominated by DSF whilst sheltered areas such as gullies are dominated by WSF (see Online Resource 1 for details on forest types). Typical fire intervals (i.e. the time elapsed between fires, which is not the same as fire frequency, i.e. the number of fires over a period of time) are between 5-20 years in DSF and 20-100 years in WSF (Murphy et al. 2013) and fires are generally of mixed fire severity (Collins et al. 2021). Short-interval fires (<5 years) are more likely to drive changes in forest composition and structure, compared to fire occurring at longer intervals (Arno & Allison-Bunnell 2002; Lewis et al. 2012; Cawson et al. 2017). Most dry and wet sclerophyll forests in the study region have burned 1–3 times since the 1970s, when reliable fire history records began (Bradstock et al. 2009; Price and Bradstock 2010), with a smaller proportion (~10%) burning in excess of three times (Hammill et al. 2013). The occurrence of severe and destructive wildfires has increased across the broader temperate biome in response to warmer drier conditions (Sharples et al. 2016; Abram et al. 2021; Collins et al. 2021), with large wildfires (> 100, 000 ha) occurring



Fig. 1 Composite image of the study region showing site locations (DSF=small black circles; WSF=stars), pre-fire drought severity and fire frequency combinations (colour shading) within the Sydney Basin bioregion (a). Sites were placed within four major firegrounds burnt in 2013. **b** shows location of Sydney Basin bioregion (magenta shading) within the con-

text of Australia. Pre-fire drought severity was determined by calculating the 6-monthly Standardized Precipitation-Evapotranspiration Index (SPEI) for October 2013. Fire frequency was calculated between June 1993–December 2014 (low ≤ 2 fires; high ≥ 3 fires) across the study area in 1993/94, 2001–03, 2006/07, 2013/14 and again in 2019/20 following our study.

Fire history

The study focussed on areas of the Sydney basin that were most recently burnt by large fires in October 2013 (Fig. 1), to control for the potentially confounding effects of time since fire. Two large fires occurred in the north of the region, which also experienced severe pre-fire drought (SD) and two fires occurred in the south, which experienced mild/moderate pre-fire drought (MD; Fig. 1). Major, widespread fires also occurred within the study region during 1993/1994, 2001/2002 (NPWS 2016). Antecedent fire frequency was calculated as the number of fires that occurred over a 20-year between 1993 and 2013 and was categorised as low (1-2 fires; LF) or high (3 or more fires; HF). Fire history data were obtained from the New South Wales National Parks and Wildlife Service (NPWS 2016).

Drought severity

Drought severity was estimated by calculating the Standardized Precipitation-Evapotranspiration Index (SPEI, for calculation see Vicente-Serrano et al. 2010). SPEI represents the climatic water balance (i.e. precipitation minus potential evapotranspiration) expressed as the standard deviation from average values calculated over a 30-year period (e.g. 1980-2010). Negative SPEI values represent water deficit relative to long-term conditions, whilst positive values represent increased water availability relative to long-term conditions. We calculated SPEI at 6-monthly time scale, which is considered adequate for detecting the effects of drought in temperate eucalypt forests (Pook 1986; Pook et al. 1997). SPEI values between -1 and +1 are considered to be within the range of normal climatic variability, whilst values below -1 represent increasingly severe drought (Slette et al. 2019); however, values of -0.5 or lower have been considered to be representative of drought conditions in temperate Australia (Ma et al. 2015). Study sites were categorised as either mild/moderate drought (MD; SPEI=0 to -1.4) or severe drought (SD; SPEI = < - 1.4). This threshold divided the study area into two approximately equal-sized (e.g. number of pixels) areas, each containing substantial areas of DSF and WSF. For example, values below -1.4 were restricted to warmer areas at lower elevations (e.g. in northern and western parts of the study region) whilst values above -1.4 occurred closer to the coast and at higher elevations (e.g. in southern and eastern parts of the study region, Fig. 1). Thus, some broad scale correlation between drought severity and climate may have existed in our study. To minimise confounding effects, sites were placed within narrow climatic bounds (see *Study design*).

