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Fire Ecology

FIELD NOTE

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

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Abstract

Background Climate change is driving global fire regimes toward greater extremes, potentially threatening plant species that are adapted to historic fire regimes. Successful conservation of threatened plant species depends upon improving our understanding of how they respond to these changing fire regimes in fire prone regions. The 2019–2020 Australian megafires burnt at very high to extreme severity across an unprecedented extent and overlaid a complex history of prescribed burns and wildfires, providing an ideal foundation to study the consequences of multiple fire regime elements. We examined the recruitment response of *Pomaderris bodalla*, one of many threatened obligate-seeding shrub species growing in wet sclerophyll (mesic) forest in south-east Australia. We surveyed seedling recruitment at sites across a gradient of fire severity and frequency. Our aims were to (i) confirm in vitro results that suggest a positive relationship with fire severity; (ii) determine the species response to fire frequency and (iii) identify the nature of the effect of fire severity and fire frequency in combination.

Results We found that recruitment had a positive response to fire severity, peaking at high severity sites as soil temperatures reached optimal levels for dormancy-break but declining, while still remaining positive, at moderate and 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 and this effect appeared to be additive with fire severity.

Conclusion Our findings indicate that increased fire frequency poses an ongoing threat to *P. bodalla* and similar obligate-seeding shrub species. The hump-shaped relationship with fire severity suggests that future large-scale extreme fires will cause seed mortality-induced reduction in recruitment, with the potential to exacerbate the negative effects of high fire frequency. Informed management of threatened species requires detailed knowledge of species responses to multiple fire regime elements, and novel fire response traits like seed dormancy can provide beneficial insights for robust conservation strategies.

Keywords Fire regimes, Fire management, Threatened species, Obligate seeder, Physical dormancy, Temperate pyric humid forests, Fire frequency, Fire severity

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Resumen

Antecedentes El cambio climático está conduciendo los regímenes de fuego a mayores extremos, amenazando potencialmente a plantas que históricamente han estado adaptadas a esos regímenes. La conservación exitosa de plantas amenazadas depende de que podamos mejorar nuestro entendimiento de cómo esas plantas responden a cambios en esos regímenes en regiones propensas al fuego. Los mega-incendios de 2019–2020 en Australia quemaron con una severidad sin precedentes (de alta a extrema) a lo largo de grandes extensiones y se superpusieron a una compleja historia de quemas prescriptas e incendios, proveyendo de una idea fundacional para estudiar las consecuencias de los múltiples elementos de los regímenes de fuego. Examinamos la respuesta al reclutamiento de Pomaderis bodalla, una de las muchas especies de arbustos que se reproducen obligadamente por semilla en bosques esclerófilos mésicos en el sudeste de Australia. Relevamos el reclutamiento de plántulas en sitios a través de un gradiente de severidad y frecuencia de fuegos. Nuestros objetivos fueron; (1) confirmar, in vitro, los resultados que sugieren una relación positiva con la severidad del fuego; (2) determinar la respuesta de la especie a la frecuencia del fuego, y (3) identificar la naturaleza del efecto de la severidad y la frecuencia del fuego de manera combinada.

Resultados Encontramos que el reclutamiento tuvo un efecto positivo con la severidad del fuego, con picos en sitios que tuvieron una alta severidad cuando las temperaturas del suelo alcanzaron niveles óptimos como para romper la dormancia, pero declinaron, aunque permanecieron todavía positivas, en sitios con severidades moderadas y extremas. El patrón de respuesta igualó los estudios in vitro, que habían establecido que las semillas de P. bodala físicamente dormantes tuvieron un rompimiento mínimo de la dormancia a temperaturas de fuego relativamente baja, un pico alto de rompimiento de la dormancia a temperaturas de fuego relativamente altas, y una inducción a mortalidad inducida por el calor a temperaturas del fuego extremas. La frecuencia del fuego tuvo un efecto general negativo en el reclutamiento, con menor reclutamiento en sitios quemados frecuentemente, siendo este efecto aparentemente aditivo con la severidad del fuego.

