Fire Ecology

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Time since fire shapes plant immaturity risk across fire severity classes

Ella S. Plumanns-Pouton[1]* , Matthew H. Swan[1], Trent D. Penman[1], Luke Collins[2,3] and Luke T. Kelly[1]

Abstract

Background When fire intervals are shorter than the time required for plants to reproduce, plant populations are threatened by "immaturity risk." Therefore, understanding how the time between fires influences plants can inform ecosystem management. Quantifying periods of immaturity risk requires investigating the influence of fire intervals across plant life stages, but most studies are indiscriminate of maturity. As fire regimes are multidimensional, it is also important to consider other characteristics of fires such as severity. We conducted a field study in heathy woodland that investigated how fire severity and fire interval influence immaturity risk to serotinous resprouter species, by examining if fire severity interacts with the time since the fire to influence the occurrence of mature individuals and relative abundance of three species: silver banksia (*Banksia marginata Cav.*), prickly teatree (*Leptospermum continentale Joy Thomps*), and heath teatree (*Leptospermum myrsinoides Schitdl*).

Results Regression modeling revealed a strong, positive influence of time since the last fire on the proportion of quadrats at a site with mature plants, for all three species. We only detected a small and uncertain influence of fire severity on the proportion of quadrats with mature heath and prickly teatree, and did not observe an effect of fire severity on the maturity of silver banksia. Interestingly, no relationships were observed between time since fire and the relative abundance of plants. That is, only when plant life stages were considered did we detect an effect of fire on plants. Populations of the three species were mostly immature in the first 7 years post-fire, suggesting if sites were uniformly burnt in this time frame, there could be increased risk of local extinctions.

Conclusions Our study highlights the importance of examining population processes, such as reproduction, in addition to plant relative abundance. Surprisingly, we did not detect strong differences in plant maturation across fire severity classes; low occurrence of mature plants in recently burnt areas indicated that immaturity risk was high, regardless of fire severity. Ecological studies that distinguish between plant life stages will help to predict the impacts of fire on populations and enhance decision-making. We recommend fire intervals of ≥ 8 years to protect serotinous resprouter plants in heathy woodland vegetation of southern Australia.

Keywords Australia, *Banksia marginata*, Fire regimes, Fire severity, Interval squeeze, Resprouters, *Leptospermum continentale*, *Leptospermum myrsinoides*, Serotiny, Heathland

*Correspondence:
Ella S. Plumanns-Pouton
ellap@student.unimelb.edu.au
[1] School of Ecosystem and Forest Sciences, The University of Melbourne, Grattan Street, Parkville, VIC 3010, Australia
[2] Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, 506 Burnside Road West, Victoria, BC V8Z 1M5, Canada
[3] Department of Environment and Genetics, La Trobe University, Bundoora, VIC 3086, Australia

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Resumen

Antecedentes Cuando los intervalos entre fuegos son menores que el tiempo requerido por las plantas para reproducirse, las poblaciones son amenazadas por el "riesgo de inmadurez". Por lo tanto, el entender como el tiempo entre fuegos influencia la vida de las plantas, nos puede brindar información sobre el manejo de ecosistemas. La cuantificación del período de "riesgo de inmadurez" requiere investigar la influencia de los intervalos de fuego sobre los estadios de vida de las plantas, aunque la mayoría de los estudios no discriminan sobre su estado de madurez. Como los regímenes de fuego son multidimensionales, es también importante considerar otras características de los fuegos, como su severidad. Condujimos un estudio de campo en un bosque de brezos que investigó cómo la severidad del fuego y el intervalo entre fuegos influencian el riesgo de inmadurez en especies serótinas, examinando si la severidad del fuego interactúa con el tiempo entre fuegos para influenciar la aparición u ocurrencia de individuos maduros y su abundancia relativa en tres especies: banksia plateada (Banksia marginata Cav.), *prickly teatree* (Leptospermum continentale Joy Thomps), y *heath teatree* (Leptospermum myrsinoides Schitdl).

Resultados Los modelos de regresión revelaron una muy fuerte y positiva influencia del tiempo entre el ultimo fuego en la proporción de parcelas en un sitio con plantas maduras, para todas estas especies. Detectamos solo una pequeña e incierta influencia de la severidad del fuego en la proporción de parcelas con plantas maduras de *heath* y *prickly teatree*, y no observamos un efecto de la severidad del fuego en la madurez de banksia plateada. De manera interesante, ninguna relación fue observada entre el tiempo desde el último fuego y la abundancia relativa de estas plantas. Esto significa que sólo cuando los estadios de vida de las plantas fueron considerados, detectamos un efecto del fuego sobre las plantas. La mayoría de las poblaciones de las tres especies consideradas estaban inmaduras en los siete primeros años del post-fuego, sugiriendo que si los sitios fuesen quemados de manera uniforme en este tipo de esquema, podría incrementarse el riesgo de extinciones locales.

Conclusiones Nuestro estudio enfatiza la importancia de examinar los procesos a nivel poblacional, como la reproducción, de manera adicional a la abundancia relativa de las plantas. Sorprendentemente, no detectamos diferencias marcadas en maduración de las plantas entre diferentes clases de severidad; la baja ocurrencia de plantas maduras en áreas quemadas recientemente indica que el riesgo de inmadurez es alto independientemente de la severidad del fuego. Los estudios ecológicos que distinguen entre distintos estadios de vida de las plantas ayudan a predecir los impactos del fuego en poblaciones y ayudan a mejorar los procesos de decisión. Recomendamos intervalos de ≥ 8 años para proteger las plantas serótinas en bosques de brezos de Australia.

Background

Fire directly influences the ability of plants to complete their life cycles and thus shapes plant population dynamics (Baltzer et al. 2021; Gosper et al. 2022). While many species have fire-related traits (Lamont et al. 2020; Lamont et al. 2019), ongoing fire regime changes, including higher frequency of severe fires (Collins et al. 2022), threaten the ability of plants to complete their life cycles (Gallagher et al. 2022; Nolan et al. 2022). Thus, quantifying the influence of multiple components of fire regimes on plant abundance and demography is essential to understand and manage the impacts of fire on plant populations (Enright et al. 2015; Tulloch et al. 2016).

The time since and between fires determines if plants can establish, grow, and reproduce (Burrows, et al. 2008; Harvey et al. 2017). Fire must be at sufficient intervals for plants to mature and develop a viable seed bank (Penman and Penman 2010). Short fire intervals can threaten plant populations through "immaturity risk," a concept that highlights the important role of mature individuals in accumulating sources of population persistence

(Zedler 1995). If the period is too short between fires, individuals do not have sufficient time to reach maturity, and this prevents persistence through recruitment and even resprouting (McColl-Gausden et al. 2022; Turner et al. 2019). Most research on immaturity risk focuses on obligate seeders (plants that do not resprout post-fire) (Whelan and Ayre 2020), yet some "resprouter" species are also vulnerable to immaturity risk, because they only produce shoots after a fire if they are mature, and post-fire require time to grow above-ground vegetation and restore below-ground resprouting organs (Clarke et al. 2013; Enright et al. 2011). Determining how much of a species' population is mature at different lengths of time since fire can therefore provide important information on the suitability of different fire frequencies for maintaining those populations (Burrows et al. 2008; Kraaij et al. 2013).

The characteristics of fire events are also important to consider (Steel et al. 2021). Fire severity—the consumption of plant material caused by fire intensity (Keeley 2009)—is an important fire characteristic that influences the reproductive status and recruitment of plants (Assal

et al. 2018; Fairman et al. 2016). For example, for some eucalypt species, exposure to high-severity fires can promote a higher density of recruitment post-fire than low-severity fires (Bennett et al. 2016). High-severity fire can stimulate increased flowering and cone production across a wide range of plants (Thomsen and Ooi 2022). Yet, high-severity fire can also cause seed death and limit seed dispersal, especially when fire temperatures are extreme (Bradstock et al. 1994; Gill, Hoecker, and Turner 2021). Studies on plant reproduction after fire do not usually account for fire severity (Brennan and Keeley 2019; Gosper et al. 2022), even though fire severity influences recruitment and time to maturity (McCaw 2008). We reason that incorporating both fire severity and time since fire into ecological studies will help to disentangle the influences of the multiple components of the fire regime and understand plant life cycles under future fire regimes.

In this study, we test whether fire severity influences the relationship between time since fire and reproductive maturity. We do this using field data collected within a Mediterranean-type "heathy woodland" ecosystem in southeastern Australia. We quantify the proportion of quadrats at a site that contains individuals exhibiting reproductive maturity (flower and seed production), across a time since fire gradient following either low- or high-severity fire. We do this for three serotinous facultative seeder species that resprout to a juvenile stage post-fire, and therefore require several years to regain maturity after the fire (Falster et al. 2021). Serotinous or canopy-stored seed typically has very short longevity once released from its protective casing (Enright et al. 2007; Su et al. 2019). Serotinous plants also typically mature at a slower rate than non-serotinous plants (Enright et al. 2007) and are therefore at higher immaturity risk. This is why canopy seeders, such as the taxa we have selected for study, are often used as benchmark species for determining appropriate intervals between fires (Bradstock and Kenny 2003).