Pre-fire drought severity varied considerably at broad scale within the study region, with fires in the northern part of the region burning under severe drought and fires in the southern part of the region burning under mild/moderate drought (Fig. 1). Most areas returned to non-drought conditions in the six months following October 2013. SPEI was calculated using spatially gridded climate data at $0.05^{\circ} \times 0.05^{\circ}$ resolution for the 6-month period prior to and after the 2013 fire. Field sites were only placed in areas where post-fire SPEI indicated that drought conditions were no longer present, to avoid the confounding effects of post-fire drought on juvenile mortality and recruitment. Thus, there was substantial variability in pre-fire drought severity and minimal variation in post-fire drought conditions across the study regions. Climatic data used to calculate SPEI was obtained from the SILO database (SILO 2019). SPEI was calculated using the function 'spei' in the 'SPEI' package in R (Vicente-Serrano et al. 2010).

Study design

The study design incorporated drought severity (MD; SD), fire frequency (LF; HF) and forest type (DSF; WSF) with 13-14 replicate sites per treatment combination (n = 111). Sites were distributed broadly across the study region to obtain sufficient spatial variability in drought severity (see Drought severity for details; Fig. 1). Study sites occupied narrow bounds of mean annual temperature and rainfall (e.g. ±2 °C and 200 mm across sites in each sampling area, based on 30 years of weather observations spanning the period 1970-2000) to control for climatic variability. The density of mature trees (e.g. > 10 cm DBH), recorded in an enclosing 50 m \times 20 m quadrat at each site, was broadly similar between the fire and drought classes within each forest type (see Fig. S1, Online Resource 2). All DSF sites were last burnt at moderate-high severity, with a high amount of scorching and consumption of canopy foliage (canopy 70–100% burnt; severity classes 3–5, Hammill and Bradstock 2006), whereas all WSF sites were burnt at low-moderate severity, with a mix of unburnt and scorched canopy foliage (canopy <70% burnt; severity classes 1–2, Hammill and Bradstock 2006). Because the topography of the study region limits the prevalence of high severity fires in gullies (Bradstock et al. 2010), fire severity could not be matched between forest types (i.e. not enough area was available for sampling high severity fire in WSF). Consequently, we have contrasted the 'common' fire severity patterns between forest types: high severity in DSF and low/moderate severity in WSF (Bradstock et al. 2010).

A 50 m \times 5 m plot was established at each site following established forest measurement protocols (McElhinny et al. 2006, 2005). DSF plots were confined to the top of ridges along contours (i.e. perpendicular to the direction of the slope), whereas WSF plots were confined to gully bottoms or lower slopes, adjacent to creeks along contours (see Online Resource 1 for examples of typical sites). Plot aspect varied between sites to minimise aspect bias. Plots were selected randomly within a few kilometres of access roads and within the treatment levels. Plots were placed at least 50 m from roads and trails (Marcantonio et al. 2013; Zamani et al. 2020) and at least 300-500 m (Bradstock et al. 2010) apart to reduce the effect of spatial autocorrelation. All plots were surveyed between February 2018 and July 2018.

Field methods

All juvenile trees between 2.5 and 10 cm diameter at breast height over bark (DBH) were identified and individually measured within a 50 m×5 m plot. Species were identified using the keys provided by Klaphake (2012) and Brooker and Kleinig (1999). Juvenile stems that arose from dead stems > 10 cm DBH were included, whilst juvenile stems that arose from live stems > 10 cm DBH were not included, i.e. when trees were multi-stemmed, the largest living stem was used to determine the maximum DBH. When stems were closely spaced (e.g. within 10–20 cm of each other), a 1 m long steel rod (4 mm diameter) was used to probe between stems to determine whether they were connected by a sub-surface lignotuber. To determine whether a juvenile was a new post-fire seedling or a surviving resprout (Fig. 2), the base of the stem was excavated of soil and manually checked for small burnt stems/lignotuber with evidence of fire damage. The DBH of each juvenile tree was measured over bark at 1.3 m above the ground on the uphill side of the tree.