Conclusiones Nuestros hallazgos indican que el incremento en la frecuencia de los fuegos significa una amenaza continua a P. bodalla y otras especies de arbustos similares que se reproducen por semilla. La relación del tipo de curva normal con la severidad del fuego sugiere que los futuros fuegos extremos de gran escala causarán un aumento en la mortalidad de plántulas y reducción en el reclutamiento, con el potencial de ser exacerbados por la alta frecuencia de los incendios. Para el manejo, la información sobre las especies amenazadas requiere de un detallado conocimiento de las respuestas de las especies a los elementos múltiples de los regímenes de fuegos, y las nuevas respuestas sobre las características de los fuegos (i.e. la dormancia de semillas) pueden proveer de nuevas perspectivas para estrategias más robustas de conservación.

Background

Climate change is the leading driver of more frequent and extreme fire events (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 high 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 impacts on fire regimes are already pervasive, such as through land use changes causing increased ignitions from the growing urban-fire interface (Duane et al. 2021) and from the use of fire for management (Archibald et al. 2013), particularly for the protection of human assets and lives. Land management seeks to actively alter fire regimes, intending to minimise the extent and severity of wildfires, both by implementing strategies such as prescribed burns to reduce fuel loads and by suppressing uncontrolled wildfires (Bowman et al. 2011). As severe and uncontrollable wildfires become more frequent (Duane et al. 2021), it is critical that land managers have knowledge of how flora, particularly threatened species, might respond to more frequent and severe fires.

Plant responses to fire regimes are typically understood in terms of two primary functional groups: 'resprouters', which can resprout post-fire from protected epicormic or basal buds, and 'obligate seeders', which are killed by fire and rely on soil- or canopy-stored seed banks for persistence (Bond & Midgely 2001; Pausas et al. 2004). Increased fire frequency is a significant threat, decreasing the time in which plants can regenerate and replenish seed banks or energy storage organs (e.g. lignotubers) during the inter-fire period and therefore reducing their capacity to respond to and persist through subsequent fires (Keith 1996; Auld and Ooi 2017; Gallagher et al. 2021). However, while these functional groups can provide broad indications of potential threat, incorporating other traits into such groups may refine predictions. Furthermore, over half of all threatened species globally require species-specific interventions (Bolam et al. 2022) and species-specific ecological knowledge is required to implement these actions in an informed way (Scheele et al. 2018).

In recent years, a number of obligate seeders, including dominant tree species, in Australia have undergone declines due to increased fire frequencies (Fairman et al. 2016). Climate change is exacerbating this threat, by producing drier and hotter conditions which promote more frequent fire while also stressing plants, slowing growth and lengthening the time required between fires for plants to mature (e.g. Bowman et al. 2016; Henzler et al. 2018). Altered fire severity, which deviates from historical norms, is also understood to be a potential threat to the persistence of plant species and ecosystems (Etchells et al. 2020; Landesmann et al. 2021). Fire severity here refers to the level of fuel consumption during a fire. It is useful as a proxy for fire intensity (i.e. the energy output of the fire *sensu* Keeley 2009) and through this tends to correlate positively with soil heating (Bradstock and Auld 1995). Obligate seeders are less affected by high severity fire, compared to resprouters (Pausas and Keeley 2014), as many are killed even at lower severities. However, extremely severe 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 severity fires may pose a threat, by killing off fire sensitive adult plants aboveground but failing to stimulate recruitment from seeds in the soil that require fire-related temperature cues (Le Breton et al. 2020).

While there is a good functional understanding of how fire can threaten plants, knowledge gaps remain around how multiple fire regime elements, such as frequency and severity, combine to impact plant species and the ecosystems in which they occur (Basset et al. 2017; Barker et al. 2021). Furthermore, there is a lack of fundamental ecological knowledge for many individual threatened species (Nolan et al. 2021a). Interactive or additive impacts on recruitment are highly likely, particularly under climate change (Kelly et al. 2020). For example, Palmer et al. (2018) investigated the impacts of fire severity on *Acacia* species in east Australian dry sclerophyll forests and found that while increasingly high severity fire resulted in the death of all mature plants, it promoted higher recruitment, therefore leaving behind a smaller residual seed bank (Palmer et al. 2018). The authors concluded that the population was at greater risk from even a single subsequent fire event, if it were to occur after a short interval. In Spain, serotinous obligate seeding *Pinus* species were found to have suffered negative additive impacts from high severity and frequent fire (Fernández-García et al. 2019). Severity and frequency clearly combine to impact post-fire recovery and persistence. Consequently, there is a growing need to improve and quantify our understanding of how these fire regime elements may, together, threaten species persistence.

