Fire frequency and severity mediate recruitment success of a threatened shrub following a megafire

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Research Article

Keywords: fire regimes, fire management, threatened species, obligate seeder, physical dormancy, temperate pyric humid forests, Australia, fire frequency, fire severity, Pomaderris bodalla

Posted Date: July 19th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1801417/v1

Version of Record: A version of this preprint was published at Fire Ecology on November 2nd, 2023. See the published version at https://doi.org/10.1186/s42408-023-00217-z.

Abstract

Background Climate change is driving global fire regimes to become more extreme, potentially threatening plant species that are adapted to less extreme, historic fire regimes. Developing a better understanding of how threatened plant species might respond to a more extreme fire regime is key to successful future conservation in fire prone regions. The Australian megafires in 2019-2020 were unprecedented in the extent of vegetation burnt at very high to extreme severity and overlaid a complex history of prescribed burns and wildfires. These conditions established an ideal foundation for a case study of consequences for a threatened obligate-seeding shrub, *Pomaderris bodalla*, which grows in wet sclerophyll (mesic) forest on the south-east coast of Australia. We sought to confirm the response of this species to extreme severity fires, by surveying seedling recruitment at sites across a gradient of fire severity, exposed to a history of different fire frequencies. Our aims were to identify i) whether there was an interaction between the two fire regime elements and ii) whether the threshold for the usual positive relationship between fire severity and seedling recruitment could be exceeded under future fire regimes.

Results We found that recruitment had a hump-shaped response to fire severity, peaking at high severity sites as soil temperatures reached optimal levels for dormancy-break but declining at extreme severity sites. The pattern of response matched *in vitro* studies, which had established that physically dormant *P. bodalla* seeds had minimal dormancy broken at low fire-related temperatures, peak dormancy broken at high fire-related temperatures, and heat-induced mortality at extreme temperatures. Fire frequency had an overall negative effect on recruitment, with fewer recruits at more frequently burnt sites, however a significant interaction highlighted that this effect was driven mainly at high severity burn sites.

Conclusion Our findings indicate that while the species may persist at higher severity fires in the future, albeit with lower levels of recruitment, increased fire frequency poses an ongoing threat to *P. bodalla* and similar species. Fire management informed by species and ecosystem fire response traits can be a boon to conservation efforts, but requires detailed knowledge of species responses to all elements of the fire regime.

Background

Climate change is driving global fire regimes to become more extreme (Duane et al. 2021), with the now common megafires both a symptom and symbol of these changes. In areas affected by megafires, greater areas of vegetation are being burnt at higher severity (Collins et al. 2021) and more frequently (Nolan *et al*. 2021a; Le Breton et al. 2022). Species in fire prone regions are adapted to specific combinations of the elements that make up fire regimes (e.g. fire frequency, season and severity), and consequently a change in any one element has the potential to threaten species persistence, and degrade the ecosystems in which they occur (Miller et al. 2019). Anthropogenic changes to fire regimes are already pervasive, through land use changes and from the use of fire for management (Archibald et al. 2013), particularly in the context of protection of human assets and lives. Fire management seeks to actively alter fire regimes, intending to minimise the extent and severity of natural fires, both by

implementing prescribed burns to reduce fuel loads and by suppressing uncontrolled wildfires. As severe and uncontrollable wildfires become more frequent due to climate change, it is critical that land managers have knowledge of how flora, particularly threatened species already challenged by anthropogenically altered fire regimes, might respond to a more extreme fire regime.

The effects that changes to different elements of the fire regime may have on plant species demography and persistence are becoming increasingly well understood, with impacts differing depending on plant functional response. Species which can resprout from protected epicormic or basal buds are called 'resprouters', while species which are killed by fire and rely on soil- or canopy-stored seed banks for persistence are called 'obligate seeders'. Increased fire frequency is considered a significant threat to plant species, decreasing the time in which plants can regenerate and replenish seed banks or energy storage during the inter-fire period, and therefore reducing their capacity to respond to and persist through subsequent fires (Auld & O'Connell 1991; Keith, 1996; Enright et al. 2015; Auld & Ooi 2017; Gallagher et al. 2021). Resprouters are generally considered more resilient to increases in fire frequency than obligate seeders, although there are limits to what they can tolerate (Fairman *et al.* 2016; Nolan et al. 2021b). In recent years, whole forests of obligate seeders in Australia have been observed to undergo declines due to increased fire frequencies (Fairman *et al.* 2016). Climate change is further increasing the threat posed by too frequent fire, with drier and hotter conditions which simultaneously shorten fire intervals and lengthen the time it takes for plants to mature (Enright et al. 2015).

Altered fire severity is also commonly understood to be a potential threat to the persistence of plant species and ecosystems (Etchells et al. 2020; Landesmann et al. 2021). Resprouters, particularly epicormic resprouters, tend to be at greater risk when exposed to higher severity fires compared to obligate seeders (Pausas & Keeley 2014). Greater canopy consumption and heat are more likely at higher severities, and more likely to kill the buds from which resprouters regenerate after fire (Etchells et al. 2020). Additionally, the tendency for high severity fires to follow severe dry periods and droughts means resprouters are being burnt at high severity in an already compromised state (Nolan et al. 2021b). Obligate seeders are less affected by high severity fire, as many are killed even at lower severities. However, extremely severe and intense fires can result in temperatures that will kill both canopy seed banks (e.g. Offord et al. 2004) and seeds in the soil (Palmer et al. 2018). For some species, lower severities may actually pose more of a threat by killing off fire sensitive adult plants while failing to stimulate recruitment from seeds that require fire-related temperature cues (Le Breton et al. 2020).