We propose two alternative hypotheses for how time since fire and fire severity may interact to drive the proportion of mature plants at a site (represented by the variable "Proportion of quadrats with mature individuals" in Fig. 1). Under hypothesis 1 (Fig. 1A), we predict that the time immediately following the fire is a period of "high immaturity risk" for populations exposed to high-severity fire and less of a risk ("low immaturity risk") for populations exposed to low-severity fire. This is because low-severity fires may allow for some mature individuals to persist post-fire (Rodman et al. 2021), but high-severity fires are more likely to completely reduce a population to a juvenile state (Pellegrini et al. 2017). Individuals that retain above-ground vegetation after low-severity

fires would form some protection to plant populations at exposure to a second fire (Burrows and Middleton 2016), whereas high-severity fires would leave populations exposed to local extinction if fire passed again at a time when plants have not reached maturity (i.e., plant survival could be reduced). If a fire-free period is maintained until plants reach maturity, then perhaps counterintuitively, it is then plausible for there to be a higher proportion of mature plants in those populations that were exposed to high- rather than low-severity fires. This is because high fire temperatures may maximize germination rates (Auld and Bradstock 1996) and produce more individuals that later mature. By contrast, under hypothesis 2 (Fig. 1B), mortality rates of mature plants are expected to be high irrespective of fire severity, with no distinguishing effect of fire severity on the proportion of mature plants. Under this hypothesis, the difference between low- and high-severity fires is simply not distinct enough to differentially kill individuals. Therefore, under a continued fire-free period, there may be a positive relationship between time since fire and reproductive maturity (Muir, et al. 2014), which will plateau over time, for populations that are exposed to both high- and low-severity fires. These hypotheses are both plausible and require empirical testing.

Methods

Study area, site selection, and fire mapping

The study was completed in heathy woodland vegetation of Gariwerd (the Grampians National Park, the Black Range National Park, and Cherry Pool State Forest; Fig. 2), Victoria, Australia ($-37.21°$ S, $142.39°$ E). The region has a cool temperate climate, with four distinct seasons. Annual rainfall was 900 mm in 2020, 31 mm less than the 10-year average (930 mm $2010-2020$; http://www.bom.gov.au/jsp/ncc/cdio/weatherData, Halls Gap, 37.14° S, 142.52° E). Soils are typically nutrient-poor acidic sands. The area has a long history of fire, including skillful application by Indigenous peoples such as the Djab Wurrung, Eastern Maar, Gunditjmara, Jaadwa, Jardwadjali, Jupagulk, Wergaia, and Wotjobaluk Nations. The area has experienced several large wildfires since 1939, including in 2006 (127,000 ha), 2013 (35,000 ha), and 2014 (55,000 ha), and prescribed burning by government agencies has been applied since the 1970s. Some locations have remained unburnt since 1939 (Fig. 2A).

Heathy woodland vegetation is made up of evergreen schlerophyllous shrubs and trees, including the *Ericaceae*, *Fabaceae*, *Myrtaceae*, and *Proteaceae* families (Specht and Moll 1983). Tree cover is dominated by brown stringybark (*Eucalyptus baxteri (Benth.) Maiden & Blakely ex J.M.Black*), which grows to a maximum
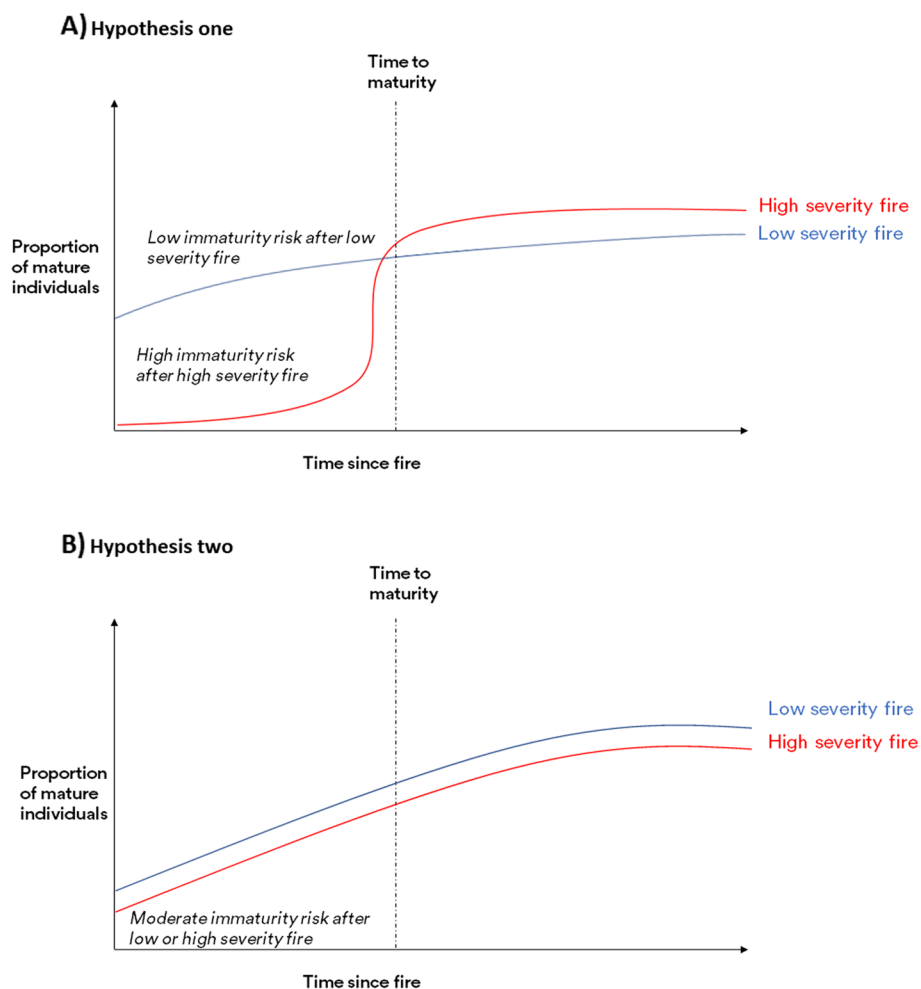
Fig. 1 Alternative conceptual models of how time since fire and fire severity could influence the proportion of mature plants. **A** Under hypothesis 1, the recent time since fire is a high immaturity risk point for populations exposed to high severity fire, because the population is in a juvenile state and unlikely to persist if another fire occurs. Whereas, areas exposed to low-severity fire retain some mature individuals which protects plant populations after repeat fires. **B** Under hypothesis 2, the early years since fire are a time of high immaturity risk for all individuals, regardless of fire severity. Thus, forming a mostly linear relationship between time since fire and the proportion of mature individuals for both high and low-severity fires

height of approximately 8 m (Enright and Goldblum 1998). Midstorey shrubs include species such as scrub sheoak (*Allocasuarina paludosa Sieber ex Spreng*) and beaked hakea (*Hakea rostrata F.Muell. ex Meisn*). All sites included in the present study had tree cover, which is necessary to calculate fire severity using the method we applied.

We used a space for time substitution approach to assess the effect of time since fire and fire severity on plant populations. Thirty-five sites were selected to represent variation in time since fire, including in areas burnt at low and high severity. Time since the last fire was calculated using a spatial fire history database that uses satellite imagery, on-ground mapping, and historical records, acquired from the Victorian Government

(Department of Environment Land Water and Planning 2022), and later ground truthed by EPP and MS. We selected sites for the study that had burnt between 1990 and 2020, the range of fire histories mapped by satellite imagery at a resolution that enables calculation of fire severity (Collins et al. 2020). Fire severity was mapped with Landsat imagery (30-m resolution) using the approach described in Collins et al. (2020).