The impacts of changes to different elements of the fire regime, individually 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 six functional groups in the global temperate-boreal forests and woodlands biome and dominate much of the continent's east coast (Fig. 1; Keith and Mac Nally 2020). These forests are highly biodiverse, store significant carbon sinks and are adapted to extremely high severity and low frequency fire, recurring over multi-decadal time scales (Keith and Mac Nally 2020).

Obligate seeders are a key functional type in subcanopy and understory flora in temperate pyric humid forest, with long-lived soil-stored seed banks which can lay dormant for decades (Keith and Mac Nally 2020). Up to 82% of shrub species in these forests possess some form of seed dormancy (Collette and Ooi 2021), often with fire-linked cues for breaking dormancy and stimulating recruitment (Keith and 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 and Ooi 2021). Optimal germination is often tied to temperatures over 80 °C among species with physically dormant seeds (Auld and 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 can therefore 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 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 extreme severity

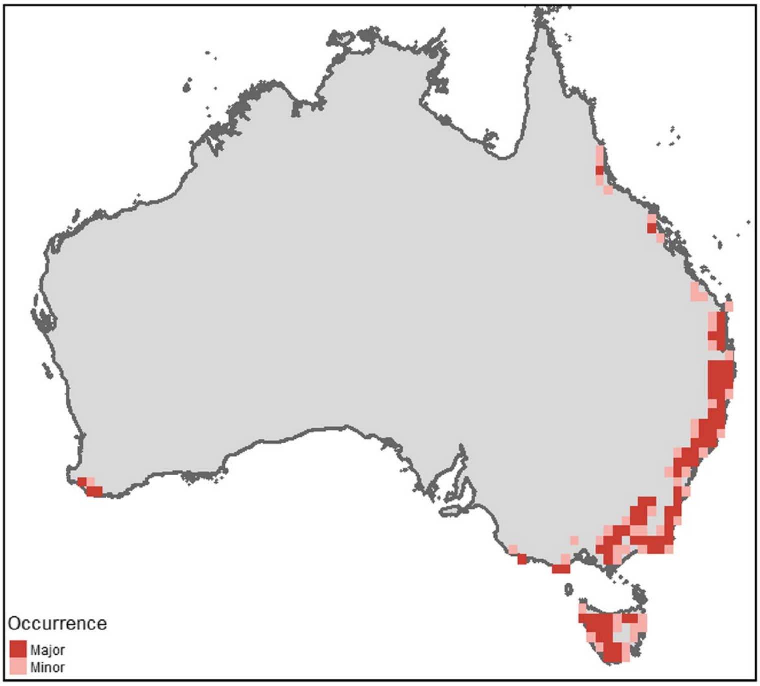

Fig. 1 Map of the global distribution of the temperate pyric humid forests functional group, within the temperate-boreal forests and woodland biome, adapted from Keith and Mac Nally 2020. The two occurrence levels, major and minor, are defined as > 20% of cell area and < 20% of cell area respectively (Keith and Mac Nally 2020)

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; Auld et al. 2022; Le Breton et al. 2022).

The aim of this study was to explore how fire frequency and 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) and 8 to 10 years to mature and produce seed (Le Breton and Auld 2019). This species was chosen as it exemplifies the obligate seeding life history strategy. *Pomaderris* generally have limited capacity to resprout following fire and *P. bodalla* in particular has never been observed resprouting in response to fire. Additionally, the relatively numerous populations (for a threatened species) with pre-fire population data and documented dormancy breaking and germination thresholds together make *P. bodalla* useful model species for this study. Specifically, we sought to (1) confirm 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, (2) investigate how the species responded to fire frequency and (3) determine whether this effect was mediated by fire severity. We hypothesised that *P. bodalla* populations would have high post-fire recruitment following higher severity fires, but this effect would diminish in populations burnt relatively more frequently in the past due to a depleted soil-stored seed bank.