Mortality (whole-tree/genet) was defined as a dead standing stem or downed stem/associated stump representing an individual that had died due to the most recent fire (Fig. 2). Stumps and logs were measured if they met the following criteria: (a) determined to be a product of the most recent fire by being allocated a decay state of '1' or less (wood hard and intact, see criteria described by Gordon et al. 2018 and Roxburgh et al. 2006); (b) had most likely been felled via fire scar formation and collapse, evidenced by a fire scar/break point, rather than collapse due to wind damage (see Bendall et al. 2022b). Mortality of juveniles smaller than 2.5 cm DBH was unable to be determined, as charred stems in this size-class looked similar to other non-eucalypt plant genera.

Data analysis

We fitted Bayesian regression models to analyse the influence of fire frequency and drought severity on each of the following response variables: the probability of juvenile mortality; the number of post-fire seedlings; the post-fire replacement balance (number of seedlings minus the number of dead juveniles); and the total post-fire juvenile abundance (number seedlings plus the number of surviving resprouts). For all models, the single predictor was a four-level categorical variable giving the combination of fire frequency (low versus high) and drought severity (mild/moderate versus severe).

Individual juvenile mortality was modelled as a Bernoulli process via a logit-link function. A weighting term was included to down-weight observations for downed stems since these had been measured across a larger plot area for an additional purpose in our related study on mature trees (see Bendall et al. 2022b). Site was included as random effect as the treatment categories varied at the site-level, rather than at the level of an individual tree. The number of post-fire seedlings was modelled as following a negative binomial distribution parameterised in terms of mean and dispersion. A model was fitted in which, for each combination of drought and fire classes,



Fig. 2 Diagram showing trees in various size-classes and potential effects of fire on mortality, recruitment and replacement amongst size-classes

the priors for distribution parameters were informed by overall priors. We chose this model structure to impose some shrinkage across drought and fire classes to ensure more reliable inferences given the relatively small number of sites within each fire and drought class, and also to deal with the occurrence of several large outlier values in the data. Since the fitted negative binomial distributions could be strongly right-tailed, we monitored posterior median values rather than posterior means. The model for post-fire replacement balance followed a similar structure as that for the number of post-fire seedlings. However, since the data included negative values, it was treated as continuous and modelled using a location-scale t-distribution, with the mean and standard deviation parameters specific to each drought and fire combination, and a global shape parameter learned by the model to reduce the influence presence of several large outliers in the data. Whilst this method monitored posterior means rather than posterior medians, it shared the same intent as in the other models, i.e. to provide and intuitive summary of the central tendency/most likely values.

Models were fitted via Markov Chain Monte Carlo using R version 3.5.0 (R Core Team 2020). The juvenile mortality model was fitted using the 'brm' function in the brms package (Bürkner 2017). The models of post-fire seedlings and post-fire replacement balance were fitted using the JAGS program (Plummer 2003) via the 'run.jags' function in the runjags package (Denwood 2016).

For each model, we sampled four Markov chains, each consisting of at least 5000 model iterations. We assessed model convergence using the diagnostic statistic of Gelman and Rubin (1992) and checked for acceptable levels of serial autocorrelation by ensuring that the statistic was less than 1.1. Additional posterior predictive checks, both visual and using a test statistic, were performed to assess model fit (e.g. WAIC, Pareto k diagnostic, Vehtari et al. 2017). All assessed models yielded Pareto k estimates either or < 0.5 or < 0.7, with the exception of the count of post-fire seedlings (DSFonly) where a very small number of estimates (1.8%)fell between Pareto k values of 0.7-1 (see the output of the code provided in the data repository for visual checks of model fit: https://github.com/eli-bendall/EB. Ch3.scripts). Separate Markov Chains for each model were then combined into a matrix of samples from the joint posterior distribution of model parameters, which we subsequently used to derive predictions of probabilities/tree count per site amongst the treatments (Kruschke 2015; Suzuki 2019). We then used the posterior model parameters to estimate the distribution of difference in response between contrasting drought and fire classes. These calculations are referred to in the results as 'median posterior difference', i.e. the median value of summarised difference calculations. Credible intervals were calculated as highest posterior density intervals (HPDI), in order to display the central 50% of model predictions and lower/upper 95% bounds of model predictions.