Severity mapping included defining the perimeter and start and end dates of all fires included in the present study, using Landsat imagery to form pre- and post-fire images, and deriving eight spectral indices from those images (including normalized burn ratio, normalized difference vegetation index, normalized difference water index, visible atmospherically resistant index, modified
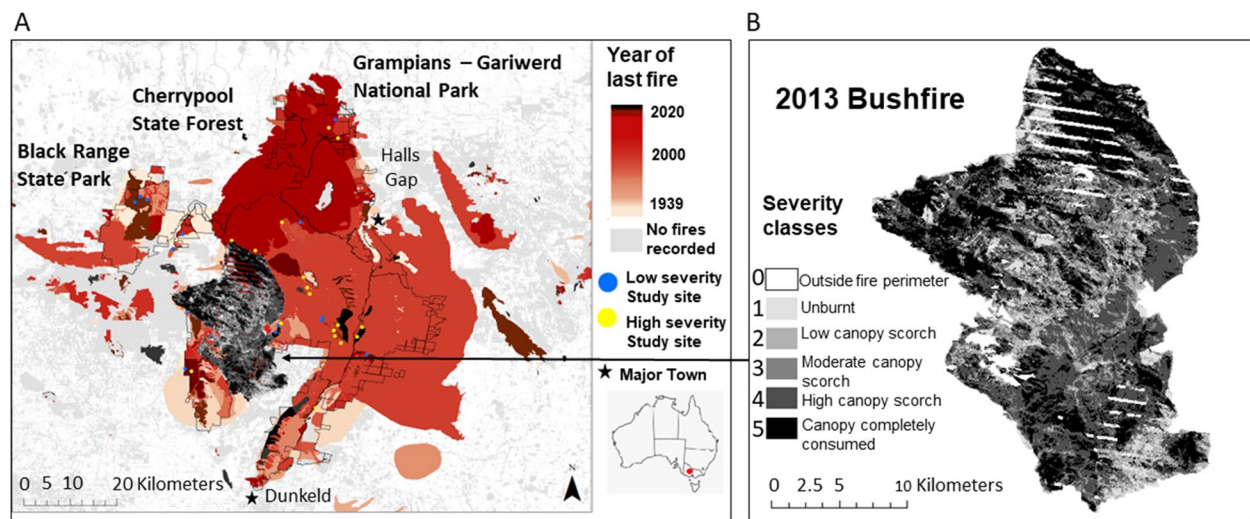
Fig. 2 A Map of the study area, Gariwerd, Australia, with time since the last fire shown (1939–2020). **B** An inset of fire severity mapped for a single fire from 2013. In panel A, study sites are represented in yellow for high severity (severity classes 4, high canopy scorch; 5, canopy completely consumed) and blue for low severity (severity class 2, low canopy scorch). Grey areas show the native vegetation with no fires recorded. Stars indicate regional town centers. The right panel (B) shows an example of the fire severity variation for a 2013 fire. Severity classes are shown on a scale from 0 to 5 (0, outside the mapped fire perimeter; 1, unburnt within the fire perimeter; 2, low canopy scorch (understory burnt, < 20% of canopy scorched); 3, moderate canopy scorch (understory burnt, 20–80% of canopy scorched); 4, high canopy scorch (understory burnt, > 80% of canopy scorched); 5, canopy completely consumed). Horizontal striping in the severity map is due to a commonly occurring Landsat 7 line scan error

soil adjusted vegetation index, burn area index, mid-infrared bi-spectral index, and char soil index) (Collins et al. 2020). A random forest machine learning algorithm was then applied to assign pixels to one of five severity classes: unburnt, low canopy scorch (< 20% scorch), moderate canopy scorch (20–80% scorch), high canopy scorch (> 80% scorch), and canopy consumption. The model has been trained and tested using 43 fires across southeastern Australia, including fires occurring in our study area, and found to have very high classification accuracy (> 89%) for the unburnt, high crown scorch, and canopy consumed classes and high accuracy for the low (81%) and moderate scorch (72%) classes (Collins et al. 2020; 2021). In the present study, pixels were reclassified into either "high" (high canopy scorch, canopy consumption) or "low" (low canopy scorch) and assessed in the field by EPP and MS to ensure study sites were established in the desired fire severity classes. Moderate canopy scorch was avoided when selecting sites because it was considered an ambiguous severity class in heathy woodlands that are shrubby-statured in nature.

In summary, sites ranged from 1 to 23 years post-fire, and 21 of the sites were burnt at high severity and 14 at low severity (Supporting Information Table S2). Sites constituted a 100-m transect that covered consistent severity pixels, fire history, vegetation type, and topography and were oriented away from roads. Sites were a minimum of 500 m apart to reduce spatial dependence.

Field survey methods

Surveys of vascular plants were completed in late summer to autumn (March to May 2021) along a 100-m transect. We recorded the presence and maturity of all species within 33 quadrats (1 m²) that were distributed every 3 m across the transect. Plant maturity was defined as either "seeds" (if visible fruit was present), "flowers" (if flowers were visible), or "immature" (no indication of maturity). This was collected hierarchically, with seed as the "highest" marker of maturity. Maturity information was recorded per quadrat. In cases where multiple individuals of the same species were observed in a quadrat as flowering and/or with seeds, we only recorded the higher observation of seeds. However, the occurrence of multiple individuals in one quadrat was rare. The occurrence of species within each of the 33 quadrats, from zero to 33, was used as a measure of relative abundance, expressed as a proportion out of 33 (hereafter "relative abundance"). The proportion of quadrats with mature individuals was calculated as the number of quadrats containing the species exhibiting maturity (seed or flowers), based on the total number of quadrats that contained the species at a site (hereafter "proportion of quadrats with mature individuals").

Statistical analysis

We modeled only serotinous species, a group for which reproductive maturity could be identified because they

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produce or hold propagules throughout the year. We limited the analysis to three species that were present at ≥ 25 sites: silver banksia (*Banksia marginata Cav.*), prickly teatree (*Leptospermum continentale Joy Thomps*), and heath teatree (*Leptospermum myrsinoides Schitdl*). After the fire, mature individuals from these three species have been recorded to resprout basally to a juvenile state, while immature individuals are fire-killed (Falster et al. 2021). The study species also germinate their seeds post-fire, at which point their seed bank is exhausted (Falster et al. 2021). We constrained model estimates to 0–15 years post-fire because there were limited data points for the three study species at longer times since the fire. We considered this to be sufficient time to investigate how maturity was influenced by time since fire and fire severity, and plausibly related to immaturity risk; the two teatree species have been observed to mature at 3–5 years post-fire and silver banksia at 5–10 years post-fire (Falster et al. 2021).

We used generalized additive models (GAMs) to quantify the influence of time since fire and fire severity on the relative abundance of species, and the proportion of quadrats with mature plants (Wood 2017). GAMs are a form of regression in which the predictor does not take a predetermined, linear form, and instead uses a smoothing function (Simpson 2018; Wood 2017). They have been widely used to model fire-biota relationships (Haslem et al. 2011).

The response data were proportional (relative abundance: presence at between 0 to 33 quadrats; and proportion of quadrats with mature individuals: with the proportion of mature individuals calculated as a function of quadrats in which a species was present). We ran three alternative models for each combination of species and response variable (i.e., relative abundance and proportion of quadrats with mature individuals). First, we analyzed the univariate influence of time since fire on the relative abundance or proportion of quadrats with mature individuals. Second, we built models that included time since fire and fire severity as additive predictors of the plant measures. Third, we modeled the interactive effects of time since fire and fire severity on the plant measures. We trialed model building using a binomial link function through the R package mgcv (Wood 2011), but the models exhibited overdispersion. The betabinomial distribution is regularly used to model proportions arising from counts that are overdispersed (Douma and Weedon 2019). We built models using a betabinomial distribution in the R statistical package brms, a package that employs a Bayesian framework (Bürkner 2017). Each regression model comprised four Markov Chain Monte Carlo simulations with 4000 iterations. We specified a half Student *T* distribution for all priors: the intercept, standard deviation of the smooth term, and overdispersion priors. The half Student *T* distribution was considered a "moderately skeptical" prior (Gelman 2006) for the modeled data as predictions were representative of the observed data rather than predetermined priors (Lemoine 2019). The default brms overdispersion prior was considered overly flat due to an emphasis on lower values, and thus overly informative. Sensitivity analysis indicated that minor changes to the priors within the brms framework made no marked difference to regression model outputs (Supporting Information Table S3). Thus, we only present the results of the half Student *T* distribution in the main text.

We explored model effects and their uncertainty primarily using plots of model predictions. We also obtained a Bayesian measure of *R*-squared ("Bayes R^2") as a measure of model fit and reported the 2.5% and 97.5% quantiles around this measure. We built mean estimates (estimated marginal means) from the model using the ggeffects package (Lüdecke 2018) and displayed these and confidence intervals (highest posterior density intervals) using the package ggplot2 (Wickham 2016). Finally, we conducted posterior predictive checks with 50 posterior draws to test the predictive accuracy of the models using the MgcViz package (Fasiolo et al. 2020). All statistical analyses were performed in R Studio using version 1.4.1717/R version 4.1.1 (R Core Team 2021; RStudio Team 2020).

