

Resilience of Resprouting Temperate Forests is Diminished by Coupled Severe Drought and Fire

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Research Article

Keywords: drought effects, Eucalyptus, fire effects, temperate forest, tree mortality, tree recruitment

Posted Date: November 3rd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-1041787/v1>

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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 juvenile trees (balance of recruitment minus mortality) following fire. We compared dry ridgetop and wet gully assemblages 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. This result indicated that topographic position (i.e. wet gullies) did little to moderate 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. Future increases in the frequency of coupled severe drought and fire will likely increase the susceptibility of resilient temperate forests to major changes in structure and function.

Introduction

The structure and function of forests are dependent on factors affecting tree demography (Bowman *et al.* 2009; Allen, Breshears & McDowell 2015; Cobb *et al.* 2017). Disturbances affect demographic processes such as mortality and recruitment of new trees from seedlings through to maturity, which may reduce 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 destabilize 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, Nock & Flannigan 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, Breshears & McDowell 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, Nitschke & Bennett 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, Nitschke & Bennett 2016). Low mortality rates of mature trees and the rapid recovery of biomass in resprouting forests 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).

In contrast to mature trees, juvenile plants 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, Murphy & Russell-Smith 2009; Prior, Williams & Bowman 2010; Fairman *et al.* 2017). If mortality of juvenile trees exceeds replacement by new recruits, transition from a forest to an alternative state 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; Fensham *et al.* 2017; Collins 2020).

Severe drought may interact with fire to affect the juvenile pool in a number of ways: (i) causing hydraulic failure, leading to mortality pre-fire (Matusick *et al.* 2013; Fensham *et al.* 2017; Nolan *et al.* 2021); (ii) depleting carbohydrate stores pre-fire and potentially reducing post-fire resprouting success (Rosas *et al.* 2013; Chapter 2); (iii) reducing the availability of canopy-stored seed by inhibiting reproduction or causing premature release of canopy stored seed (Pook, Gill & Moore 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, Mast & Feddema 2013). Thus, severe drought combined with frequent fire could potentially diminish the standing 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 behavior (Bradstock *et al.* 2010; Collins *et al.* 2019a). Ridgetop environments are generally dry with low nutrient availability, while gully environments retain higher levels of moisture and soil nutrients (McColl 1969). Topographic gradients in moisture availability typically drive 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 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'. Eucalypt species are resilient to fire, with most species possessing canopy-held 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; Merchant *et al.* 2007), including well-developed storage organs used for post-disturbance resprouting (Burrows 2013), conferring resilience under extreme disturbance regimes (e.g. Collins 2020). Dry sclerophyll forests (DSF), which dominate ridgetops on poorer soils are typically composed of small-medium sized trees 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, usually with understories of soft-leaved plants and have a relatively high proportion of fire- and drought-sensitive species compared to DSF.

Our study investigated the effect of antecedent drought and fire frequency on the survival and recruitment response of juvenile eucalypts to wildfire, across two contrasting vegetation types (DSF, WSF). We addressed the responses of mature tree (e.g. >10 cm DBH) in a separate, complimentary article. Specifically, this study focused on 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 is driving spatial variation in the effects of drought and fire across these forests.

Methods

Study area

The Sydney Basin bioregion covers approximately 45,000 km² along the eastern seaboard of southeastern Australia (Figure 1). Soils are mainly of low fertility, derived from sandstone and shale parent material (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). DSF dominates ridgetops and WSF dominates gullies, with most forested land occurring within the National Park estate (see Online Resource 1 for details on vegetation types). Typical fire intervals 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). Fires occurring at very short intervals (<5 years) are likely to result in changes to forest structure and composition, when compared to areas burnt at longer intervals (Arno & Allison-Bunnell 2002; Lewis *et al.* 2012; Cawson *et al.* 2017). Most 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 & Bradstock 2010), with a smaller proportion