How frequency and severity combine to impact plant species and the ecosystems in which they occur remain underexplored (Basset *et al.* 2017; Barker, Price & Jenkins 2021), especially under climate change scenarios currently playing out (Kelly et al. 2020), but are highly likely to have interactive or additive impacts on recruitment. For example, Palmer et al. (2018) investigated the impacts of fire severity on *Acacia* species in east Australian dry sclerophyll forests and found that increasingly high severity fire promoted higher recruitment, therefore leaving behind a smaller residual seed bank (Palmer et al. 2018). While this high severity fire resulted in a strong recruitment response, they concluded that the population was at greater risk from even a single subsequent fire event, if it were to occur after a short interval.

Fernández-García et al. (2019) found that serotinous obligate seeding *Pinus* species in Spain suffered additive negative impact by high severity fires and fire frequency. Severity and frequency clearly have the capacity to interact and modify their impacts on species post-fire recovery and persistence. Consequently, to enable effective conservation, there is an urgent need to improve and formalise our understanding of how these interactions may threaten species persistence.

The impacts of changes to different elements of the fire regime, both alone and in combination, are likely to vary across ecosystems (Enright et al 2015; Nolan et al. 2021b) depending on how much the current regime diverges from the historical regime. Temperate pyric humid forests in Australia are one of the six functional groups in the global temperate-boreal forests and woodlands biome and dominate much of the continent's east coast (Keith & Mac Nally 2020). Fire management and large-scale shifts in land use since European invasion led to frequent higher severity fires for land clearing by colonists and later frequent lower severity hazard reduction burning aimed at reducing fuel loads (NSW NPWS 2011). These forests are highly biodiverse, significant carbon sinks and are adapted to extremely high severity and low frequency fire, recurring over multi-decadal or century-scale time scales.

One of the key functional types in subcanopy and understory flora in temperate pyric humid forest is obligate seeding, with long-lived soil-stored seed banks which can lay dormant for decades before being stimulated to germinate by fire-related cues (Keith & Mac Nally 2020). Up to 82% of shrub species in these forests possess some form of dormancy (Collette & Ooi 2021), often with fire-linked cues for breaking seed dormancy and stimulating recruitment (Keith & Mac Nally 2020). Species with physically dormant seeds, which possess an impermeable seed coat that requires heating or physical scarification to break dormancy (Ooi et al. 2014), account for around 40% of shrub species with dormancy in the region (Collette & Ooi 2021). Optimal germination is often tied to temperatures of over 80°C among species with physically dormant seeds (Auld & O'Connell 1991; Ooi et al. 2014), believed to be an adaptation to fire (Keeley et al. 2011). Seeds requiring dormancy-breaking temperatures of 100°C or more, like many of those within the genus *Pomaderris*, are therefore likely to be adapted to high fire severity (Ooi et al. 2014; Le Breton et al. 2020). Fire severity and soil-heating is therefore likely to drive variation in germination and recruitment response of physically dormant species, while the obligate-seeding strategy is highly sensitive to fire frequency.

In south-eastern Australia, the 2019–2020 fire season burnt around 10 million ha in a series of the large megafires (Nolan et al. 2020; Gallagher et al. 2021), including over 21% of the temperate forest biome (Boer et al. 2020). The area burnt at high severity during these fires was proportionally similar to past fires, however, the sheer extent of the ~ 1.8 million ha burnt at extremely high severity was unprecedented in modern fire records (Collins et al. 2021). The fire footprint overlaid a complex fire history of frequently overlapping smaller fires and in doing so pushed much of the landscape below the minimum fire intervals required for regeneration and species persistence (Gallagher et al. 2021; Le Breton et al. 2022). How then may species respond to a fire that represents, at an event level, the conditions these species are adapted to (i.e. severe wildfire), while at a regime level, conditions that may pose a threat (i.e. frequent, mixed severity fires)?

The aim of this study was to explore how fire frequency and fire severity affect the post-fire recruitment of fire-sensitive species through a case study of an obligate seeding shrub, *Pomaderris bodalla* N.G.Walsh & Coates, which requires high temperature germination cues for optimal recruitment (Le Breton et al. 2020). Specifically, we sought to determine whether high temperature thresholds required for breaking physical seed dormancy in *P. bodalla*, observed *in vitro*, translated to a response to fire severity in the field, and how this effect was mediated by fire frequency. We hypothesise that *P. bodalla* populations will have high post-fire recruitment following higher severity fires, but this effect will be diminished in populations that have been burnt more frequently in the past due to a depleted soil-stored seed bank. We tested three main predictions: i) seedling recruitment will increase with fire severity, ii) seedling recruitment will decrease with fire frequency, and consequently iii) the highest levels of seedling recruitment will be observed following higher severities and lower frequencies of fire, while the lowest levels of recruitment will be observed following lower severity and higher frequency fires.

Methods

Study species and region

Pomaderris bodalla N.G. Walsh & G. Coates is an obligate seeding shrub endemic to the south-eastern coast of Australia in New South Wales (Fig. 1a). The majority of the population occurs between Moruya (-35.920, 150.093) and Merimbula (-36.891, 149.901) but there are two disjunct records in the upper Hunter Valley (-32.278, 150.902) c. 400 km north of the core population (Fig. 1a). The southern populations tend to be patchily distributed in moist open forest in sheltered gullies and the riparian zone in the foothills of the southern escarpment (Walsh & Coates 1997), while the northern records occur on more exposed slopes in open woodland (Bell, 2001, 2008). Mean annual rainfall varies from 829 mm at the southern extent of its range to 636 mm at the northern extent (Australian Bureau of Meteorology 2021). *Pomaderris* are typically killed by fire, though some species have the capacity to resprout following partial canopy scorch (Le Breton et al. 2020), and they recover from physically dormant seeds in soil-stored seed banks (Le Breton et al. 2020). *In vitro* germination trials have revealed that seeds require exposure to high fire-associated temperatures to overcome their physical dormancy. Germination was minimal at temperatures below 100°C, which appears to be at or near the optimum temperature for dormancy break given that little to no mortality was observed (Le Breton et al. 2020). Notably, temperatures of 100°C or higher indicate a close association with fire, given such high temperatures in the soil are unlikely to occur otherwise (Le Breton et al. 2020) and heat-related mortality is limited to higher temperatures still. Consequently, the relationship between germination response and fire-related soil temperatures is hump-shaped, peaking around 100°C and declining at higher temperatures.