Results

Relative abundance of plants

There was no observable relationship between time since fire on the relative abundance of silver banksia, prickly teatree, or heath teatree in the 15-year period considered (Fig. 3A). For example, heath teatree was predicted to occur at approximately 50% of quadrats across the range of fire histories surveyed (Fig. 3A). Although the inclusion of fire severity as an additive or interactive effect slightly improved model explanatory power for all three species (Table 1), we did not observe marked changes in relative abundance that were associated with fire severity (Fig. 3A). For models of the abundance of each species, the mean estimate of relative abundance was similar for high severity and low-severity fire, and confidence intervals overlapped across most of the time since fire gradient.

Proportion of reproductively mature individuals

In contrast to models of relative abundance, time since fire had a strong influence on the proportion of quadrats with mature individuals—for all three species (Fig. 3B). For example, for silver banksia, the predicted proportion of quadrats with mature individuals increased from 13% (1 year post-fire) to 58% (15 years
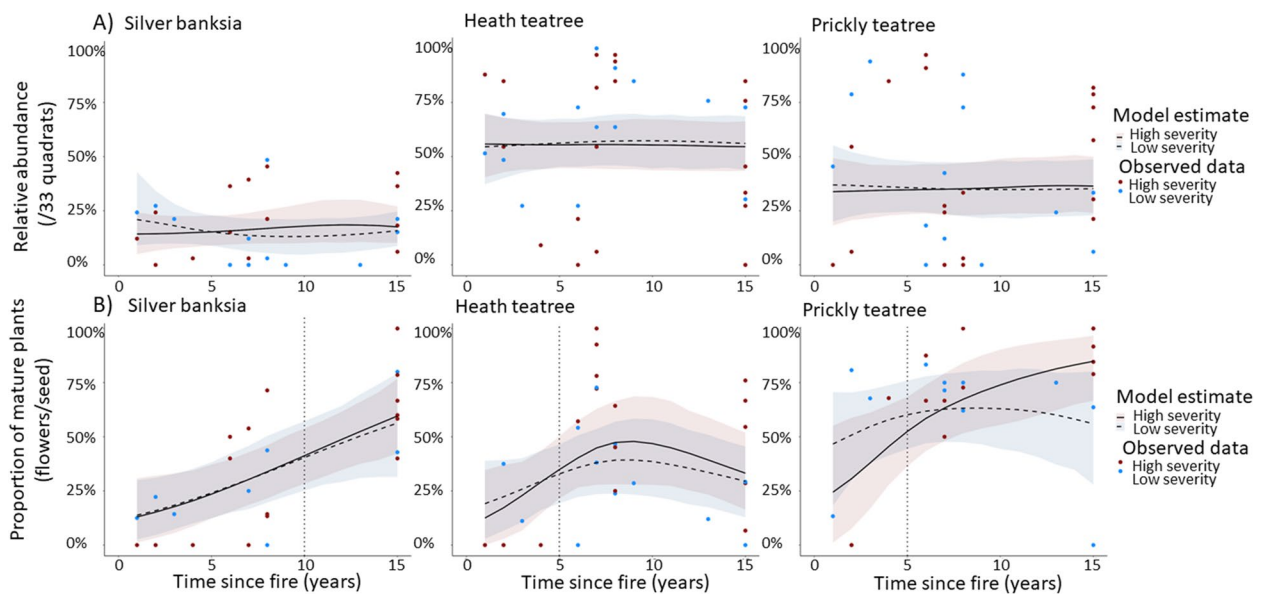
Fig. 3 Influence of time since fire and fire severity on relative abundance (top row) and proportion of quadrats with mature individuals (bottom row), for silver banksia, heath teatree, and prickly teatree in Gariwerd, Australia. The *x*-axis shows the time since the fire in years for all plots. In the top row, the *y*-axis demonstrates the relative abundance of individuals at a site from 0 to 33 quadrats, converted to a percentage of 0 to 100%. In the bottom row, the *y*-axis demonstrates the proportion of quadrats with mature individuals at a site. For each plot, the full line shows predicted models (sometimes called estimated marginal means) for high fire severity, while the dotted line shows the predicted models for low fire severity. Red-colored shading demonstrates the confidence intervals (specifically, highest posterior density intervals) for high fire severity while blue-colored shading demonstrates the confidence interval for low fire severity. The points show the observed data, colored in red and blue for high and low fire severity, respectively. For the bottom row, the vertical dotted line represents the time to maturity obtained from the Victorian Vital Attributes database; 5 to 10 years for silver banskia and 3 to 5 years for the teatree species, respectively

Table 1 Outputs from regression models of plant distributions from Gariwerd, Australia, as a function of fire history. For each model, the Bayes R^2 (and 2.5% and 97.5% quantiles) are displayed

Response variable	Model predictors	Species	Bayes R^2	Q2.5	Q97.5
Relative abundance	Time since fire	Silver banksia	0.03	0.00	0.14
		Prickly teatree	0.02	0.00	0.09
		Heath teatree	0.03	0.00	0.13
	Time since fire + fire severity	Silver banksia	0.08	0.01	0.22
		Prickly teatree	0.04	0.00	0.14
		Heath teatree	0.07	0.00	0.20
	Time since fire * fire severity	Silver banksia	0.07	0.00	0.29
		Prickly teatree	0.02	0.00	0.08
		Heath teatree	0.03	0.00	0.13
Proportion of quadrats with mature individuals	Time since fire	Silver banksia	0.69	0.54	0.76
		Prickly teatree	0.72	0.60	0.81
		Heath teatree	0.27	0.14	0.45
	Time since fire + fire severity	Silver banksia	0.68	0.53	0.76
		Prickly teatree	0.72	0.59	0.81
		Heath teatree	0.54	0.29	0.68
	Time since fire * fire severity	Silver banksia	0.64	0.42	0.75
		Prickly teatree	0.78	0.65	0.88
		Heath teatree	0.40	0.15	0.64

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post-fire). All species demonstrated an increase in the proportion of quadrats with mature individuals at a site from 1 to 10 years post-fire. The variation explained by the models was moderate to high (0.27–0.72 Bayes R^2, Table 1). Model predictions (Fig. 3B) for all three species showed that time since fire has a strong effect on maturity regardless of fire severity. While the mean estimates for the interactive model of prickly teatree show a small amount of differentiation by fire severity class, the overlapping confidence intervals around the mean estimates for fire severity type show that this difference is highly uncertain.

The inclusion of fire severity as an additive or interactive effect did not consistently improve the fit of models of reproductive maturity (Table 1). For prickly teatree, the variance explained in the model with an interaction term for fire severity was higher (0.78 Bayes R^2, Table 1) than the models with an additive term for fire severity (0.72 Bayes R^2, Table 1) and without fire severity (0.72 Bayes R^2, Table 1). In the first 5 years since fire, the mean estimates from models of this species that included an interaction term indicated a moderately higher proportion of quadrats with mature individuals in areas burnt by low-severity fire than high-severity fire (Fig. 3). The influence of fire severity was also supported by the stronger influence of time since fire under high severity fire. However, the confidence intervals of the low-severity and high-severity estimates largely overlap, and thus, we do not interpret this as a strong interactive effect. From approximately 5 years post-fire, all sites had high proportions of quadrats containing mature prickly teatree, but the sites that experienced high severity fires had marginally larger proportions of quadrats with mature plants than the sites that experienced low severity fires (clearest from about 13 years post-fire) (Fig. 3B).

For the proportion of mature heath teatree occurring in quadrats, the model with an additive term for fire severity explained more variation in the data (0.54 Bayes R^2, Table 1) than the model with an interactive term for fire severity (0.40 Bayes R^2, Table 1) and without fire severity (0.27 Bayes R^2, Table 1). Yet, graphical exploration of model predictions did not indicate a strong effect of fire severity for heath teatree; the mean estimates from the model with an interaction term were similar for low and high severity fire and had confidence intervals that overlapped across almost the full range of time since fire (Fig. 3B). For silver banksia, the inclusion of fire severity as an additive (0.68 Bayes R^2, Table 1) or interactive term (0.64 Bayes R^2, Table 1) in the model of mature plants did not explain more variation in the data, relative to the base model (0.69 Bayes

R^2, Table 1). We did not detect an effect of fire severity when assessing these model predictions graphically, with model estimates and confidence intervals aligning for low and high-severity fire in the interactive model (Fig. 3B).

Discussion

We aimed to understand the combined influence of time since fire and fire severity on three serotinous resprouter species, and what this means for immaturity risk. Time since fire clearly influenced the proportion of quadrats with mature plants (and therefore the period of immaturity risk) for all three species. Fire severity was observed to have a small and uncertain effect on one species, a marginal and uncertain effect on another species, and no effect was detected on a third species. To our knowledge, this study is one of the first empirical tests of the relationship between fire severity, time since fire, and plant maturity in Mediterranean-type ecosystems. While clear relationships between fire and reproductive maturity were observed, no relationship was observed between fire and plant abundance, highlighting the importance of empirical studies that examine plant life cycles and population processes.