(~10%) burning in excess of three times (Hammill, Tasker & Barker 2013). The occurrence of extreme 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 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 focused on areas of the Sydney basin that were most recently burnt by large fires in October 2013 (Figure 1), to control for the potentially confounding effects of time since fire. The fires occurred in four different sub-regions across the Sydney Basin, with two sub-regions experiencing mild/moderate drought (MD) and two experiencing severe drought (SD; Fig. 1). Fire frequency was calculated for each sub-region as the number of fires that occurred between 1993 and 2013 and was categorized 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 quantified by using the Standardized Precipitation-Evapotranspiration Index (SPEI, Vicente-Serrano *et al.* 2010). SPEI is an index of the climatic water balance (i.e. precipitation minus potential evapotranspiration) expressed as the number of standard deviation units from average values calculated over a 30 year period (e.g. 1980–2010). Negative SPEI values indicate increased water deficit relative to long-term conditions, while positive values indicate surplus water availability relative to long-term conditions. We calculated SPEI at a 6-monthly time scale, which is sufficient for detecting drought stress in temperate eucalypt forests (Pook 1986; Pook, Gill & Moore 1997). Slette *et al.* (2019) suggest SPEI values between -1 and +1 can be treated as falling within the range of normal climatic variability, while values below -1 represent progressively more severe drought conditions; however, values at or below -0.5 have been considered to be representative of drought conditions in temperate Australia (Ma *et al.* 2015). We partitioned sub-regions in our study into either mild/moderate drought (MD; SPEI = 0 to -1.4) or severe drought (SD; SPEI = < -1.4). This threshold was chosen as it divided the study area into two approximately equal-sized and climatically coherent regions, each contain substantial DSF and WSF populations. For example values below -1.4 were restricted to typically drier, warmer areas at lower elevation in the north-west of the study region while values above -1.4 occurred along the coastal fringe and in cooler areas with higher elevation (Fig. 1).

In the six months preceding the 2013/14 fire season, drought severity varied considerably within the study region, with fires in the northern sub-regions burning under severe drought and fires in the southern sub-regions burning under mild/moderate drought (Fig. 1). Most areas returned to low drought/normal conditions in the six months following October 2013. For each sub-region, SPEI was calculated using spatially gridded climate data at 0.05° x 0.05° resolution for the 6-month period prior to and after the

2013 fire. Field sites were only placed in areas where post-fire SPEI had returned to normal/near normal, 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 'SPEI' package in R (Vicente-Serrano *et al.* 2010).

Study design

The study design incorporated drought severity (MD; SD), fire frequency (LF; HF) and vegetation type (DSF; WSF) in a fully factorial manner, with 14 replicate sites per treatment combination ($n = 112$). The 112 sites were evenly distributed across the four sub-regions (28 sites per sub-region) to obtain sufficient spatial variability in drought severity (Fig. 1). Sub-regions occupied narrow bounds of mean annual temperature and rainfall ($\pm 2^\circ\text{C}$ and 200 mm across sites within each sub-region) to control for climatic variability. 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 & 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 & 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 vegetation types. Consequently, we have contrasted the 'common' fire severity patterns between vegetation types: high severity in DSF and low/moderate severity in WSF (Bradstock *et al.* 2010).

A 50 m x 5 m plot was established at each site following established forest measurement protocols (McElhinny *et al.* 2006; McElhinny *et al.* 2005). DSF plots were confined to the top of ridges along contours, 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 minimize aspect bias. Plots were selected randomly within a few kilometers of access roads and within the treatment levels identified in a GIS. Plots were placed at least 50 m from roads and trails to avoid edge effects and at least 300–500 m apart to reduce the effect of spatial autocorrelation. 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 the 50 m x 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, while 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 that maximum DBH. When stems were closely-spaced, 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 lignotuber presence. The DBH of each juvenile stem was measured over bark at 1.3 m above the ground on the uphill side of the tree.

Mortality 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 downed stems were only included if they were determined to be a product of the most recent fire based on criteria described by Gordon *et al.* (2018) and Roxburgh *et al.* (2006); and had most likely been felled via fire scar formation and collapse, evidenced by a fire scar/break point. 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).