The present study focusses on the core populations in the southern extent of *P. bodalla's* range (Fig. 1a). These populations primarily occur in Bodalla and Moruya State Forests and Kooraban National Park. Logging of native timbers has historically occurred across all three areas and continues in both State Forests, however the practice ceased in Kooraban National Park when it was gazetted in 2001 (NSW NPWS 2011). The gullies and riparian areas in which *P. bodalla* occurs within this region are dominated

by wet sclerophyll forest communities within the temperate pyric humid forests functional group (Keith & Mac Nally 2020). Although fires in these forest types are naturally infrequent and of high severity, the broader landscape has a complex history of lower severity burns implemented by the Yuin people (NSW NPWS 2011). After European invasion, frequent high severity fires were used for land clearing by colonists and later, frequent low intensity hazard reduction burning has been aimed at reducing fuel loads (NSW NPWS 2011; Fig. 1b). During the 2019–2020 fire season close to 50% of the wet sclerophyll forests in NSW were burnt (Le Breton et al. 2022) at some of the highest severities observed in the state (Collins et al. 2021). It is estimated these fires impacted around 47% of the known populations of *P. bodalla* (Fig. 1c).

Surveys and population estimates

Ten populations (Fig. 1b) were chosen for survey based on their fire history, how frequently they had been burnt and whether they had been burnt during the 2019–2020 fire season. Fire history and frequency data were obtained from statewide fire history mapping from 1960–2020 (Le Breton et al. 2022) and fire severity classes for the 2019–2020 fires were obtained from the NSW SEED data portal (https://www.seed.nsw.gov.au/). We obtained two fire severity classification datasets, as different methods have been found to be more or less accurate in different vegetation types. These were FESM severity classification (https://datasets.seed.nsw.gov.au/dataset/fire-extent-and-severity-mapping-fesm), based on the fire extent and severity algorithm (Gibson et al. 2020) and the Google Earth Engine Burnt Area Map (GEEBAM; https://datasets.seed.nsw.gov.au/dataset/google-earth-engine-burnt-area-map-geebam; DPIE 2020). All sites had *P. bodalla* population data from previous surveys conducted within the 5 years prior to the 2019–2020 megafires (Miles 2019; Le Breton et al. 2020).

Surveys were conducted in June 2021 (15 months post-fire). *Pomaderris bodalla* typically flowers in spring but the species is readily distinguishable from co-occurring *Pomaderris* species based on the presence of rusty stellate hairs on stems and new growth of mature plants and seedlings. Populations were primarily sampled using belt transects with the aim of conducting a total count of individuals at all sites whenever possible; one population was surveyed using randomly placed quadrats.

At each site, fire severity was visually assessed based on whether the fire had only burnt the understory (low severity), or for higher severities (moderate to extreme severity) whether there was partial (high severity) to complete canopy consumption (extreme severity). This was used to ground truth remotely sensed classification and select appropriate severity classes that both reflected conditions on the ground and fit within the broader picture presented by the remotely-sensed severity classifications.

Population area was calculated by fitting alpha hull polygons to coordinate points at population edges for larger, more dispersed populations. Where populations were more discrete, counts were made in full, and population area was based on the area encompassed within a transect. Where discontinuities > 50 m occurred between patches within a plant population, each patch had its area calculated separately; patch areas were then summed together to get the total population area (Keith 2000).

Analysis

To test our hypothesis, we followed an inferential method (Tredennick et al. 2021) and created models with covariates representing the effect of key drivers, fire severity and frequency, on seedling counts. Fire severity estimates on the ground more closely aligned with the GEEBAM severity categories than FESM, which occasionally misclassified low severity sites as unburnt. Consequently, GEEBAM fire severity categories were used for the final analysis. Fire frequency was defined as the number of times each population had been burnt between 1960 and 2020, including the 2019–2020 megafires. Site was included as a random variable and the model was weighted by patch area. A negative binomial distribution was assumed, to account for overdispersion in the count data. The generalized linear mixed effects model took the following form,

$$g\left(\mu_i\right) = x_i^{'}\beta + z_i^{'}u$$

where the expectation of the observed data is conditional on the random effect (e.g. $\mathbb{E}\left[y_i \middle| u\right] = \mu_i$) and that conditional mean μ_i inputs into a mean parameterization (McCulloch and Neuhuas 2014) of the negative binomial distribution, e.g. $y_i \tilde{N}B(\mu, \varphi)$. $x_i^{'}\beta$ are the linear covariates and coefficients and $z_i^{'}u$ are the random intercepts. $g\left(.\right)$ is the link function, for which the log-link was used.

These models were analysed in R 4.1.0 (R Core Team 2021) using the glmmTMB package (v 1.1.2, Brooks et al. 2017). The glmmTMB package handles weights by adding a simple multiplier to the log-likelihood contribution of each observation. To compare the full and null models we performed a Likelihood Ratio Test (LRT) with the base R anova() function. *Post-hoc* Tukey's HSD tests were conducted to assess differences among severity levels using means and contrasts estimated in the emmeans package (v. 1.6.3, Lenth *et al*. 2021).

Because the species is geographically restricted and limited in the number of known populations, there were limitations in the extent to which we could replicate across different fire histories and levels of severity. To provide a more detailed picture of which aspects of the fire regime were impacting which aspects of the life history of our study species we also ran a series of single factor general linear models to test the relationships between four other variables: pre-fire population density, post-fire seedling density, time since fire and fire frequency. Pre- and post-fire density was calculated for each patch where pre-fire population data was available by dividing the total count for each patch by patch area. We performed this component of the analysis at the patch scale to minimise the effect of sampling differences in methods used for pre- and post-fire data collection. We ran three GLM's testing i) pre-fire population density vs fire frequency before 2019–2020; ii) seedling density vs pre-fire population density; and, iii) seedling density vs time since last fire. Time since last fire and fire frequency were tested separately as the two are autocorrelated but effect plant species in different ways. These models were again run using the glmmTMB package (v 1.1.2, Brooks et al. 2017) and fitted with a gaussian distribution to account for the conversion of count data to density estimates. The anova function was used to test for significance of model results.