Data for all models, with the exception of the juvenile mortality model, were aggregated by site (DSF, n=56; WSF, n=55). We modelled DSF and WSF independently due to confounding of fire severity. The data and R scripts used to generate the results are provided online in a data repository (https://github. com/eli-bendall/EB.Ch3.scripts) and secondary results summaries can be found in Online Resource 2.

Results

Juvenile mortality

In dry sclerophyll forest, mortality was most likely under severe drought and low fire frequency, followed

25 (a)

20

15

10

5

0

P mortality (%)

by severe drought and high fire frequency (Fig. 3a). Mortality was less likely under mild/moderate drought and was similar across both fire frequency classes (Fig. 3a). When fire frequency was low, severe drought increased the likelihood of mortality by 11.6% compared to mild/moderate drought, whereas when fire frequency was high, the corresponding increase was 3.2%.

In wet sclerophyll forest, mortality was most likely under severe drought and was similar across both fire frequency classes (Fig. 3b). Mortality was less likely under mild/moderate drought and was similar across both fire frequency classes (Fig. 3b). When fire frequency was low, under severe drought the likelihood of mortality was higher by 5.7% compared to mild/ moderate drought. When fire frequency was high, the corresponding difference in mortality was 6.5% higher (Fig. 3b).

Recruitment and replacement balance

WSF

MOIHF

25 (b)

20

15

10

5

In dry sclerophyll forest, the number of post-fire seedlings per site was higher under severe drought and high fire frequency than any other drought-fire combination. Compared with low fire frequency sites, the number of new seedlings per site was higher under high fire frequency under severe drought, but



DSF

Fig. 3 The effect of drought severity and fire frequency on the probability of mortality for juveniles (2.5-10 cm DBH) in dry sclerophyll forest (DSF; a) and wet sclerophyll forest (WSF; b) of the Sydney Basin. X-axis indicates drought severity/fire frequency combination (MD mild/moderate drought; SD severe drought; LF low fire frequency; HF high fire frequency); colours correspond to treatment combinations; boxes and whiskers represent credible intervals for model predictions, where boxes represent the central 50% of posterior samples and whiskers represent upper and lower 95% bounds

SOILF

SDIHF

lower under mild/moderate drought (Fig. 4a). The number of dead juveniles per site was higher under severe drought than mild/moderate drought (Fig. 4c). There were approximately double the number of dead juveniles per site under severe drought compared to mild/moderate drought (Fig. 4c). The replacement of dead juveniles by post-fire seedlings was similar in all drought/fire combination, except under severe drought and low fire frequency, where replacement was negative (i.e. a mean net loss; Fig. 4e). When fire frequency was low, severe drought resulted in lower replacement by a median of 12 trees per site relative to mild/moderate drought (Fig. 4e). In contrast to sites with low fire frequency, under high fire frequency, severe drought had little effect on replacement (net gain < 1.5 tree per site), but there was much greater variability in replacement per site (Fig. 4e). The probability of decline, estimated as the proportion of posterior median replacement values fitted by the model that were less than zero, was substantial under severe drought combined with low fire frequency (approx.



Drought / fire frequency combination

Fig. 4 The effect of drought severity and fire frequency on the predicted count of post-fire seedlings (a and b), dead juveniles (d and c) and replacement (e and f) per site in dry sclerophyll forest (DSF; top row) and wet sclerophyll forest (WSF; bot-tom row) of the Sydney Basin. X-axis indicates drought severity/fire frequency combination (MD mild/moderate drought; SD severe drought; LF low fire frequency; HF high fire frequency); points are raw data and colours correspond to treatment combinations; boxes and whiskers represent credible intervals for model predictions, where boxes represent the central 50% of posterior samples and whiskers represent upper and lower 95% bounds. Scaling of y-axis intended to emphasise predictions, resulting in raw data points lying above the plot window. Number of missing points per treatment combination is given in the same order as they appear on panels from left to right; panel **a**: 3, 1, 1, 5; **b**: 2, 6, 0, 1; **c**: 0, 1, 6, 3; **d**: 2, 1, 0, 0; other panels: nil 92%) but considerably lower under all other drought/ fire combinations (29–40%).