Juvenile mortality was modelled as a Bernoulli process via a logit-link function. A weighting term was included to account for different plot sizes between standing stems and downed stems. The number of post-fire seedlings was modelled as following a negative binomial distribution parameterized in terms of mean and dispersion. A hierarchical model was fitted in which, for each combination of drought and fire classes, the priors for distribution parameters were informed by overall priors. We chose this model structure to ensure more reliable inferences given the relatively small number of sites within each combination of fire and drought classes, and 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 hierarchical 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. While this method monitored posterior means rather than posterior medians, it shared the same intent as in the other models, i.e. to obtain an estimation of the central tendency/most likely values.

Models were fitted via Markov Chain Monte Carlo using R version 3.5.0 (R Core Team 2019). The juvenile mortality model was fitted using the brms package (Bürkner 2018). The models of post-fire seedlings and post-fire replacement balance were fitted using the JAGS program (Plummer 2003) via 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 of Gelman and Rubin (1992) and checked for acceptable levels of serial autocorrelation. 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 among the treatments (Kruschke 2015; Suzuki 2019). We then calculated the difference between selected comparisons by arithmetically generating a distribution of differences that could be used to inform interpretation of the magnitude of differences among treatment combinations. Hence, 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 = 56). We modelled DSF and WSF independently due to confounding by fire severity. The data and R scripts used to generate the results are provided online in a data repository (<https://github.com/erb418/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 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

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 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. 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). While 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 substantial (49.5–77%), though the net decline was low (e.g. < 12 plants per hectare).

Juvenile abundance

In dry sclerophyll forest, post-fire abundance of live juveniles (post fire seedlings plus surviving resprouts) per site was highest under mild/moderate drought, being similar in both fire frequency classes (Fig. 5a). Abundance of live juveniles 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 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 juvenile abundance (62 individuals per site) under severe drought but there was no difference under mild/moderate drought (Fig. 5a).

In wet sclerophyll forest, post-fire abundance of live juveniles per site 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). While high fire frequency had a positive effect on juvenile abundance under both drought treatments (Fig. 5b), severe drought resulted in lower juvenile abundance compared to

mild/moderate drought, by 5 juveniles under low fire frequency and 11 plants under high fire frequency (Fig. 5b).

Discussion

Our findings suggest that severe drought preceding recent wildfires has diminished the 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 contrast to expectations, frequent fire in the preceding decades leading up to 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, as reflected in the higher post-fire juvenile abundance compared to sites with low fire frequency. Increased juvenile abundance in this context, however, likely corresponds with elevated mortality in mature trees (Fairman, Bennett & Nitschke 2019; Watson, French & Collins 2020). Numbers of 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 & 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, 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, Nock & Flannigan 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). Thus, our findings have important implications for the persistence and condition of temperate forest assemblages in future. These results are indicative of a broader global trend of forest decline and state conversion due to increasing drought and/or fire frequency (Savage, Mast & Feddema 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. The drought preceding the 2013/14 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 post-fire 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 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). Another possible contributor might be 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. If drought-adapted trees such as DSF species are able to increase flowering synchronicity due to drought, and maintain relatively high seed production, then they may be able take advantage of increased resources created via 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 toward more tolerant species, Brando *et al.* 2014) or a shift toward 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, Williamson & Bowman 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. Similarly, 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, 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). 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 forests have high resistance to low severity fire (Collins *et al.* 2019b), but must resprout to survive high severity fire (Collins 2019). 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), while numbers of surviving resprouts were also much lower (see Online Resource 2). Further, total post-fire 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.* in prep). 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 & 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, Nitschke & Bennett 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, Resco de Dios & Bradstock 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 2019/20 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; Nolan *et al.* 2021). Changes in disturbance regimes of this magnitude or

greater will challenge forest resilience paradigms and may be sufficient to cause recruitment bottlenecks in future.

Declarations

Funding

This project was completed as part of the first author's PhD candidature at the University of Wollongong. There were no external grants or funding associated with this project.

Conflicts of interest/Competing interests

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

Availability of data and material

All data are provided online in a data repository (<https://github.com/erb418/EB.Ch2.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/erb418/EB.Ch2.scripts>).