Results

Study sites experienced three levels of severity during the 2019–2020 fire season: moderate, high and extreme (Fig. 1c), and had been burnt between one and four times between 1960 and 2020 (Fig. 1b). Replication of fire frequency was limited at sites which had been burnt at moderate and extreme severity and a single site, burnt at high severity, had no fires recorded prior to 2019–2020. Seedlings could not be located at two of the 11 sites surveyed; both had small pre-fire populations of 1–2 plants and burnt within 3–7 years before the 2019–2020 megafires (Table 1).

Table 1
Study sites, fire history and population data

Site	Severity	Times burnt 1960–2020	Time since fire (years)	Pre-fire population size	Mean seedling density†
651	extreme	3	3	2*	0
657	high	4	7	1	0
662	high	2	51	87	0.27
679	extreme	2 to 4	23 to 51	191	2.29
680	high	3	20	8*	1.39
683	moderate	2 to 4	18 to 51	26	0.14
700	moderate	2	51	28	1.31
701	extreme	2	51	4*	0.9
702	moderate	3	15	34	0.67
703	high	3	15	1	0.01
704	high	1	> 60	70	26.8

Pre-fire population size sources: All pre-fire population size estimates from Miles and Canackle (2019), except where marked by * these are from Le Breton (2016). NB: Ranges of times burnt are for larger or more diffuse sites with mixed fire histories, which remain nonetheless a single population. † Mean seedling density is weighted by the area occupied by the population.

Model comparison

Seedling counts increased from moderate to high severity sites but decreased under extreme severity (GLMM: df = 2, χ^2 = 1584.59, p < 0.001; Fig. 2.) and declined with increasing fire frequency (GLMM: df = 1, χ^2 = 720.79, p < 0.001; Fig. 3.). However, there was an interaction between fire frequency and fire severity (GLMM: df = 2, χ^2 = 792.56, p < 0.001 Fig. 3) that had diverging effects depending on the level of severity. Moderate severity fire was associated with low seedling counts that declined as frequency increased. Similarly high severity fires were associated with much higher seedling counts (Tukey's Test: p < 0.001; Fig. 2) but also declined with increasing fire frequency (Fig. 3). Extreme severity fires responded quite differently with relatively low seedling counts at low frequencies but increasing significantly with fire

frequency, however, this trend was based on only three sites each of which had different fire frequency. The full model including this interaction was the best model for seedling counts when compared to the null model with no interaction (LRT: df = 2, χ^2 = 303.23, p < 0.001), supporting our hypothesis.

Single factor models

Pre-fire population density decreased as fire frequency increased and was highest in patches unburnt in the 60 years prior to the 2019–2020 fires (GLM: df = 1, χ^2 = 4.3371, p < 0.05; Fig. 4a). Post-fire seedling density, in turn, increased with pre-fire population density (GLM: df = 1, χ^2 = 6.9075, p < 0.01; Fig. 4b), and also increased with longer time since last fire (GLM: df = 1, χ^2 = 3.9779, p < 0.05; Fig. 4c). Overall seedling density was lowest at sites with short time since last fire, low pre-fire population density and high fire frequency (Fig. 4c). Long unburnt patches in general had higher post-fire seedling densities (Fig. 4c) and higher pre-fire population densities due to low fire frequency (Fig. 4a).

Discussion

The 2019–2020 Australian fire season provided a unique opportunity to test the effects of extreme fire severity across a large area of extent. The extent allowed us to explore how fire frequency and severity can interact and whether any impacts of such extreme fire regime shift could be detected in fire-adapted species. As predicted, *Pomaderris bodalla* recruitment responded negatively to increasing fire frequency, highlighting the potential that high fire frequency can limit the availability of seeds stored within the soil seed bank. Two sites appeared to have suffered local extinction after the 2019–2020 fires owing to frequent fire and low pre-fire population size. The relationship between recruitment and severity was not linear but hump-shaped, with a peak at high severity and reduced recruitment at moderate and extreme severities. The significant interaction between fire severity and frequency also appeared to be driven primarily by recruitment after high severity fires, with a clear decline with fire frequency only within this severity class. Our results provide evidence that our fire-adapted study species requires high but not extreme severity fires to produce the greatest numbers of seedlings, despite the fact that it has one of the highest dormancy-breaking temperature thresholds recorded (Tangney *et al*. in prep). This work brings up the question of how often extreme severity fires can heat soils beyond the thresholds even of those species that are fire-adapted.

The hump-shaped relationship identified between recruitment and severity reflects the pattern of response seen in *in vitro* germination studies of the physically dormant *Pomaderris bodalla* (Le Breton et al. 2020). Physical dormancy temperature thresholds of the species' seeds produced only a slight increase in proportion germinated after heating at 80°C, and close to maximal germination at 100°C and 120°C (Le Breton et al. 2020; Tangney *et al.* in prep). While fire severity does not always directly correspond to soil temperatures during fires (Stoof et al. 2013; Tangney et al. 2020), we found that when comparing across fire severity sites within the same plant community type there was a strong relationship with heating, at least as indicated by the germination response. The lack of relationship found in other studies may have been because fires had not reached the extent of extreme severity experienced in our study. The hump-

shaped relationship observed likely reflects soil heating below 100°C at moderate fire severity sites, an increase in soil temperatures to an optimum (~ 120°C) at high severity sites, but low levels of recruitment at extreme severity sites which would have reached temperatures that could overcome dormancy but offset by an increase in the occurrence of lethal temperatures or exposure times causing high mortality. Co-occurring species observed at several of the study sites also have physically dormant seeds and known dormancy breaking thresholds that support this interpretation. *Commersonia fraseri* (Malvaceae) optimal germination occurs following heating of the seeds at 80°C (Floyd 1976) and was abundant in most of the moderate severity sites and one extreme severity site. A second species, *Acacia mearnsii* (Fabaceae), has a dormancy breaking temperature threshold of ~ 110°C with 100% mortality at temperatures of 150°C (Riveiro et al. 2020); it occurred across sites burnt at all three severity levels, but was prolific at high and extreme severity sites, almost forming monocultures in some areas. The association of *C. fraseri* with moderate severity sites and *A. mearnsii* with high severity sites supports our conclusion regarding the average temperatures reached at these severity levels.