On fire and the relative abundance of plants

We did not detect an effect of time since fire or fire severity on relative abundance across the three plant species. This can be explained by the large cohorts of individuals that germinate post-fire (Bell 1999; Cowling and Lamont 1987; Roche et al. 1998) and thus are likely to appear as juveniles in data sets that include all maturities. The time scale of our study is also important. We modeled plant distributions within a 15-year period after fire, yet some changes in plant abundance potentially happen at later post-fire ages because these species live for several decades. For example, declines in abundance due to mortality, inter-specific competition, or self-thinning may occur at later post-fire ages (Gale and Cary 2021).

While measures of plant occurrence and relative abundance remain useful in some contexts (Kelly et al. 2017), the present study indicates that, on their own, measures of relative abundance may not provide enough information to accurately assess the effects of fire on plant populations in recently burnt areas. This supports previous empirical and modeling work that emphasizes the importance of considering population processes when investigating the influence of fire on vegetation (Davis et al. 2018; Enright et al. 2015; Tulloch et al. 2016) and highlights the importance of monitoring plant life stages to aid recovery after fire and inform management actions and decision making.

Reproductively mature individuals

We identified a strong influence of time since fire on the proportion of mature individuals at a site for all three species. For silver banksia and prickly teatree, the proportion of quadrats with mature individuals at a site was observed to increase up to 15 years post-fire, suggesting that some individuals are still maturing towards the cut off point of the time since fire range we modeled. Silver banksia is a good example of this, and there is evidence that it benefits from a substantial fire-free period (maturing up to the full range of our study). Previous time to maturity estimates for both the teatree species is between 3 and 5 years post-fire (Falster et al. 2021). Our new field observations document that the proportion of quadrats with mature individuals continues to increase past this timeframe. Nonetheless, prickly teatree demonstrated relatively high levels of maturity (> 50% of quadrats with mature individuals occurring) for both severity classes before five years. For heath teatree, a small number of observations of mature individuals at sites burnt at less than 5 years and, at low severity, likely indicate surviving individuals that retained maturity through a low-severity fire.

For heath teatree, the positive relationship between the proportion of quadrats with mature individuals and time since the last fire peaked just under 10 years, then begins to decline. Previous studies in other serotinous species, including types of banksia and pine, have found similar patterns of reproductive effort and time since fire, with an initial rapid increase in reproductive effort, followed by a plateau or decline (Agne et al. 2022; Keeley et al. 1999; Muir et al. 2014). This suggests inter-fire recruitment could be occurring, increasing the total number of juveniles and thus their proportion at samples within a site. Inter-fire recruitment could also be occurring in combination with self-thinning; in this case, when the maximum capacity of mature individuals is reached, the survival rate of individuals may be reduced by competition (Gale and Cary 2021). An alternative explanation is that larger species have reached an age post-fire where they change light availability within the site (such as prickly teatree).

Contrary to what we expected under hypothesis 1, the results of the present study did not indicate a clear influence of fire severity on the maturity of plants along a time since fire gradient. Instead, the models provide stronger support for hypothesis 2: mortality rates of mature plants are high irrespective of fire severity, thus causing no distinguishing effect of fire severity on the proportion of quadrats with mature individuals. The consistent proportion of mature silver banksia plants across severity classes may be due to their tolerance of a large range of temperatures for canopy seed release (Enright and Lamont 1989). Some banksia species release seed from 150 to 400

degrees, and thus, seed release is only partially explained by energy-dependent responses (e.g., melting of the resin that holds follicles closed) (Enright and Lamont 1989). Silver banksia also often occurs as small shrubs in this landscape, and this may contribute to a higher probability of being consumed even at low severities. For silver banksia, there was no evidence from the model estimates that high-severity fires are reducing the ability for species to mature and thus complete their life cycles.

Mature plants were recorded directly after fire: 1 year at sites exposed to low-severity fire for prickly teatree and silver banksia, and 2 years for heath teatree, indicating survival of some mature individuals (Fig. 3). Even though statistical modeling did not highlight strong or interactive effects of fire severity on the study species, this likely shows that mature individuals can persist under some forms of low-severity fire and perhaps act as safeguards at exposure to short-interval fire. For example, for silver banksia, 3 sites that were burnt at low-severity fire less than 3 years prior demonstrate between 15 and 25% of quadrats containing those species had mature individuals. For heath and prickly teatree, up to 40 and 80% of quadrats contained mature plants at 2 years post-fire. The ability to tolerate fire intervals at shorter time frames than the juvenile period has been observed in oak-leaved banksia (*Banksia quercifolia R.Br.*), and attributed to variation in the passage of fire, including severity (Burrows and Middleton 2016). The possibility of surviving mature individuals under low-severity fire is important because most estimates of immaturity risk assume that individuals are killed by fire or return to a juvenile state after fire (Henzler et al. 2018; McColl-Gausden et al. 2022). We think that it is plausible that stronger effects of fire severity, and related characteristics such as fire intensity, could be observed at finer resolutions than the present study—and if different types of lower severity burns were implemented in the landscape.

After around 7 years post-fire, a moderately higher proportion of mature prickly teatree occurred at sites that experienced high-severity fire than low-severity fire. This may be explained by the temperature of fires: heat-stimulated germination may be greater under moderate to high temperatures that do not exceed lethal thresholds. Lower temperatures, closer to the minimum necessary to stimulate germination, may result in less germination (Auld and Bradstock 1996; Bradstock and Auld 1995; Moreira and Pausas 2012). This is consistent with a higher proportion of quadrats with mature individuals of prickly teatree at the time post-fire recruits are likely to have matured. Shifts in resource availability, such as reduced competition for light or an increase in ash-related minerals such as phosphorus and potassium, may also explain these patterns (Lamont and Runciman

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1993; Negrón-Ortiz and Gorchov 2000). This observed pattern of higher proportions of mature prickly teatree under high-severity fire continues until the end range of our study (15 years), well after the maturation of plants establishing or regrowing after the most recent fire is expected. We hypothesize that the experience of initially lower competition post-high severity fire may contribute to more rigorous growth at later ages post-fire (Resco de Dios 2016), subsequently creating competition that prevents recruitment. Studies of other species have demonstrated more rigorous growth, including height and shrub coverage, under high-severity fire (Crotteau et al. 2013; Pausas et al. 2002; Resco de Dios 2016).

Several studies have demonstrated a strong influence of fire severity on plants (Bassett et al. 2017; Busby, Moffett, and Holz 2020). It is possible that the influence of fire severity is less pronounced in fire-prone heathy woodlands of southeastern Australia than in other ecosystems that might be less fire-habituated or more topographically varied. In a comparable Mediterranean-type shrubland ecosystem in Chile, fire severity did not influence vegetation regeneration (Smith-Ramírez et al. 2022). Shrubby chaparral ecosystems in the western USA also persist through high-fire severity fire, due to strong regeneration traits of plant species (Airey Lauvaux et al. 2016). However, for the neighboring mountainous and topographically varied conifer forests, fire severity can be an important factor in plant composition (Strand et al. 2019) and plant species diversity (Richter et al. 2019). Even where severity has a pronounced effect, the influence of fire severity can be strong in the short term (months to years), but disappear after one to two decades (Meng et al. 2015; Romme et al. 2016). The early post-fire time frame of this study therefore provided a sound basis for detecting potential effects of severity on the three study species.

We now highlight the several ways forward for studies of plant maturity, fire severity, and time since the last fire. First is how fire severity is measured. Although fire severity modeling was assessed in the field, there is variation within a 30-m resolution that may influence individual plants and therefore populations and individuals. In particular, low-severity fires can be patchier than high-severity fires, and patchy fires are likely to influence the vegetation heterogeneously (Ooi et al. 2006). Research on fine-scale variation in severity, including assessing how the configuration of fires influences individual plants, will be important to progress work on demographics and life cyles (Ooi, et al. 2006). In the present study, we modeled "low" severity fires that had < 20% of the canopy scorched, and it is possible that lower severity or patchier fires could be applied (e.g., cultural burning, ecological burning, and other forms of deliberate fire use). Investigating these very low severities may reveal new patterns in immaturity risk.

The second way forward is investigating fire severity and time since fire interactions across different plant functional types (such as obligate seeders, in addition to facultative seeder species). For example, there is some evidence that soil-stored obligate seeding species in the *Leucopogon* genus may be able to tolerate frequent fires if they are low in severity and spatially heterogenous (Ooi et al. 2006). Furthermore, differences in low- and high-severity fires might violate assumptions about which plant traits are resilient to fire regimes (Enright et al. 2014). For example, non-fire-killed species can experience resprouting failure and plant death after high-severity fire (Bennett et al. 2016; Berris et al. 2022), and fire severity may reduce the availability of the soil-stored seed bank and thus reduce resilience to recurring fire events (Palmer et al. 2018). It is possible that species that are less abundant than those we modeled will be more susceptible to fire severity impacts and therefore more targeted studies for rare and threatened species may be useful.