Author's contributions

Eli Bendall, Ross Bradstock and Luke Collins conceived the ideas; Eli Bendall, Ross Bradstock and Luke Collins designed the methodology; Eli Bendall collected the data; Eli Bendall and Michael Bedward analysed the data; Eli Bendall led the writing of the manuscript; Ross Bradstock, Luke Collins, Micheal Bedward and Andrea Leigh contributed to the writing of the manuscript; Eli Bendall prepared Online Resource 1. *All authors contributed critically to the drafts and gave final approval for publication.*

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Figures

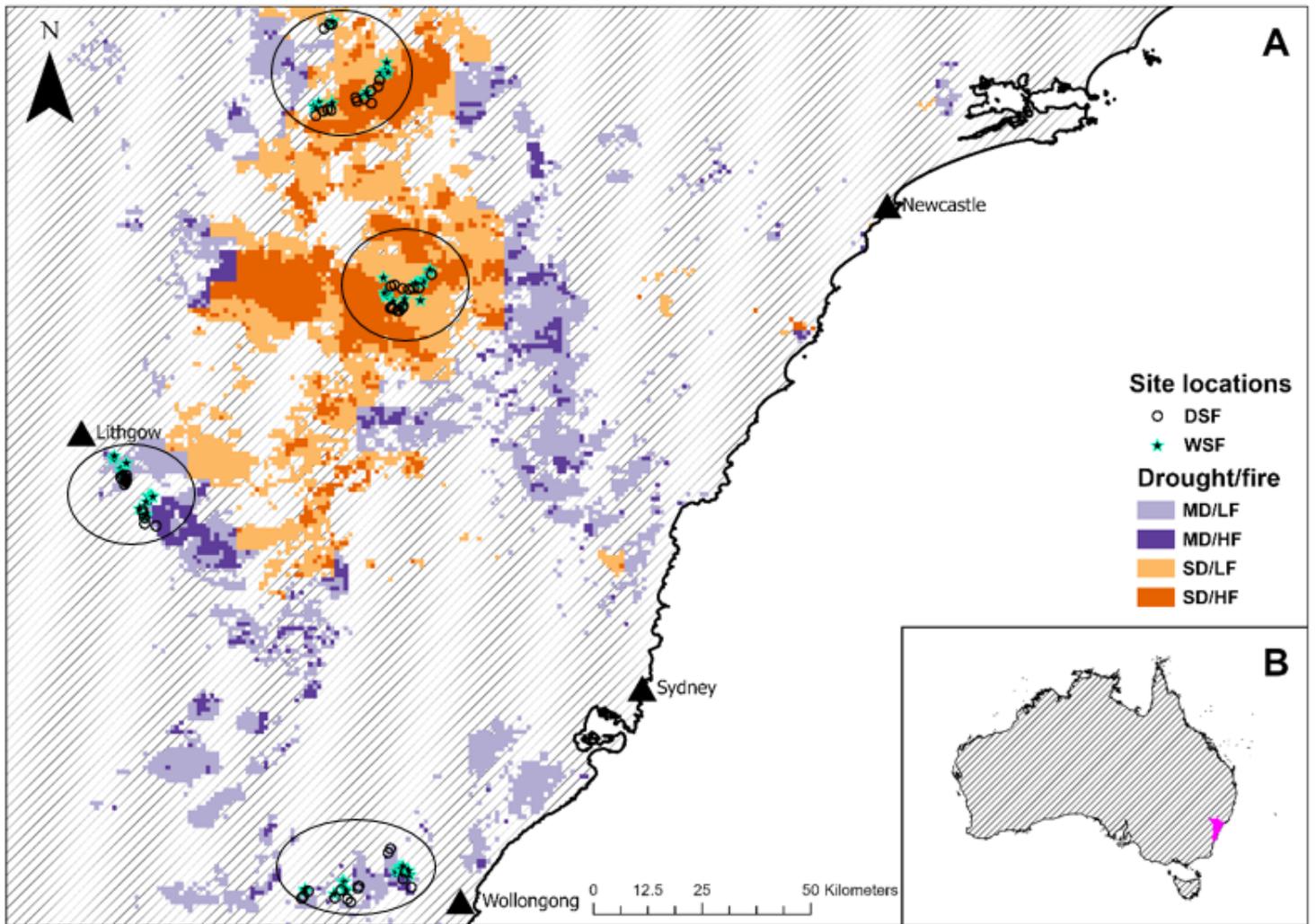


Figure 1

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 (panel A). Sites were clustered within four sub-regions (large black ellipses). Panel B shows location of Sydney Basin bioregion (magenta shading) within the context of Australia. Pre-fire drought severity was determined by calculating 6-monthly the Standardized Precipitation-Evapotranspiration Index (SPEI) for October 2013. Fire frequency was calculated between June 1993 – December 2014 (low ≤ 2 fires; high ≥ 3 fires).