Methods

Study species and region

Pomaderris bodalla is an obligate-seeding shrub endemic to the south-eastern coast of Australia in New South Wales (Fig. 2a). The species is characterised by a mixture of rusty and stellate hairs on leaves and new growth and can grow to a height of over 4 m (Le Breton et al. 2020). 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. 2a). 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). Our study focusses on populations in the southern extent of the species range (Fig. 2a). These populations primarily occur in Bodalla and Moruya State Forests and Kooraban National Park where they tend to be patchily distributed in moist open forest in sheltered gullies and the riparian zone in the foothills of the southern

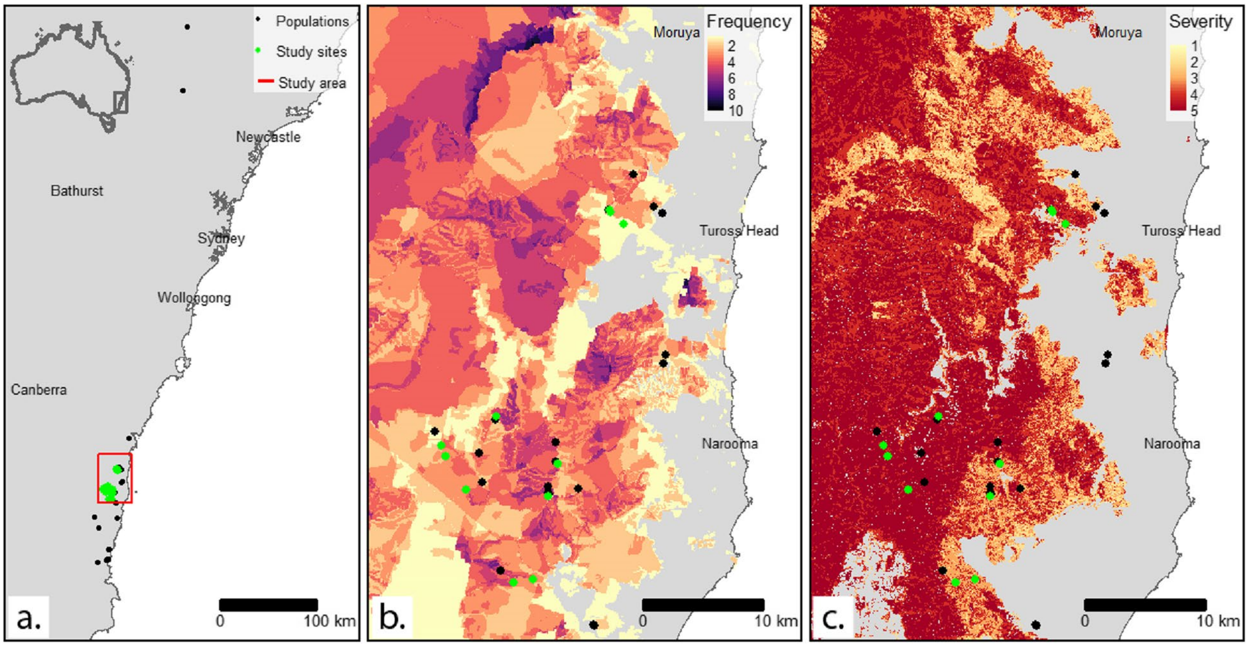

Fig. 2 Maps of **a** the distribution of *Pomaderris bodalla* on the south-east coast of Australia, **b** fire frequency (number of fires between 1960 and 2020) across the study area and **c** GEEBAM severity (DPIE 2020) of the 2019–2020 fire season across the study area

escarpment (Walsh and Coates 1997). This habitat is dominated by wet sclerophyll forest communities within the temperate pyric humid forests functional group (Keith and 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 severity hazard reduction burning has been aimed at reducing fuel loads (NSW NPWS 2011; Fig. 2b). 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 (Collins et al. 2021). It is estimated these fires impacted 47% of the known populations of *P. bodalla* (Fig. 2c).