The coincidence of extreme severity fire coupled with high frequency fire means that *Pomaderris bodalla* and similar species suffer additive negative effects. Our analysis indicates that the number of potential recruits within the soil are already small due to frequent fires reducing population density, and thus the number of mature plants that can produce seed (Fig. 4a), while shorter time since fire intervals limit the time for seed bank accumulation (Fig. 4c). The size of the soil seed bank is limited by the number of times a site has burnt because the number of mature individuals are reduced when the average fire interval approaches the primary juvenile period maintained by a species (Keith 1996; Nolan et al. 2021b). This means that there can also be a cumulative effect of frequent fire on population size of perennial species even if the interval exceeds the primary juvenile period, because there are fewer years where annual seed input into the soil seed bank occurs. The number of potential recruits is then further depleted by high seed mortality due to extreme severity fires causing lethal soil temperatures over large extents. The result is that where extreme severity fires overlap with high fire frequency, the impact on the species is much greater because both may negatively impact the soil seed bank largely independently of one another while exacerbating the negative impacts of the other. Longer time since last fire can potentially offset the effects of reduced population size by increasing the number of annual inputs plants contribute to the soil-stored seed bank.

The concept of fire frequency depleting the soil seed bank of obligate seeding species is well established (Enright et al. 2015; Kelly et al. 2020) and the negative relationship observed between *P. bodalla* recruitment and increasing fire frequency in the field matches our initial prediction. Although replication of sites at the lowest and highest end of the frequency spectrum was limited (n = 1 & 3 sites respectively), there was a clear negative relationship. We observed two extreme examples where higher frequency fire (3–4 fires in 60 years) and short fire intervals (3–7 years) appear to have eliminated two populations, where both already had small pre-fire populations (Miles 2019). The primary juvenile period of *P. bodalla* is unknown but is believed to be around 8–10 years (Le Breton & Auld 2019) and most species require an additional 2–4 years to begin producing sufficient viable seed for seed bank replenishment (Kenny 2013). The maximum observed frequency was four fires over 60 years, which should on average result in long

enough intervals for the species to replenish the soil seed bank. However, there would likely still be depletion of the soil seed bank through attrition and time lost to repeated cycles of recruitment and maturation compared to less frequently burnt sites.

The unexpected interaction between fire severity and frequency was driven by the expected decline in seedlings with increased frequency, but masking of this effect at moderate or extreme severities. This appears to be driven by the very limited amount of seedling emergence at either end of the severity gradient, caused by a minimal loss of dormancy at the moderate end, and seed mortality at the upper end. This significant interaction runs counter to the relationship observed in serotinous pine forests in Spain, where frequency overrode severity as it increased (Fernández-García *et al.* 2016). However, this again could result from the extreme nature of the fires in our study, suggesting that we have found evidence for the severity threshold for maximal *P. bodalla* recruitment and potentially other species in temperate humid pyric forests in which it occurs. We should note that the low levels of replication, particularly at extreme severities, warrants caution in interpreting some of our results, and provides motivation to continue to collect data to test our general hypothesis. Nevertheless, our findings are broadly consistent with past research on interactions between fire severity and frequency.

The observation that the seed bank can become a limiting factor at higher fire frequencies aligns with findings of studies on the effects of severity and frequency on *Acacia* species with physical dormancy in drier parts of the country (Palmer et al. 2018) and non-dormant *Eucalyptus* in similar vegetation, although via different mechanisms (Bennett et al. 2016). Some 411 obligate-seeding species were impacted by the 2019–2020 fires and considered at risk of poor recovery based on the threat of fire frequency alone (Gallagher et al. 2021). Many of these species and others will also be at risk from the impacts of fire severity or interactions between the two elements of the fire regime. However, few studies have quantified this interaction and severity impacts cannot therefore be confidently incorporated into predictive frameworks. Our study provides preliminary evidence for detrimental effects of extreme severity fires, particularly combined with the additive impacts of high fire frequency, on recruitment during future events like the 2019–2020 megafires. The observed decline in seedling densities at areas burnt at extreme severity suggests that species with similar life histories to *P. bodalla* will face increased pressure during future extreme fire seasons that follow this trend. Additionally, while climate change increases the likelihood of severe fire seasons it will also increasingly interact with the post-fire establishment of species via mechanisms such as drought (Parmesan & Hanley 2015). This process, where plant species are squeezed by climate-change driven reductions in the length of fire intervals and delays in recruitment and development, lengthening the time between fires required by species ('interval squeeze' *sensu* Enright et al. 2015), is likely to increase the risk faced by obligate seeding species (Le Breton et al. 2022).