Finally, more work is needed on the numbers of mature plants in a given population that increase the risk of local extinction (or immaturity risk) faced by a population (Gosper et al. 2013). In some cases, 50% maturity of a local population is taken as a threshold for sustaining a species, but uncertainty remains on the true proportion of mature plants needed to sustain populations of different species and groups (Gosper et al. 2013; Muir et al. 2014). For example, canopy seed bank production is likely to increase for several years post-maturation time, and therefore, it may be several years post-maturation time before a local population would have sufficient seed store to not be at immaturity risk. A resprouting hakea species (*Hakea decurrens*) from the same region demonstrates peak cone production at 12 years (Enright and Goldblum 1998). It would also be useful to quantify the trajectory of flowering to fruiting.

Conclusions

Differentiating across plant life stages is important to understand how fire influences plant populations. Our research has demonstrated that accounting for maturity can reveal new and important relationships that are not visible from relative abundance data that pool all life stages. As the climate changes, and "squeezes" the fire intervals through which species can persist (Enright et al. 2015), understanding reproductive maturity will help to identify species at risk of extinction. In the heathy woodlands we studied, fire intervals ≤ 8 years are unlikely to support the reproduction of serotinous resprouter species if they are applied across large areas. In particular, silver banksia and heath teatree will continue to accumulate seed store well after 8 years. A wide range of conservation actions is possible including a mix of fire suppression, fuel reduction, and ecological restoration.

Abbreviation
TSF   Time since fire

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00185-4.

> **Additional file 1: Table 2.** List of site numbers with corresponding time since fire and fire severity values. **Table 3.** Sensitivity analysis for the choice of priors for one model (interactive model) for one example species (Prickly teatreeat). We show the priors chosen in this study (top row), compared against default priors (second row), and a range of other plausible combinations of priors. We specify the priors input for the intercept, standard deviation of smooth terms, and dispersion parameter, and the model outputs including Bayes R^2._, and the 2.5% and 97.5% quantiles.

Authors' contributions

EPP, MS, TP, and LK conceived the ideas and hypotheses and designed the methodology. LC developed the fire severity maps. EPP collected the field data. EPP conducted the statistical analyses of the data. EPP, MS, TP, LC, and LK interpreted the results. EPP produced the first draft. EPP and LK led further the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Availability of data and materials

The datasets generated and analyzed during the current study are available in the Figshare repository, https://doi.org/10.26188/22272769.

Declarations

Competing interests

The authors declare that they have no competing interests.

References

Agne, Michelle C., Joseph B. Fontaine, Neal J. Enright, Sarah M. Bisbing, and Brian J. Harvey. 2022. Demographic processes underpinning post-fire resilience in California closed-cone pine forests: The importance of fire interval, stand structure, and climate. *Plant Ecology* 223 (7): 751–767. https://doi.org/10.1007/s11258-022-01228-7.

Assal, Timothy J., Mauro E. González, and Jason S. Sibold. 2018. Burn severity controls on postfire Araucaria-Nothofagus regeneration in the Andean Cordillera. *Journal of Biogeography* 45 (11): 2483–2494. https://doi.org/10.1111/jbi.13428.

Auld, Tony D., and Ross A. Bradstock. 1996. Soil temperatures after the passage of a fire: Do they influence the germination of buried seeds? *Austral Ecology* 21 (1): 106–109. https://doi.org/10.1111/j.1442-9993.1996.tb00589.x.

Baltzer, Jennifer L., Nicola J. Day, Xanthe J. Walker, David Greene, Michelle C. Mack, Heather D. Alexander, Dominique Arseneault, Jennifer Barnes, Yves Bergeron, Yan Boucher, et al. 2021. Increasing fire and the decline of fire adapted black spruce in the boreal forest. *Proceedings of the National Academy of Sciences* 118 (45):e2024872118.https://doi.org/10.1073/pnas.2024872118.

Bassett, Michelle, Steven W J Leonard, Evelyn K Chia, Michael F Clarke, and Andrew F Bennett. 2017. Interacting effects of fire severity, time since fire and topography on vegetation structure after wildfire 396:26–34.https://doi.org/10.1016/j.foreco.2017.04.006.

Bell, David T. 1999. Turner review no. 1: the process of germination in Australian species. *Australian Journal of Botany* 47 (4):475–517.https://doi.org/10.1071/BT98007.

Bennett, Lauren T., Matthew J. Bruce, Josephine MacHunter, Michele Kohout, Mihai A. Tanase, and Cristina Aponte. 2016. Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire. *Forest Ecology and Management* 380: 107–117. https://doi.org/10.1016/j.foreco.2016.08.047.

Berris, Karleah K., Ruby M. H. Jones, Xiangning Kok, Adrian K. J. McCafferty, Johannes K. Skirrow, Trish Mooney, Karleah K. Berris, Ruby M. H. Jones, Xiangning Kok, Adrian K. J. McCafferty, et al. 2022. The effect of inter-fire interval and fire severity on seedling germination and resprouting in Allocasuarina verticillata. *Australian Journal of Botany* 70 (5): 384–395. https://doi.org/10.1071/BT22016.

Bradstock, Ross, and A., and B. J. Kenny. 2003. An application of plant functional types to fire management in a conservation reserve in Southeastern Australia. *Journal of Vegetation Science* 14 (3): 345–354. https://doi.org/10.1111/j.1654-1103.2003.tb02160.x.

Bradstock, Ross, and A., and T. D. Auld. 1995. Soil temperatures during experimental bushfires in relation to fire intensity: Consequences for legume germination and fire management in South-Eastern Australia. *Journal of Applied Ecology* 32 (1): 76. https://doi.org/10.2307/2404417.

Bradstock, Ross A., A.M. Gill, S.M. Hastinga, and P.H.R. Moore. 1994. Survival of serotinous seedbanks during bushfires: Comparative studies of Hakea species from Southeastern Australia. *Australian Journal of Ecology* 19 (3): 276–282. https://doi.org/10.1111/j.1442-9993.1994.tb00490.x.

Brennan, Teresa J., and Jon E. Keeley. 2019. Postfire population dynamics of a fire-dependent cypress. *Plant Ecology* 220 (6): 605–617. https://doi.org/10.1007/s11258-019-00939-8.

Bürkner, Paul-Christian. 2017. Brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* 80 (1):1–28.https://doi.org/10.18637/jss.v080.i01.

Burrows, Neil, and Ted Middleton. 2016. Mechanisms enabling a fire sensitive plant to survive frequent fires in South-West Australian eucalypt forests. *Fire Ecology* 12 (1): 26–40. https://doi.org/10.4996/fireecology.1201026.

Burrows, Neil D., G. Wardell-Johnson, and B. Ward. 2008. Post-fire juvenile period of plants in South-West Australia forests and implications for fire management. *Journal of the Royal Society of Western Australia* 91: 163–174.

Busby, Sebastian U., Kevan B. Moffett, and Andrés Holz. 2020. High-severity and short-interval wildfires limit forest recovery in the central Cascade Range. *Ecosphere* 11 (9):e03247.https://doi.org/10.1002/ecs2.3247.

Clarke, P.J., M.J. Lawes, J.J. Midgley, B.B. Lamont, F. Ojeda, and G.E. Burrows. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197 (1): 19–35. https://doi.org/10.1111/nph.2012.197.issue-110.1111/nph.12001.

Collins, Luke, Ross A. Bradstock, Hamish Clarke, Michael F. Clarke, Rachael H. Nolan, and Trent D. Penman. 2021. The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters* 16 (4).044029.https://doi.org/10.1088/1748-9326/abeb9e.

Collins, Luke, Hamish Clarke, Michael F. Clarke, Sarah C. McColl Gausden, Rachael H. Nolan, Trent Penman, and Ross Bradstock. 2022. Warmer and drier conditions have increased the potential for large and severe fire seasons across south-eastern Australia. *Global Ecology and Biogeography* 31: 1933–1948. https://doi.org/10.1111/geb.13514.

Collins, Luke, Greg Mccarthy, Andrew Mellor, Graeme Newell, and Luke Smith. 2020. Remote sensing of environment training data requirements for fire severity mapping using Landsat imagery and random forest. *Remote Sensing of Environment* 245:111839.https://doi.org/10.1016/j.rse.2020.111839.

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Cowling, Richard, and M., and Byron B. Lamont. 1987. Post-fire recruitment of four co-occurring Banksia species. *The Journal of Applied Ecology* 24 (2): 645. https://doi.org/10.2307/2403899.

Davis, Kimberley T., Philip E. Higuera, and Anna Sala. 2018. Anticipating fire-mediated impacts of climate change using a demographic framework. *Functional Ecology* 32 (7): 1729–1745. https://doi.org/10.1111/1365-2435.13132.