In wet sclerophyll forest the number of new seedlings per site was highest under mild/moderate drought and high fire frequency and was zero under all other drought/fire combinations (Fig. 4b). Whilst high fire frequency had a positive effect on the number of new seedlings per site under mild/moderate drought (Fig. 4b) this effect was lost under severe drought, e.g. severe drought resulted in a lower number of new seedlings compared to mild/moderate drought, by 7 (Fig. 4b). The number of dead juveniles per site was very low across all treatments (e.g. < 1 dead juvenile per site; Fig. 4d), with little difference across drought severity or fire frequency categories (Fig. 4d). The replacement of dead juveniles by post-fire seedlings was highest under mild/moderate drought and high fire frequency and effectively zero under all other drought/fire combinations (Fig. 4f). High fire frequency had a positive effect on replacement under mild/moderate drought, with higher replacement by 8.5 juveniles per site, although this effect was negligible under severe drought (Fig. 4f). The probability of decline (median predicted replacement < 0) was very low under mild/moderate drought and high fire frequency (< 0.5%). Under all other drought/fire combinations the probability of decline was moderate to substantial (49.5–77%), though the net decline was low (e.g. < 12 juveniles per hectare).

Total juvenile abundance

In dry sclerophyll forest, total post-fire abundance of live juveniles (post-fire seedlings plus surviving resprouts, i.e. 'total juveniles') per site was highest under mild/moderate drought, being similar in both fire frequency classes (Fig. 5a). Total juvenile abundance per site was slightly lower under severe drought and high fire frequency and lowest under mild/moderate drought and low fire frequency (Fig. 5a). Relative to moderate drought, severe drought reduced median total juvenile abundance by 16 and 79 individuals under high fire frequency and low fire frequency, respectively (Fig. 5a). High fire frequency, compared with low fire frequency, resulted in higher median total juvenile abundance (62 individuals per site) under severe drought but there was no difference under mild/moderate drought (Fig. 5a).

In wet sclerophyll forest, total juvenile abundance was higher under high fire frequency in both drought severity classes and similarly low under low fire frequency in both drought severity classes (Fig. 5b). Whilst high fire frequency had a positive effect on total juvenile abundance under both drought treatments (Fig. 5b), severe drought resulted in lower total juvenile abundance compared to mild/moderate drought, by 5 juveniles under low fire frequency and 11 juveniles under high fire frequency (Fig. 5b).

Discussion

Our findings suggest that severe drought preceding recent wildfires has diminished the total pool of juvenile trees across two broadly distributed eucalypt forest communities in southern Australia. The decline in the juvenile pool was driven by increased fire-related mortality under severe drought conditions, rather than by a reduction in seedling recruitment. In our related study addressing the fate of mature trees (i.e. > 10 cm DBH) at these study sites, we did not detect this effect. However, in that study we did conclude that smaller trees were potentially at elevated risk of mortality under severe disturbance regimes (e.g. too frequent fire) due to a number of factors related to tree characteristics (see Bendall et al. 2022b). In contrast to expectations, frequent fire in the preceding decades leading up to coupled severe drought and fire in 2013 did not produce negative, synergistic effects on juvenile mortality, replacement or total post-fire abundance. On the contrary, high fire frequency may have offset the effect of severe drought in 2013, bolstering the number of juveniles (e.g. via release from competition), as reflected in the higher post-fire total juvenile abundance compared to sites with low fire frequency. In our related study (Bendall et al. 2022b), we found that smaller-sized mature trees on ridgetops (e.g. 10-15 cm) experienced a 10-20% increase in mortality due to high fire frequency (though a corresponding decrease in surviving adult density was present only in the severe drought class, see Online Resource 2), so it is plausible that reduced competition with overstorey trees may have resulted in increased total juvenile abundance in the present study. Others have also noted that increased juvenile abundance likely corresponds with elevated mortality in mature trees (Fairman et al. 2019; Watson et al.