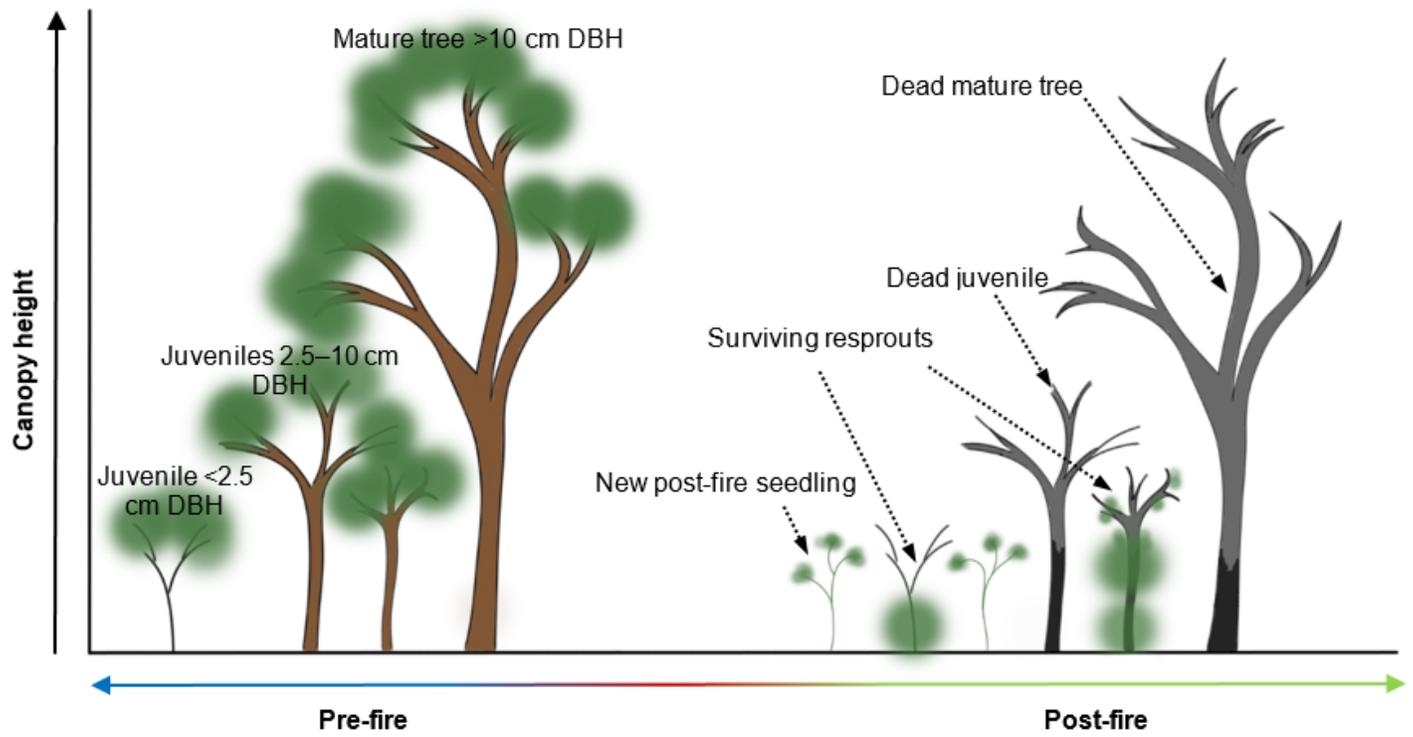


Figure 2

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

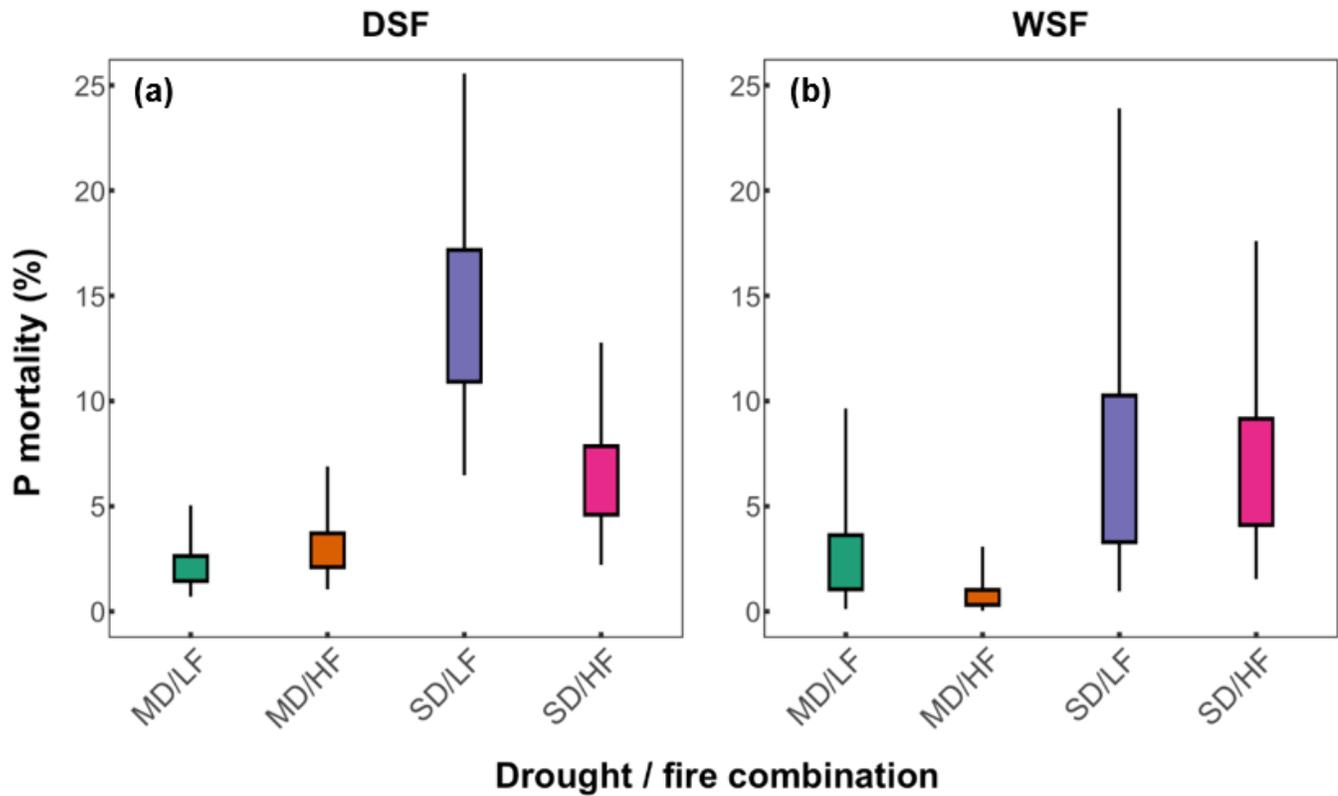


Figure 3

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; panel a) and wet sclerophyll forest (WSF; panel 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.