The patterns observed in our study are potentially widespread. Up to 40% of shrub species in Australian temperate humid pyric forests have physically dormant seeds (Collette & Ooi 2017) and may be subject to fire frequency and severity interactions. The conditions for these types of interactions occur globally, across the Americas, Europe and southern Africa, in temperate and Mediterranean forests that have historically been subject to a regime of infrequent intense fires (Archibald et al. 2013). Consequently,

further research into the extent of fire frequency and severity interactions as event- and regime-based effects of fires on plants is needed at multiple scales. Interpreting impacts in light of their adaptations and the conditions they evolved under can help to improve our understanding of species historic relationship with fire and disentangle it from their relationship with anthropogenic fire. In the interim, our findings can provide some guidance for how land and fire managers and conservationists can incorporate fire severity and frequency interactions in practice. For *P. bodalla* and species with similar life histories – fire sensitive obligate seeders with physical dormancy broken by high fire-related temperatures – high severity fires can be a net positive. However, following an extreme severity fire, maximal germination and depletion of the soil seed bank will render species vulnerable to an overall decline if burnt again too soon. Ultimately, these processes will result in local extinctions as we observed at two sites in this study. Increasing fire frequency as a fuel management strategy may inadvertently impair the resilience of those species and forests adapted to lower frequency fire. Fire management informed by species and ecosystem fire response traits can be a conservation asset but requires detailed knowledge of species responses to all elements of the fire regime.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Fire severity data (GEEBAM v2p1, NSW DPIE 2020) is publicly available and can be accessed at https://datasets.seed.nsw.gov.au/dataset/google-earth-engine-burnt-area-map-geebam.

Fire frequency compiled by Le Breton et al 2022 is publicly available at https://doi.org/10.6084/m9.figshare.15111333.v1.

Species distribution data is publicly available via the Atlas of Living Australia and seedling abundance, prefire population size and all other relevant species data will be made available on figshare at the time of publication.

All code used to compile and analyse this data will also be made publicly available on Zenodo at the time of publication.

Competing interests

The authors declare that they have no competing interests

Funding

This work was funded by an Australian Research Council Linkage Project (LP180100741) and a grant from the New South Wales (NSW) Department of Planning, Industry and Environment's Saving Our Species program. MKJO is supported by funding from the NSW Department of Planning, Industry and Environment, via the NSW Bushfire Risk Management Research Hub.

Authors' contributions

TDLB and MKJO conceived the idea; TDLB, MKJO, and MBL designed the research; TDLB, LC and CD conducted the surveys and gathered the data; TDLB analysed the data; and TDLB, MKJO, MBL and CD wrote and edited the manuscript. The authors declare no competing interests.

Acknowledgements

We acknowledge the Yuin people as the Traditional Custodians of the Country this work was undertaken on. We recognise their continuing connection to the land and acknowledge that they never ceded sovereignty. We pay our respects to Elders past and present.

This work was funded by an Australian Research Council Linkage Project (LP180100741) and a grant from the New South Wales (NSW) Department of Planning, Industry and Environment's Saving Our Species program. MKJO is supported by funding from the NSW Department of Planning, Industry and Environment, via the NSW Bushfire Risk Management Research Hub. We thank Jackie Miles and Anna Murphy for their previous survey work on this species; NSW National Parks and Wildlife Services and NSW Forestry Corporation for their permission to access these sites.

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Figures

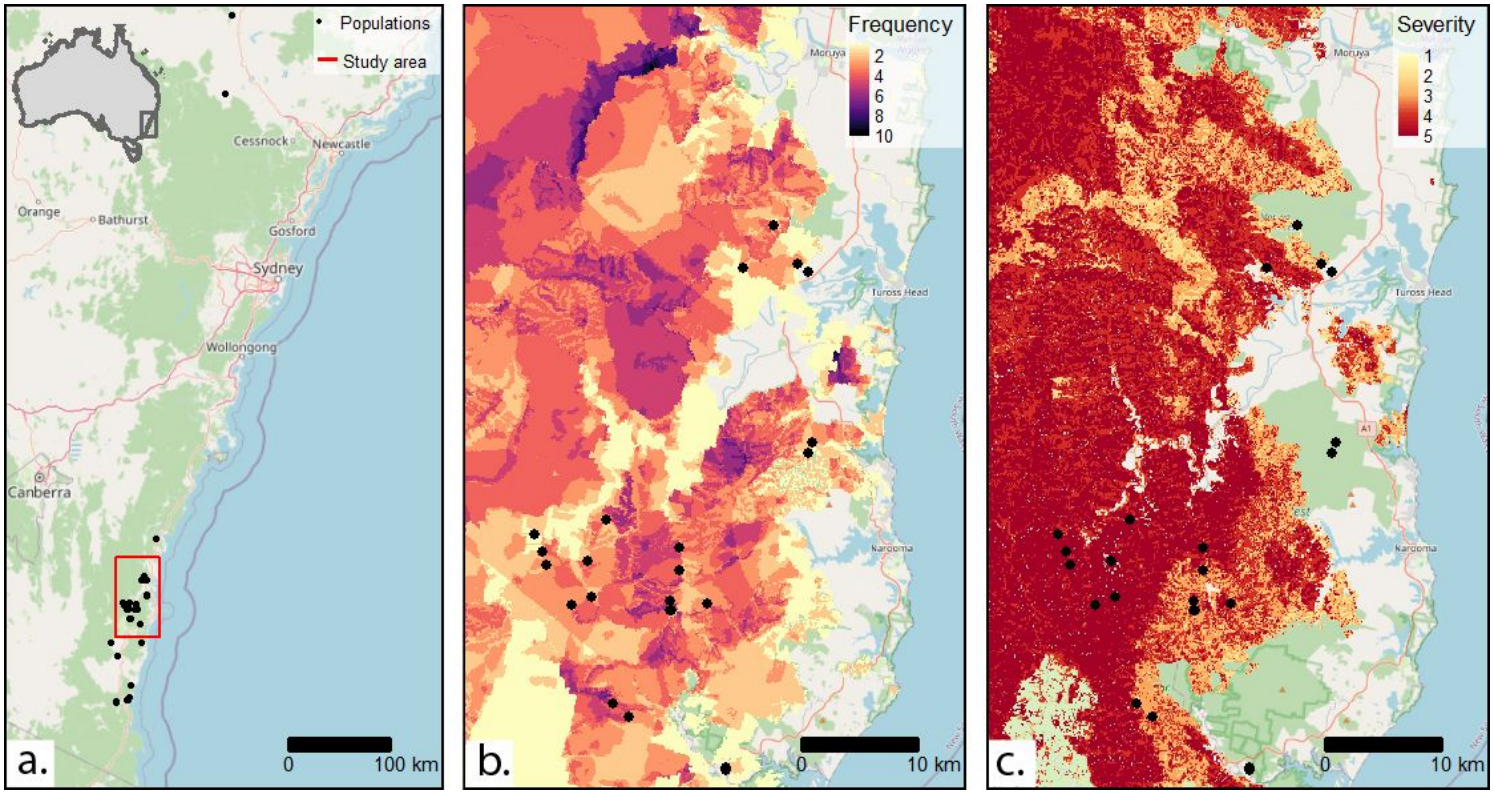

Figure 1

Maps of a) the distribution of *Pomaderris bodalla* on the south-east coast of Australia; b) fire frequency (1960-2020) across the study area; and c) GEEBAM severity (DPIE 2020) of the 2019-2020 fire season across the study area.