Pomaderris are typically killed by fire, though some species have the capacity to resprout following partial canopy scorch, and they recover from physically dormant seeds in soil-stored seed banks (Le Breton et al. 2020). The primary juvenile period of *P. bodalla* is unknown; however, recruits have been observed to develop buds 3.5 years post-fire (Dunne, C 2023 Personal observation in litt. August 3 2023). It is currently believed that the species requires 8 to 10 years between fires to produce a sufficient seed bank for persistence (Le Breton and Auld 2019). In vitro germination trials have revealed that seeds require exposure to high fire-associated temperatures to overcome their physical dormancy. Germination was minimal for heat shock treatments up to 80 °C (< 18% germination; Le Breton et al. 2020); however, 100 °C appears to be optimum for dormancy break, given that no mortality was observed (100% germination; 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.

Surveys and population estimates

Eleven populations with pre-fire population data were burnt during the 2019-20 fire season (Fig. 2b) and these populations had a mix of fire histories and burn frequencies. Fire history and frequency data were obtained from statewide fire history mapping from 1960 to 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 the FESM severity classification (https://datasets.seed.nsw.gov.au/dataset/fire-extent-and-severity-mapping-fesm), based on the fire extent and a severity algorithm (Gibson et al. 2020) and the Google Earth Engine Burnt Area Map (GEEBAM; https://datas ets.seed.nsw.gov.au/dataset/google-earth-engine-burnt-area-map-geebam; DPIE 2020). The GEEBAM is divided into four severity classes relating to the level of fuel consumption as measured by change in pre- and post-fire satellite imagery. The classes are unburnt, subcanopy burnt, subcanopy and partial canopy burnt, and subcanopy and canopy both burnt. While there are acknowledged accuracy issues in the GEEBAM dataset for areas burnt at lower severity, the study area was amongst the most severely burnt areas during the 2019–2020 fire season according to both GEEBAM and FESM mapping.

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 or stellate hairs on stems and new growth of mature plants and seedlings (Fig. 3). At each site, fire severity was visually estimated by the presence of dead understory shrubs, burn scar height and whether the fire had only burnt the understory (low severity) or, for higher severities, whether there was partial (high severity) to complete canopy consumption (inferred by the absence of leaves in the canopy and the absence of leaf litter on the ground) (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 classes. 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.

Populations were sampled with the aim of conducting a total count of individuals at all sites whenever possible, in order to contribute to a project on the species response to the 2019–2020 fires independent of the present study. Post-fire populations varied greatly in their dimensions with the smallest occurring within a single square metre and the largest over several hundred square metres. Some sites were densely occupied and linear, while others were more diffuse. Consequently, all but one population was surveyed using 2 m wide transects of variable number and length, depending on the dimensions of the population, with counts from contiguous quadrats each metre along the transect (Keith 2000). The remaining population, which had a high density of seedlings but a small spatial footprint was instead surveyed using ten randomly placed quadrats. This approach was thought to be more likely to accurately capture the number of seedlings in this population and transects would have artificially inflated the number of zeroes by extending beyond the bounds of this highly localised population.

Analysis

To test our hypothesis, we created four competing models of increasing complexity (Table 1) with covariates representing the effect of key drivers, fire severity and frequency, on seedling density. 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. Consequently, whilst models could include both fire frequency and severity terms, we excluded an interaction term due to insufficient replication. Although data on time since last fire and pre-fire population size were also available, we decided against including these variables as models for two main reasons: (i) within a bounded time frame time since fire is strongly influenced by fire frequency, and both influence pre-fire population size confounding the analysis; (ii) our primary interest in this study is the effect of fire frequency and severity on

Fig. 3 Left: Typical *Pomaderris bodalla* seedling with rust-coloured stems from light hairs. Right: Example of *P. bodalla* seedling density following high severity fire

Table 1 Model design

Model Name	Model
Null model	Seedling density ~ random effects (site)
Severity model	Seedling density ~ fire severity + random effects (site)
Frequency model	Seedling density ~ fire frequency + random effects (site)
Full model	Seedling density ~ fire severity + fire frequency + random effects (site)

seedling density; the inclusion of intermediate variables poses a risk of biasing the causal inference resulting from the analysis (Arif and MacNeil 2022).