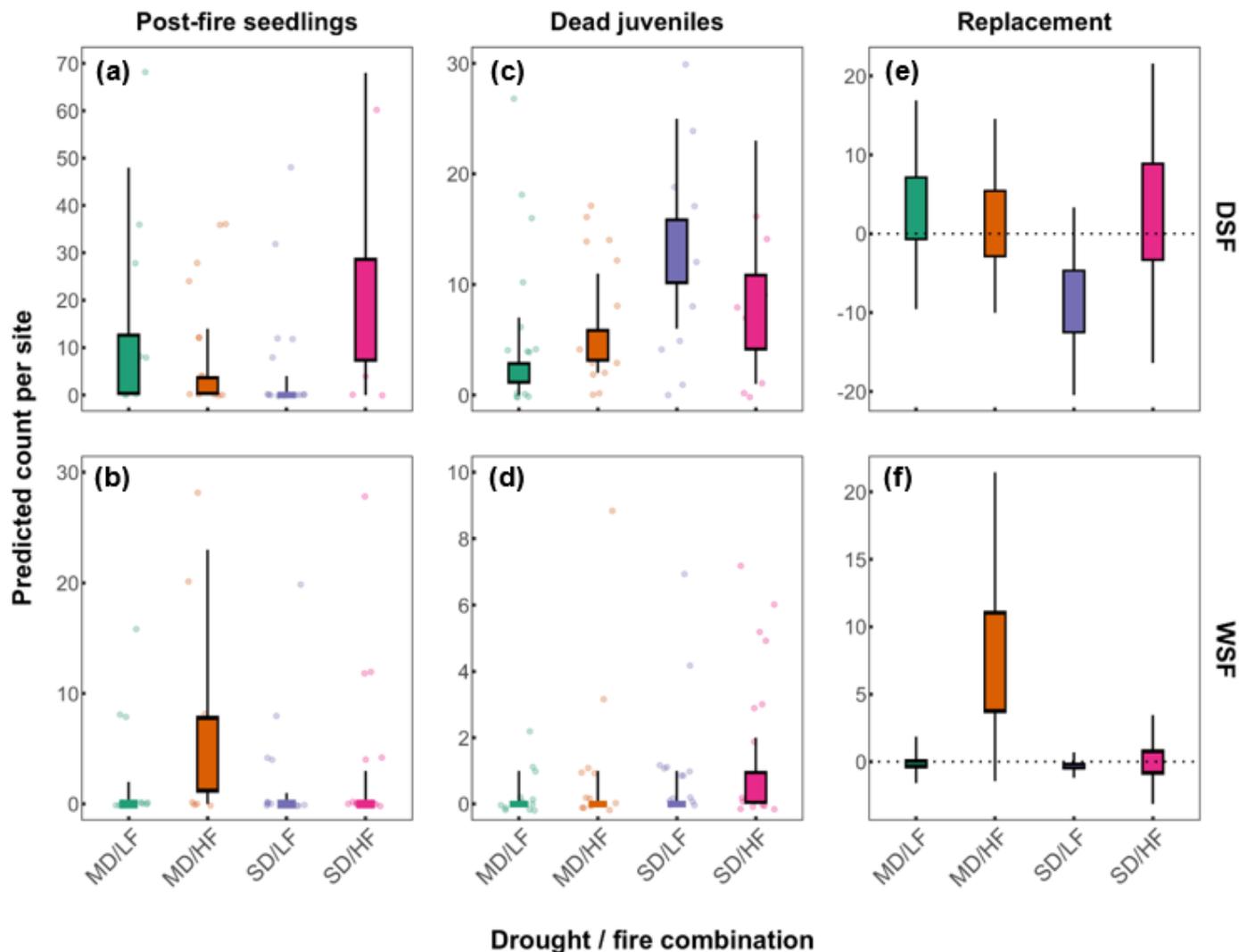


Figure 4

The effect of drought severity and fire frequency on the predicted count of post-fire seedlings (panels a & b), dead juveniles (panels d & c) and replacement (panels e & f) per site in dry sclerophyll forest (DSF; top row) and wet sclerophyll forest (WSF; bottom 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.