Drought / fire frequency combination

Fig. 5 The effect of drought severity and fire frequency on the predicted count of all live juveniles (post-fire seedlings plus surviving resprouts, i.e. 'total juveniles') per site in dry sclerophyll forest (DSF; **a**) and wet sclerophyll forest (WSF; **b**) of the Sydney Basin. X-axis indicates drought severity/ fire frequency combination (*MD* mild/moderate drought; *SD* severe drought, *LF* low fire frequency, *HF* high fire frequency); points are raw data and colours correspond to treatment com-

2020). Post-fire seedlings at our study sites likely experienced natural thinning between the fire in 2013 and sampling period in 2018, though seedling densities generally stabilise after ~5 years following fire in resprouting eucalypt forests (McCaw and Middleton 2015).

It is important to note that juvenile mortality was probably underestimated in our study due to difficulties in reliably counting dead stems < 2.5 cm DBH (unidentifiable stems were excluded from analyses), which are often consumed by fire or are indistinguishable from other dead plant genera. Thus, replacement of dead juveniles by post-fire seedlings is likely to have been net-negative rather than close to zero in many cases. Both forest types in our study may therefore experience declines in tree recruitment, given that both the frequency and severity of drought and wildfire are increasing under climate change (Wotton et al. 2010; Abram et al. 2021; Collins et al. 2021). Severe drought and extreme fire regimes are known to be increasing mortality rates of mature trees in forests similar to those in our study and other forests globally (Allen et al. 2010; Brando et al. 2014; Fairman et al. 2017). However, we found little evidence of this in

binations; boxes and whiskers represent credible intervals for model predictions, where boxes represent the central 50% of posterior samples and whiskers represent upper and lower 95% bounds. Scaling of y-axis intended to emphasise predictions, resulting in raw data points lying above the plot window. Number of missing points per treatment combination is given in the same order as they appear on panels from left to right; **a**: 3, 3, 0, 3; **b**: 3, 9, 0, 2

our study system (see Bendall et al. 2022b) and suggest that such changes are likely restricted to smaller trees with characteristics that may increase the risk of mortality, such as previous fire damage. Nonetheless, our findings likely still have important implications for the persistence and condition of temperate forest assemblages in future, as the persistence of mature trees ultimately depends on successful recruitment. Our results therefore align with a broader global trend of forest decline and state conversion due to increasing drought and/or fire frequency (Savage et al. 2013; Brando et al. 2014).

Contrary to our predictions, the probability of juvenile mortality was similar between dry sclerophyll species and wet sclerophyll species, suggesting that topographic heterogeneity in ridge-gully systems may not moderate the effects of drought and fire on mortality of juvenile trees. We found similar patterns for mature trees at the same sites (Bendall et al. 2022b). The drought preceding the 2013/2014 fire season dried litter fuels sufficiently to facilitate the encroachment of fire into the gullies (see Collins et al. 2019a), likely with sufficient intensity to cause widespread topkill of juveniles (Lawes et al. 2011). Also contrary to our predictions, recruitment of postfire seedlings in dry sclerophyll forest was promoted by severe drought and high fire frequency, albeit with increased variability, when compared to mild/moderate drought (Fig. 4a). One explanation for this may be lower live mature tree density (see Fig S.1, Online Resource 2) and/or relatively high shrub mortality during severe drought (Pratt et al. 2014) and with frequent fires (Bradstock & Myerscough 1988; Bradstock & Bedward 1996), reducing competition with post-fire eucalypt seedlings. An alternate or complimentary explanation could be that environmental constraints, such as drought, can increase flowering synchronicity in some tree species and thus pollination efficiency (Bogdziewicz et al. 2017). Note, however, that subsequent seed production may be reduced by drought (Bogdziewicz et al. 2017). It might be possible that drought-adapted eucalypts increase flowering synchronicity during drought and manage to produce and retain seed, though research on this topic is lacking (Butt et al. 2015). If drought-adapted trees such as DSF species are able to increase flowering synchronicity due to drought, and maintain relatively high seed production, then seedlings may be able take advantage of increased resources created via lower tree density, elevated shrub mortality or impoverished shrub reproduction.