Seedling density was calculated by dividing the number of seedlings counted per quadrat by the total area of the quadrat. Fire frequency was defined as the number of times each population had been burnt between 1960 and 2020, including the 2019–2020 megafires. This was considered to be the best proxy for fire frequency given that the dataset is limited in the length of time it covers, preventing adequate measurement of all fire intervals. Site was included as a random variable.

These models were analysed in R 4.1.0 (R Core Team 2021) using generalised linear mixed effects models with a Tweedie error distribution in the mgcv package (v 1.8–35, Wood et al. 2017), where the random effect for site was represented by a penalised regression term. To compare the four models, we performed manual ranking using Akaike's Information Criteria (AIC) and compared each model against the null model using a likelihood ratio test (LRT) with the mgcv anova.gam() 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).

Results

Study sites were burnt at three different levels of severity during the 2019–2020 fire season, moderate, high and extreme (Fig. 2c), and had been burnt between one and four times between 1960 and 2020 (Fig. 2b). 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 were burnt 3–7 years before the 2019–2020 megafires (Table 2).

Model comparison

AIC ranking indicated that the full model which included both fire severity and frequency was the best performing of the four models, followed by the model which included only frequency (Table 3). Comparing each model against the null indicated that fire frequency and severity have a significant effect on seedling density both alone and in combination (Table 3).

Table 2 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^a	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^a	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^a	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 ^{a}; 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

Table 3 Model comparison

Model name	AIC index	Df	Deviance	*p*-value
Null model	1338.9	NA	NA	NA
Severity model	1283.6	3.12	60.9	0.002*
Frequency model	1257.9	1	83.17	> 0.001*
Full model	1249.3	3	95.6	> 0.001*

Seedling density response

Under the full model, fire severity had a positive effect on seedling density (GAM: df = 2, F-value = 6.96, $p < 0.005$; Fig. 4), with the strongest effect observed at sites burnt at high severity ($M = 9.76$) where average seedling density was around five times higher than at moderate ($M = 1.06$) or extreme severity sites ($M = 2.30$; Tukey's test: $p < 0.05$; Fig. 2). Increasing fire frequency had a negative influence on seedling density (GAM: df = 1, F-value = 39.90, $p < 0.0001$; Fig. 5).

The model indicated that the effects of fire severity and fire frequency were additive, whereby seedling density exhibited the same general relationship with fire severity, but fire frequency acting as a modifier reducing average seedling density across severity levels as frequency increased (Fig. 5). However, given the low replication at different levels of severity and the prediction of negative values in the model, the effect of frequency in general and at different levels of severity should be treated with caution.

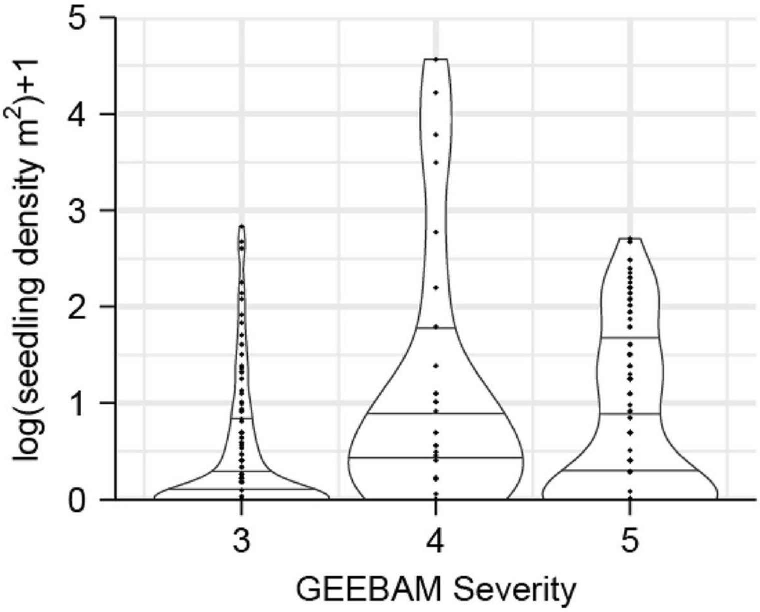

Fig. 4 Violin plot of seedling counts per quadrat by fire severity (GEEBAM) for *Pomaderris bodalla*. GEEBAM severity levels correspond to moderate (3), high (4) and extreme (5) severity. The seedling counts per quadrat have been transformed using the formula log(x) + 1 to allow better visualisation of the zero heavy data. The lines within each violin plot represent quartiles within the data