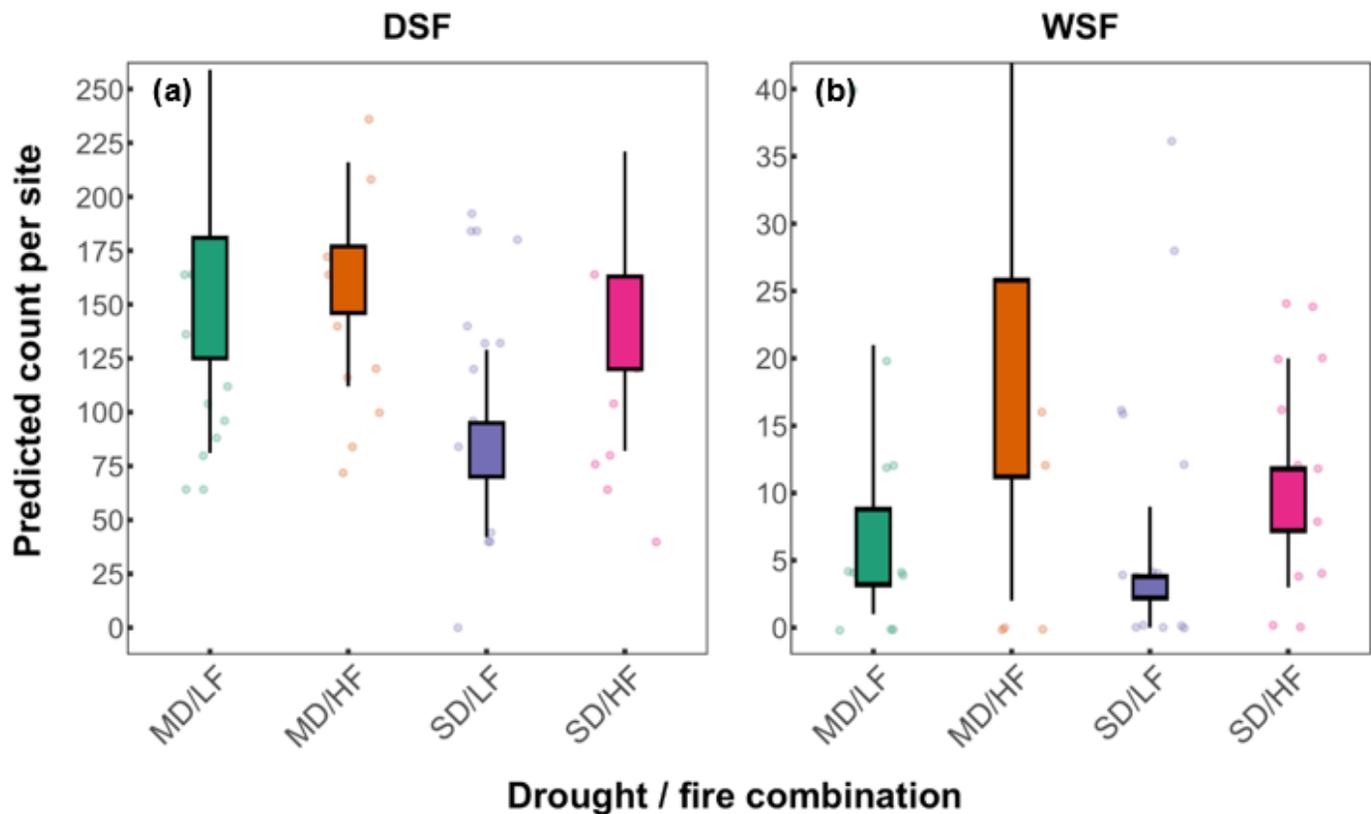


Figure 5

The effect of drought severity and fire frequency on the predicted count of live juveniles (post-fire seedlings plus surviving resprouts) per site in dry sclerophyll forest (DSF; panel a) and wet sclerophyll forest (WSF; panel 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 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, 3, 0, 3; (b): 3, 9, 0, 2.

Supplementary Files

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- [OnlineResource1.pdf](#)
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