Department of Environment Land Water and Planning. 2022. *Fire history records of fires primarily on public land. Victorian State Government*. Melbourne, Victoria. data.vic.gov.au.

Douma, Jacob C., and James T. Weedon. 2019. Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution* 10 (9): 1412–1430. https://doi.org/10.1111/2041-210X.13234.

Enright, Neal J., and D. Goldblum. 1998. Demography of a non-sprouting and resprouting Hakea species (Proteaceae) in fire-prone eucalyptus woodlands of Southeastern Australia in relation to stand age, drought and disease. *Plant Ecology* 144: 71–82.

Enright, Neal, and J., J. B. Fontaine, V. C. Westcott, J. C. Lade, and B. P. Miller. 2011. Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecology* 212 (12): 2071–2083. https://doi.org/10.1007/s11258-011-9970-7.

Enright, Neal J., and Byron B. Lamont. 1989. Fire temperatures and follicle-opening requirements in 10 Banksia species. *Australian Journal of Ecology* 14 (1): 107–113. https://doi.org/10.1111/j.1442-9993.1989.tb01012.x.

Enright, Neal J., Joseph B. Fontaine, Byron B. Lamont, Ben P. Miller, and Vanessa C. Westcott. 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *Journal of Ecology* 102 (6): 1572–1581. https://doi.org/10.1111/1365-2745.12306.

Enright, Neal J., Joseph B. Fontaine, David M.J.S.. Bowman, Ross A. Bradstock, and Richard J. Williams. 2015. Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* 13 (5): 265–272. https://doi.org/10.1890/140231.

Enright, Neal. J., E. Mosner, B. P. Miller, N. Johnson, and Byron B. Lamont. 2007. Soil vs. canopy seed storage and plant species coexistence in species-rich Australian shrublands. *Ecology* 88 (9):2292–2304.https://doi.org/10.1890/06-1343.1.

Fairman, Thomas A., Craig R. Nitschke, and Lauren T. Bennett. 2016. Too much, too soon? A review of the effects of increasing wildfire frequency on tree mortality and regeneration in temperate eucalypt forests. *International Journal of Wildland Fire* 25 (8): 831–848. https://doi.org/10.1071/WF15010.

Falster, Daniel, Rachael Gallagher, Elizabeth H. Wenk, Ian J. Wright, Dony Indiarto, Samuel C. Andrew, Caitlan Baxter, James Lawson, Stuart Allen, Anne Fuchs, et al. 2021. AusTraits, a curated plant trait database for the Australian flora. *Scientific Data* 8 (1): 254. https://doi.org/10.1038/s41597-021-01006-6.

Fasiolo, Matteo, Raphaël Nedellec, Yannig Goude, and Simon N. Wood. 2020. Scalable visualization methods for modern generalized additive models. *Journal of Computational and Graphical Statistics* 29 (1): 78–86. https://doi.org/10.1080/10618600.2019.1629942.

Gale, Matthew G., and Geoffrey J. Cary. 2021. Stand boundary effects on obligate seeding Eucalyptus delegatensis regeneration and fuel dynamics following high and low severity fire: Implications for species resilience to recurrent fire. *Austral Ecology* 46 (5): 802–817. https://doi.org/10.1111/aec.13024.

Gallagher, Rachael V., Stuart P. Allen, Berin D. E. Mackenzie, David A. Keith, Rachael H. Nolan, Libby Rumpff, Carl R. Gosper, Geoffrey Pegg, Stephen van Leeuwen, Mark K. J. Ooi, et al. 2022. An integrated approach to assessing abiotic and biotic threats to post-fire plant species recovery: Lessons from the 2019–2020 Australian fire season. *Global Ecology and Biogeography* 31 (10): 2056–2069. https://doi.org/10.1111/geb.13478.

Gelman, Andrew. 2006. Prior distributions for variance parameters in hierarchical models. *Bayesian Analysis* 1 (3): 515–533.

Gill, Nathan S., Tyler J. Hoecker, and Monica G. Turner. 2021. The propagule doesn't fall far from the tree, especially after short-interval, high-severity fire. *Ecology* 102 (1):e03194.https://doi.org/10.1002/ecy.3194.

Gosper, Carl R., Suzanne M. Prober, and Colin J. Yates. 2013. Estimating fire interval bounds using vital attributes: Implications of uncertainty and among-population variability. *Ecological Applications* 23 (4): 924–935. https://doi.org/10.1890/12-0621.1.

Gosper, Carl R., Ben P. Miller, Rachael V. Gallagher, Janine Kinloch, Richard van Dongen, Emma Adams, Sarah Barrett, Anne Cochrane, Sarah Comer, Lachlan McCaw, et al. 2022. Mapping risk to plant populations from short fire intervals via relationships between maturation period and environmental productivity. *Plant Ecology* 223: 769–787. https://doi.org/10.1007/s11258-022-01229-6.

Harvey, J.M., A.J.M. Hopkins, M.A. Langley, C.R. Gosper, M.R. Williams, and C.J. Yates. 2017. Long-term studies of post-fire reproduction in an Australian shrubland and woodland. *Australian Journal of Botany* 65 (4): 339–347. https://doi.org/10.1071/BT17011.

Haslem, Angie, Luke T. Kelly, Dale G. Nimmo, Simon J. Watson, Sally A. Kenny, Rick S. Taylor, Sarah C. Avitabile, Kate E. Callister, Lisa M. Spence-Bailey, Michael F. Clarke, et al. 2011. Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48 (1): 247–256. https://doi.org/10.1111/j.1365-2664.2010.01906.x.

Henzler, Julia, Hanna Weise, Neal J. Enright, Susanne Zander, and Britta Tietjen. 2018. A squeeze in the suitable fire interval: Simulating the persistence of fire-killed plants in a Mediterranean-type ecosystem under drier conditions. *Ecological Modelling* 389: 41–49. https://doi.org/10.1016/j.ecolmodel.2018.10.010.

Crotteau, J.S., J.M. Varner III., and M.W. Ritchie. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. *Forest Ecology and Management* 287: 103–112. https://doi.org/10.1016/j.foreco.2012.09.022.

Keeley, Jon E. 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire* 18 (1): 116–126. https://doi.org/10.1071/WF07049.

Keeley, Jon E., and Gidi Ne'eman, and C. J. Fotheringham. 1999. Immaturity risk in a fire-dependent pine. *Journal of Mediterranean Ecology* 1: 41–48.

Kelly, Luke T., Angie Haslem, Greg J. Holland, Steven W.J.. Leonard, Josephine Machunter, Michelle Bassett, Andrew F. Bennett, Matthew J. Bruce, Evelyn K. Chia, Fiona J. Christie, et al. 2017. Fire regimes and environmental gradients shape vertebrate and plant distributions in temperate eucalypt forests. *Ecosphere* 8 (4): 227–230. https://doi.org/10.1002/ecs2.1781.

Kraaij, Tineke, Richard M. Cowling, Brian W. van Wilgen, and AnneLise Schutte-Vlok. 2013. Proteaceae juvenile periods and post-fire recruitment as indicators of minimum fire return interval in eastern coastal fynbos. *Applied Vegetation Science* 16 (1): 84–94. https://doi.org/10.1111/j.1654-109X.2012.01209.x.

Lamont, Byron B., and Helen V. Runciman. 1993. Fire may stimulate flowering, branching, seed production and seedling establishment in two kangaroo paws (Haemodoraceae). *Journal of Applied Ecology* 30 (2): 256–264. https://doi.org/10.2307/2404627.

Lamont, Byron B., Tianhua He, and Zhaogui Yan. 2019. Evolutionary history of fire-stimulated Resprouting, flowering, seed release and germination. *Biological Reviews* 94 (3): 903–928. https://doi.org/10.1111/brv.12483.

Lamont, Byron B., Juli G. Pausas, Ed.T.F. Tianhua He, and Witkowski, and Mick E. Hanley. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. *Critical Reviews in Plant Sciences* 39 (2): 140–172. https://doi.org/10.1080/07352689.2020.1768465.

Lauvaux, Airey, Carl N. Catherine, and Skinner, and Alan H. Taylor. 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. *Forest Ecology and Management* 363: 74–85. https://doi.org/10.1016/j.foreco.2015.12.016.

Lemoine, Nathan P. 2019. Moving beyond noninformative priors: Why and how to choose weakly informative priors in Bayesian analyses. *Oikos* 128 (7): 912–928. https://doi.org/10.1111/oik.05985.

Lüdecke, Daniel. 2018. Ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software* 2 (26): 772. https://doi.org/10.21105/joss.00772.

McCaw, L. 2008. Variation in age to first flowering and fruiting of Banksia baxteri and Banksia coccinea at the Stirling Range, South-Western Australia. *Journal of the Royal Society of Western Australia* 91: 269–273.