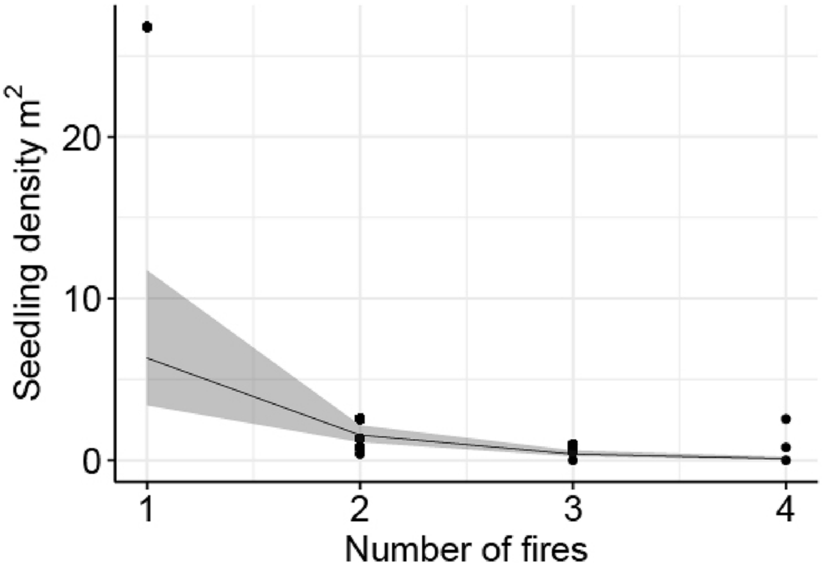

Fig. 5 Influence of fire frequency (1960–2020) on mean seedling density for *Pomaderris bodalla*. The fitted line is the full model (seedling density ~ fire severity + fire frequency + random effects (site)) which was the best fitting model in our study. The grey area around it represents 95% confidence intervals

Discussion

For species in fire prone regions, there are significant knowledge gaps surrounding impacts of multiple fire regime elements and the post-fire recovery responses of threatened species under changing fire regimes (Nolan et al. 2021a; Tangney et al. 2020). We found evidence that *Pomaderris bodalla* recruitment was greater at high and extreme, compared to moderate, fire severity, but that a seed mortality-induced decline occurred at extreme fire severity, producing an overall hump-shaped relationship. Fire frequency resulted in a monotonic decline, with lower seedling density as frequency increased, reducing any positive effects of fire severity. Interpretation of the impacts that these different fire regime elements have was benefited by utilising seed dormancy type, an important though rarely used trait for assessing fire response.

The hump-shaped but overall positive relationship identified between recruitment and severity, with both high and (to a lesser extent) extreme severity sites producing greater responses than moderate sites, is consistent with the response observed during in vitro germination studies of *P. bodalla* (Le Breton et al. 2020). The temperature thresholds required to break the physical dormancy of the species' seeds were notably high, with a slight increase in proportion germinated after heating at 80 °C, but close to maximal germination at 100 and 120 °C (Le Breton et al. 2020; Tangney et al. in prep). Our results provide evidence that *P. bodalla* 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 (Chan et al. 2022). Fire severity does not always directly correspond to soil temperatures during fires (Stoof et al. 2013; Tangney et al. 2020); however, the hump-shaped positive relationship we observed between seedling density and fire severity is consistent with the idea that soil temperature differed between severity levels. While lower recruitment occurred in the moderate severity sites, likely from insufficient dormancy-breaking temperatures, higher recruitment occurred at high severity sites presumably from optimal germination temperatures (~ 100 °C) being generated. At extreme severity sites, seedling density declined, suggesting that lethal temperatures were generated, driving higher rates of seed mortality.