Our results indicated that severe drought may increase the potential for juvenile mortality during wildfire in temperate forests (van Mantgem et al. 2009; Brando et al. 2014; Fairman et al. 2017). With reproductively immature trees at increased risk from coupled drought and fire, forest resilience may decrease in future, leading to changes in species composition (biased towards more tolerant species, Brando et al. 2014) or at the upper extreme, shift towards a non-forest state (see Bowman et al. 2013; Moser et al. 2010). Mass drought-induced mortality in forest trees has been reported globally across varying forest types (e.g. temperate, tropical, Mediterranean, Allen et al. 2010), with up to 25% mortality reported in eucalypt forests in southern Australia (Matusick et al. 2013). Frequent fire can also reduce the capacity of some eucalypt species to resprout epicormically, making them more susceptible to mortality during future fires (Fairman et al. 2019). For example, up to 80% mortality has been reported for more sensitive sub-alpine eucalypt communities following three fires at short-intervals (Fairman et al. 2017). Although resprouting forests have been considered highly resilient to disturbance (Catry et al. 2013), overall mortality can be as high as ~25% following a single high severity fire (Bennett et al. 2016; Prior et al. 2016) and juvenile mortality as high as 40% following multiple fires (Collins 2020). Our estimates of mortality are more conservative than the aforementioned studies but nevertheless suggest that juvenile trees inhabiting drier ridgetop environments are likely to experience mortality rates as high as 15% under severe drought (Fig. 3a), 11–12% greater than under mild/moderate drought. We also found that juvenile mortality on ridgetops was higher under severe drought and low fire frequency compared to severe drought and high fire frequency (Fig. 3a). One possible mechanism for this could be that low fire frequency is relatively more conducive to advanced understorey development (e.g. increased shrub density) than high fire frequency (Bradstock et al. 1997; Watson et al. 2009), leading to more severe resource limitation during severe drought (Pratt et al. 2014; Renne et al. 2019). Thus, coupled severe drought and fire could be more likely to cause mortality of juvenile trees at low rather than high fire frequency sites due to additional pressures on resource acquisition related to the density of other understorey flora.

Similarly to ridgetops, juvenile trees inhabiting moist gully environments are likely to experience mortality rates as high as 10% under severe drought (Fig. 3b), compared with 3-4% under mild/moderate drought. In our study system, the probability of mortality for mature trees due to coupled drought and fire dramatically declined if trees did not possess preexisting fire damage (i.e. basal fire scarring) and with increasing DBH (Bendall et al. 2022b). Certain bark types (e.g. hard, compact bark types) also appeared to confer greater resistance to mortality (Bendall et al. 2022b). This suggests that trees in our system may experience a temporal window of elevated vulnerability to mortality during early life stages, which tapers off differently depending on inherent resistance traits, some of which (e.g. bark type) may influence the acquisition of basal damage and thus contribute to elevated risk of mortality throughout later life stages.

In our study, recruitment of post-fire seedlings in dry sclerophyll forest was highest under severe drought and high fire frequency (Fig. 4a). It could be possible that increased juvenile mortality (see Fig. 3) promoted the establishment of new seedlings via mechanisms such as increased resource availability and release from competition (Vivian et al. 2008). Further, in our related study on mature trees at these sites (Bendall et al. 2022b) we did find elevated mortality (e.g. by 10-20%) for small trees (e.g. 10-15 cm DBH) due to high fire frequency, which adds weight to this competition release hypothesis. However, if this were the case, we would expect similar or higher levels of recruitment under severe drought and low fire frequency, principally because juvenile mortality was highest in that category for our study (Fig. 3a, 4a). One possibility for this anomaly is that competition-related changes in levels of recruitment is influenced more substantially by mortality-related changes in the overstory, rather than by the mortality of neighbouring juvenile trees. Another possibility is that forests have high resistance to low severity fire (Collins et al. 2019b), but must resprout to survive high severity fire (Collins 2020). Consequently, rates of stem mortality tend to be greater following high severity fires (Denham et al. 2016). Our study did not consider the severity of fires when quantifying fire frequency, so it is unclear whether sites were subjected to multiple high severity fire events. Contrasting both low and high fire severity across fire frequency classes in ridgetops and gullies could shed further light on the role of fire severity in moderating the flux of mortality and recruitment.