McColl-Gausden, Sarah C., Lauren T. Bennett, Dan A. Ababei, Hamish G. Clarke, and Trent D. Penman. 2022. Future fire regimes increase risks to obligate-seeder forests. *Diversity and Distributions* 28 (3): 542–558. https://doi.org/10.1111/ddi.13417.

Meng, Ran, Philip E. Dennison, Chengquan Huang, Max A. Moritz, and Carla D'Antonio. 2015. Effects of fire severity and post-fire climate on

Plumanns-Pouton *et al. Fire Ecology*   *(2023) 19:25*

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short-term vegetation recovery of mixed-conifer and red fir forests in the Sierra Nevada Mountains of California. *Remote Sensing of Environment* 171: 311–325. https://doi.org/10.1016/j.rse.2015.10.024.

Moreira, Bruno, and Juli G. Pausas. 2012. Tanned or burned: the role of fire in shaping physical seed dormancy. *PLOS ONE* 7 (12):e51523.https://doi.org/10.1371/journal.pone.0051523.

Muir, Annette M., Peter A. Vesk, and Graham Hepworth. 2014. Reproductive trajectories over decadal time-spans after fire for eight obligate-seeder shrub species in South-Eastern Australia. *Australian Journal of Botany* 62: 369–378. https://doi.org/10.1071/BT14117.

Negrón-Ortiz, Vivian, and David L. Gorchov. 2000. Effects of fire season and postfire herbivory on the cycad Zamia pumila (Zamiaceae) in slash pine savanna, Everglades National Park. *Florida. International Journal of Plant Sciences* 161 (4): 659–669. https://doi.org/10.1086/314277.

Nolan, Rachael H., Liana O. Anderson, Benjamin Poulter, and J. Morgan Varner. 2022. Increasing threat of wildfires: The year 2020 in perspective: A global ecology and biogeography special issue. *Global Ecology and Biogeography* 31: 1898–1905. https://doi.org/10.1111/geb.13588.

Ooi, Mark K.J., Robert J. Whelan, and Tony D. Auld. 2006. Persistence of obligate-seeding species at the population scale: Effects of fire intensity, fire patchiness and long fire-free intervals. *International Journal of Wildland Fire* 15 (2): 261–269. https://doi.org/10.1071/WF05024.

Palmer, Harrison D., Andrew J. Denham, and Mark K.J. Ooi. 2018. Fire severity drives variation in post-fire recruitment and residual seed bank size of Acacia species. *Plant Ecology* 219 (5): 527–537. https://doi.org/10.1007/s11258-018-0815-5.

Pausas, J.G., N. Ouadah, A. Ferran, T. Gimeno, and R. Vallejo. 2002. Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. *Plant Ecology* 169 (2): 205–213. https://doi.org/10.1023/A:1026019528443.

Pellegrini, Adam F. A., R.L. William, C.E. Anderegg, Timothy Paine, William A. Hoffmann, Tyler Kartzinel, Sam S. Rabin, Douglas Sheil, Augusto C. Franco, and Stephen W. Pacala. 2017. Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecology Letters* 20 (3): 307–316. https://doi.org/10.1111/ele.12725.

Penman, Trent, and Sandra Penman. 2010. Influence of prescribed burning on fruit production in Proteaceae. *Pacific Conservation Biology* 16 (1): 46–53. https://doi.org/10.1071/PC100046.

R Core Team. 2021. *R: a language and environment for statistical computing. R Foundation for Statistical Computing*. Vienna, Austria: R Core Team. http://www.R-project.org/.

Resco de Dios, Víctor. 2016. *When fire acts like an irrigation: competition release after burning enhances growth Trees* 30 (3): 579–580. https://doi.org/10.1007/s00468-016-1382-9.

Richter, Clark, Marcel Rejmánek, Jesse E.D. Miller, Kevin R. Welch, Jonah Maria Weeks, and Hugh Safford. 2019. The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere* 10 (10): e02882.https://doi.org/10.1002/ecs2.2882.

Roche, Shauna, Kingsley W. Dixon, and John S. Pate. 1998. For everything a season: Smoke-induced seed germination and seedling recruitment in a Western Australian Banksia woodland. *Austral Ecology* 23 (2): 111–120. https://doi.org/10.1111/j.1442-9993.1998.tb00709.x.

Rodman, Kyle C., Thomas T. Veblen, Robert A. Andrus, Neal J. Enright, Joseph B. Fontaine, Angela D. Gonzalez, Miranda D. Redmond, and Andreas P. Wion. 2021. A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *Journal of Ecology* 109 (1): 313–326. https://doi.org/10.1111/1365-2745.13480.

Romme, William H., Timothy G. Whitby, Daniel B. Tinker, and Monica G. Turner. 2016. Deterministic and stochastic processes lead to divergence in plant communities 25 years after the 1988 Yellowstone fires. *Ecological Monographs* 86 (3): 327–351. https://doi.org/10.1002/ecm.1220.

RStudio Team. 2020. *RStudio: integrated development for R. RStudio* (version 1.4.1717). Boston, MA. http://www.rstudio.com/.

Simpson, Gavin L. 2018. Modelling palaeoecological time series using generalised additive models. *Frontiers in Ecology and Evolution* 6: 149.

Smith-Ramírez, Cecilia, Jessica Castillo-Mandujano, Pablo Becerra, Nicole Sandoval, Rodrigo Fuentes, Rosario Allende, and María Paz Acuña. 2022. Combining remote sensing and field data to assess recovery of the Chilean Mediterranean vegetation after fire: effect of time elapsed and burn severity. *Forest Ecology and Management* 503:119800.https://doi.org/10.1016/j.foreco.2021.119800.

Specht, R. L., and E. J. Moll. 1983. Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In *Mediterranean-type ecosystems: the role of nutrients*, ed. F.J Kruger, D.T Mitchell, and J.U.M Jarvis, 41–65. Berlin, Heidelberg: Springer. https://link.springer.com/chapter/https://doi.org/10.1007/978-3-642-68935-2_2.

Steel, Zachary L., Brandon M. Collins, David B. Sapsis, and Scott L. Stephens. 2021. Quantifying pyrodiversity and its drivers. *Proceedings of the Royal Society b: Biological Sciences* 288 (1948): 20203202. https://doi.org/10.1098/rspb.2020.3202.

Strand, Eva K., Kevin L. Satterberg, Andrew T. Hudak, John Byrne, Azad Henareh Khalyani, and Alistair M. S. Smith. 2019. Does burn severity affect plant community diversity and composition in mixed conifer forests of the United States Intermountain West one decade post fire? *Fire Ecology* 15 (1): 25. https://doi.org/10.1186/s42408-019-0038-8.

Su, Wenhua, Yu. Jiaoe, Guangfei Zhang, Zhan Shi, Lingling Wang, Guanhua Zhao, and Rui Zhou. 2019. Comparison of the canopy and soil seed banks of Pinus yunnanensis in central Yunnan, China. *Forest Ecology and Management* 437: 41–48. https://doi.org/10.1016/j.foreco.2019.01.002.

Thomsen, Alexandria M., and Mark K. J. Ooi. 2022. Shifting season of fire and its interaction with fire severity: impacts on reproductive effort in resprouting plants. *Ecology and Evolution* 12 (3):e8717.https://doi.org/10.1002/ece3.8717.

Tulloch, Ayesha I.T.., Jean Baptiste Pichancourt, Carl R. Gosper, Angela Sanders, and Iadine Chadès. 2016. Fire management strategies to maintain species population processes in a fragmented landscape of fire-interval extremes. *Ecological Applications* 26 (7): 2175–2189. https://doi.org/10.1002/eap.1362.

Turner, Monica G., Kristin H. Braziunas, Winslow D. Hansen, and Brian J. Harvey. 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences* 116 (23): 11319–11328. https://doi.org/10.1073/pnas.1902841116.

Whelan, Robert J., and David J. Ayre. 2020. Long inter-fire intervals do not guarantee a large seed bank in a serotinous shrub (Banksia spinulosa Sm.). *Journal of Ecology*. 108 (4): 1690–1702.https://doi.org/10.1111/1365-2745.13357.

Wickham, Hadley. 2016. *Ggplot2, elegant graphics for data analysis*. New York: Springer-Verlag.

Wood, Simon N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (b)* 73 (1): 3–36.

Wood, Simon N. 2017. *Generalised addititive models: An introduction with R*, 2nd ed. London, UK: Taylor and Francis.

Zedler, P.H. 1995. Fire frequency in Southern California shrublands: biological effects and management options. In *Brushfires in California: ecology and management.*, ed. J. E. Keeley and T Scott, 101–112. Fairfield, WA, USA: International Association of Wildland Fire.

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