There were two distinct effects of high fire frequency observed during our study. The first was the general negative effect on seedling density, which likely reflects reduced recruitment due to shorter periods for building up the soil seed bank. Soil seed bank size is determined by the number and reproductive output of mature individuals, which are reduced when the average fire interval approaches the primary juvenile period maintained by a species (Keith 1996; Nolan et al. 2021b). A cumulative effect of frequent fire on population size of perennial species can also occur, even if the fire interval sometimes exceeds the primary juvenile period, because there are fewer years overall for annual seed input. The second and more extreme impact was the apparent local extinction of two populations, due to relatively high frequency fire (3–4 fires in 60 years) and short fire intervals immediately prior to the 2019–2020 fire, of 3 to 7 years. These intervals are shorter than the primary juvenile period of *P. bodalla*, which is believed to be around 8–10 years (Le Breton and Auld 2019). Two other populations had also been burnt at intervals shorter than the primary juvenile period at least once but persist today. However, in these cases, short interval fires were preceded by a longer fire-free period of 23–32 years, suggesting that this may have been long enough to accumulate a soil seed bank sufficient to offset a single short-interval event.

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. However, while this negative effect of frequency was clear, replication of sites at the lowest and highest end of the frequency spectrum was limited ($n = 1$ and 3 sites respectively), and these results need to be treated as indicative until they can be expanded upon with further study. One outlying site, with a much higher mean seedling density of 26/m^2 (Table 2), influenced the overall pattern of our results but is perhaps not unexpected. This was the only very long unburnt site, with no fire recorded prior to the 2019–2020 fires, and it appears that the combination of being long unburnt and having been burnt at high severity promoted very high recruitment.

Our results indicate that the number of potential *P. bodalla* recruits within the soil seed bank is already small at many sites due to relatively frequent fires. When sites are burnt at extreme severity, the increased likelihood of lethal soil temperatures means that recruitment from the already small soil seed bank is reduced due to higher seed mortality, rather than optimal as it would be at a high severity site with more suitable soil temperatures. When extreme severity fires overlap with high fire frequency, the impact on the species is therefore likely much greater, as the negative impacts of frequency is compounded by the increased mortality at extreme severity. 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 a different mechanism) (Bennett et al. 2016). The additive nature of these impacts is also similar to the effect of fire severity and frequency on obligate seeding serotinous pine species in Spain (Fernández-García 2019). The relationship may be more complex than it appears here as the severity of preceding fires would influence the proportion of the soil seed bank that germinates and so the size of the residual soil seed bank. It is therefore likely that there is an interaction between fire and severity that was unable to be tested in our study.

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 the additive effects of the two. However, few studies have quantified these effects together, let alone considered their interaction, and severity impacts cannot therefore be confidently incorporated into predictive frameworks. Our study provides preliminary evidence that positive effects of fire severity on physically dormant seeds can reach a threshold, beyond which seed mortality can reduce recruitment, and may exacerbate negative effects of high fire frequency. The observations of low 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 severity fires. 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 and 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).

Conclusions

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 and Ooi 2021) and may be subject to similar additive effects of fire frequency and fire severity. The conditions for such effects occur globally across areas that have historically been subject to a regime of infrequent severe fires (Archibald et al. 2013). Our findings suggest that 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. For species with similar life histories——fire sensitive obligate seeders with physical dormancy broken by high fire-related temperatures——fire frequency and fire severity likely have similar impacts, but there may be much lower thresholds for the negative effects to occur. Ultimately, these processes will result in local extinctions as we observed at two sites in this study. In order to effectively conserve species threatened by these processes detailed knowledge of species-specific responses are required. In the case of *Pomaderris*, the dormancy breaking temperature thresholds are highly species specific. Management actions, fire severity and interval prescriptions based on one species may be detrimental to another, while genus level studies may miss the species level nuance and lead to perverse outcomes for species that deviate from the norm.

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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.

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Availability of data and materials

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, pre-fire 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.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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