Wet sclerophyll forest contrasted with dry sclerophyll forest by having low numbers of post-fire seedlings overall (Fig. 4b), whilst numbers of surviving resprouts were also much lower (see Online Resource 2). Further, total juvenile abundance was clearly reduced by severe drought in both fire frequency classes (Fig. 5b). This suggests that recruitment of these relatively more sensitive species may be inherently low and that severe drought has the capacity to kill off a proportion of persisting juveniles that may have survived given fire alone. Such reductions in recruitment under severe drought may be driven by loss of seed production and germination failure (Suarez & Kitzberger 2008; Clark et al. 2016). As a consequence, gullies in drought-affected regions that are burnt may not effectively recruit new trees. However, mass recruitment may only rarely be required to sustain populations in gully environments, given the prevalence of low severity fires (Bradstock et al. 2010) and fire resistance of many resprouting eucalypts (Burrows 2013). For example, survival of mature trees in gullies at our study sites was very high and >75% either resprouted from the canopy branches or had canopies that were unaffected by fire (Bendall et al. 2022b). Nonetheless, frequent, severe drought and associated limitations on recruitment may have implications in future. Gully environments have been identified as flora and fauna survival refugia during and following fires (Meddens et al. 2018), but during drought and severe fire-weather conditions, such refugia may not be effective at limiting the severity of fires (Price and Bradstock 2012; Collins et al. 2019a).

Potential ecosystem changes

It is predicted that climate change and extreme disturbance regimes will drive ecosystem conversion (Bowman et al. 2013; Fairman et al. 2016). Increased mortality, along with reduced regeneration and recruitment, could ultimately lead to major changes in forest composition in the long term (Fairman et al. 2016). Our data indicate that coupled severe drought and fire have the potential to reduce the overall abundance of post-fire seedlings and persistent, surviving juveniles within the extensive eucalypt forests of eastern Australia. Given the relatively low mortality rates in our study (<15%), decades of continued severe disturbance would probably be required to facilitate major demographic changes in these resilient forests, as has been suggested elsewhere (see Collins 2020). However, it is important to interpret our findings in the context of recent trends of increasing drought and associated mega-fires (Kirchmeier-Young et al. 2019; Boer et al. 2020; Collins et al. 2021). For example, the 2019/20 fire season in Australia saw an unprecedented ~7 million hectares of forest burn (>21% of the extant eucalypt forest biome) (Boer et al. 2020), with 44% of this area being burnt at high severity (Bowman et al. 2021; Collins et al. 2021). Our study was conducted prior to the 2019/2020 fires, which swept through our study area and are generally accepted to have been exacerbated by chronic drought on top of record-breaking temperatures, leading to mass dieback in southern eucalypt forests (Nolan et al. 2020, 2021b). Changes in disturbance regimes of this magnitude or greater will challenge forest resilience paradigms and may be sufficient to cause recruitment bottlenecks in future.

Author contributions EB, RB and LC conceived the ideas; EB, RB and LC designed the sampling methodology; EB collected the data; EB and MBe analysed the data; EB led the writing of the manuscript; RB, LC, MBe, AL, MBo and HC contributed to the writing of the manuscript; EB prepared Online Resource 1 and 2. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability All data are provided online in a data repository (https://github.com/eli-bendall/EB.Ch3.scripts).

Code availability All R scripts used to manage data, analyse data and generate figures are provided online in a data repository (https://github.com/eli-bendall/EB.Ch3.scripts).

Declarations

Conflict of interest The authors declare that they have no conflict of interest, financial or otherwise, that could have influenced this paper.

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