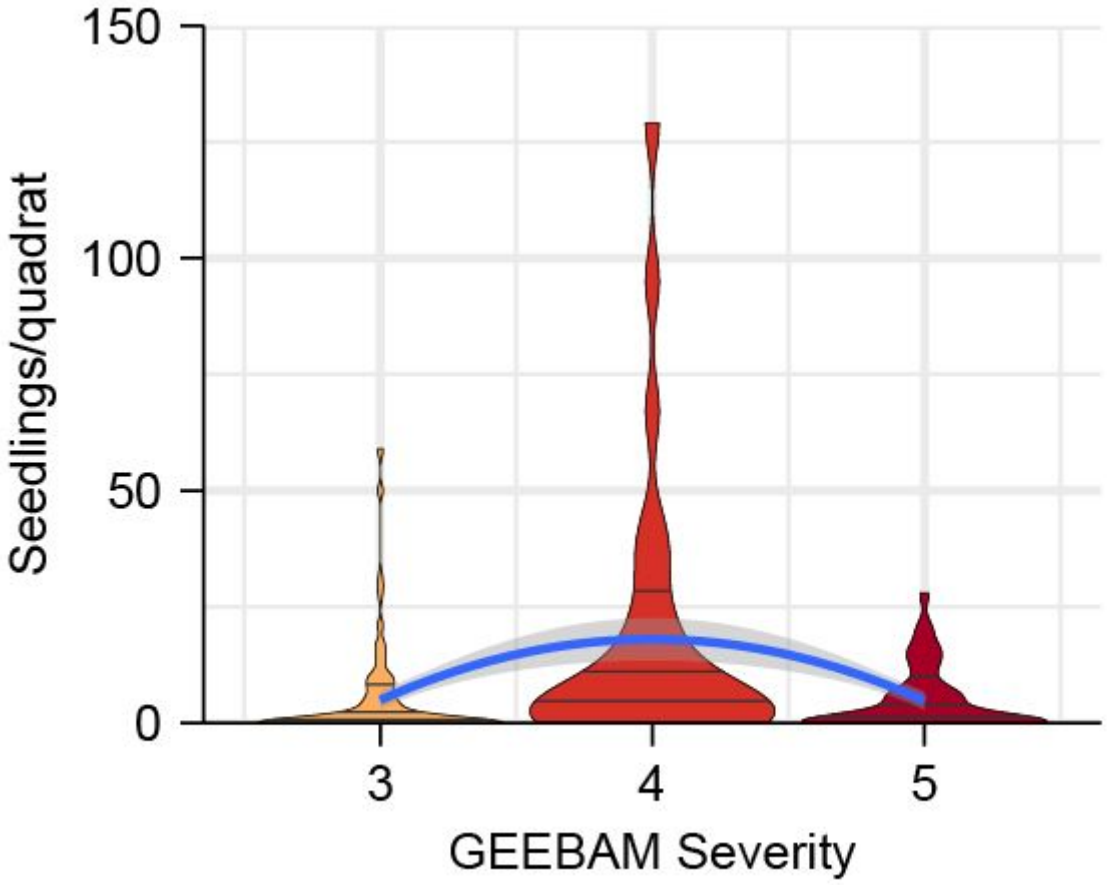

Figure 2

Boxplot of raw seedling counts per quadrat by fire severity (GEEBAM) for *Pomaderris bodalla*. GEEBAM severity levels and colouring correspond to moderate (3), high (4) and extreme (5) severity. The lines within each violin plot represent quartiles within the data. Smoothed line fitted using a quadratic equation and linear model, shaded areas represent 95% confidence intervals.

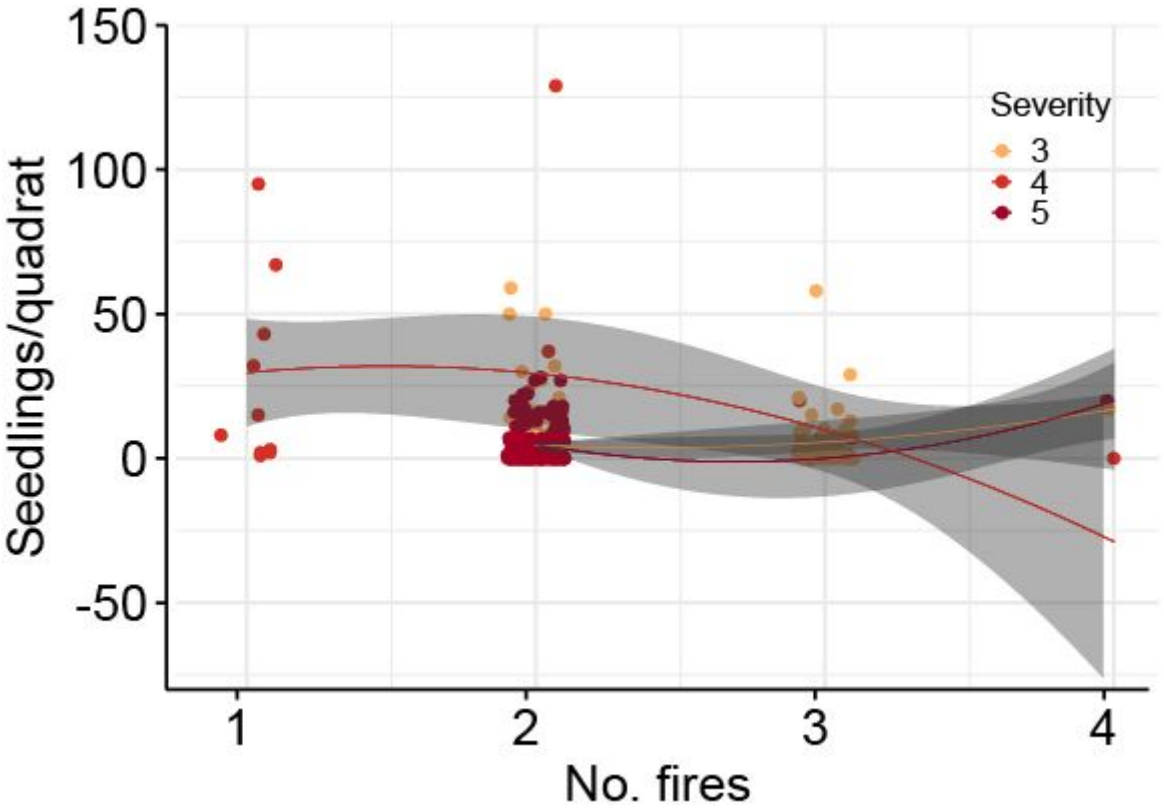

Figure 3

Influence of fire history (1960-2020) and fire severity (2019-2020 fires) on raw seedling counts per quadrat for *Pomaderris bodalla*. Smoothed lines were fitted using a quadratic equation and linear model, shaded areas represent 95% confidence intervals.

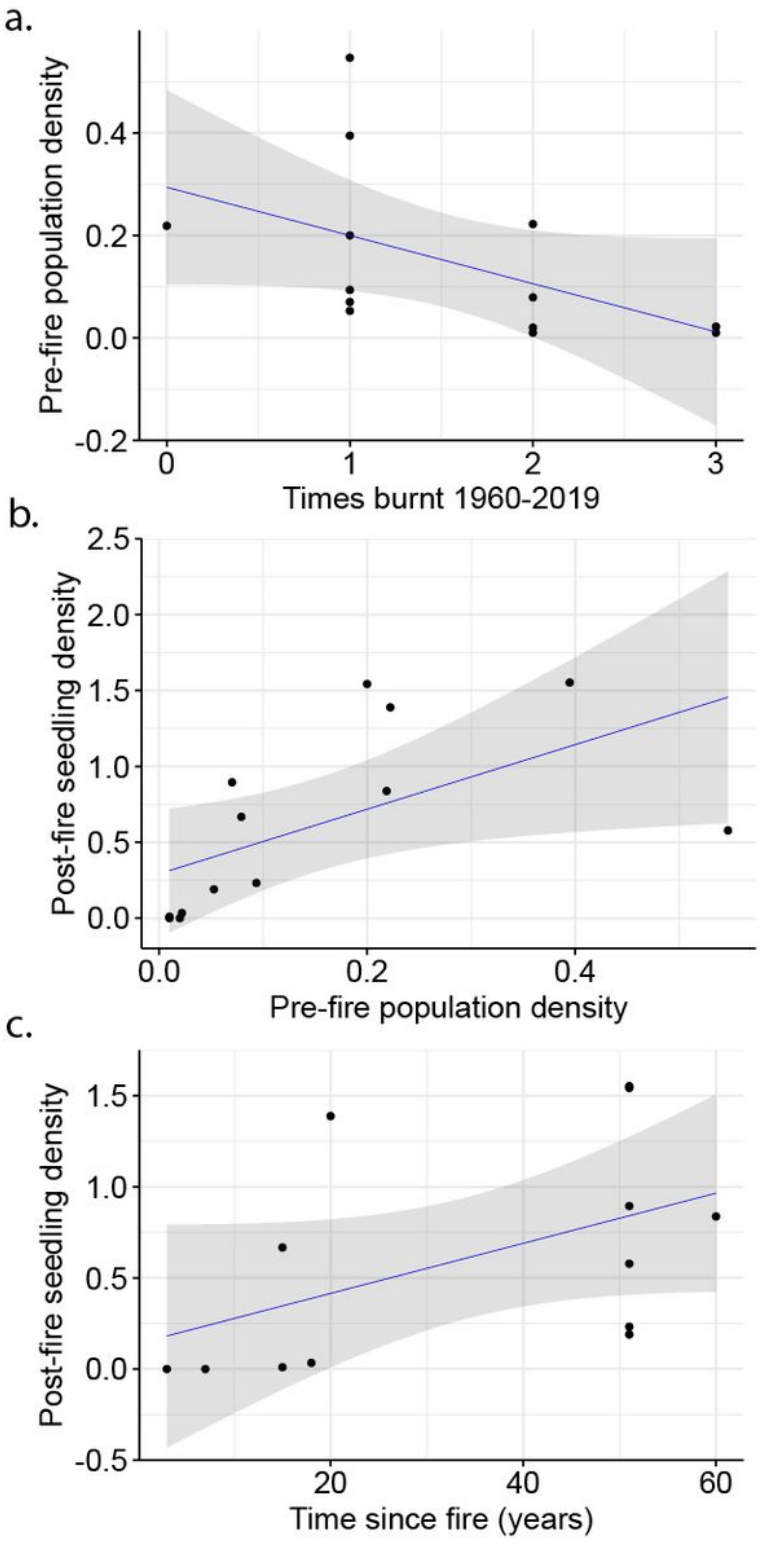

Figure 4

Patch level relationships between **a)** times burnt from 1960-2019 and pre-fire population density; **b)** pre-fire population density and post-fire seedling density; and **c)** time since fire and post-fire seedling density for *Pomaderris bodalla*. Smoothed lines were fitted using a linear model, shaded areas represent 95% confidence intervals.