Burn after growing: Investigating key life stages and seed bank development with age and height in *Banksia media* to inform fire interval

Matthew Marschall

32054194

25th of May 2026

Bachelor of Science (Honours)

Supervisor: Associate Professor Dylan Korczynskyj

I declare that the recounting of all original research within this thesis is my own and has not been previously submitted for a degree at any other academic institutions.

Matthew Marschall 25th of May 2026

Acknowledgments and Contributions

Firstly, I would like to acknowledge and pay my respects to the Goreng, Menang, Wudjari and Wadjuk people from the Noongar nation whose traditional lands this research was conducted on. Participation from the Goreng, Menang and Wudjari groups is absent in this research, therefore Noongar insights into management practices of *Banksia media* and its cultural services is missing.

I'd like to thank the boss himself, Dylan Korczynskyj. Your enthusiasm and guidance from my first year through to this project has been incredible. You've offered endless time and genuine interest in this research, leading me in the right direction at every turn. It's been a truly valuable experience that I hope to convert into an enormous employment contract. Special thanks for throwing away your holidays for field work, and for enduring some of my worst cooking.

A massive thankyou as well to Meredith Korczynskyj for field work duties. You were a crucial scrutineer and motivator to keep us in the field when considering data fraud in favour of a beach day; we would still be out there holding tape measures if not for you. Thankyou also to my housemate Bevan Grant for volunteering your time in the field. I apologise for promising 3pm knock offs and beach sessions every day, but a lie in exchange for your experience in the field was a hill I was willing to die on.

Thank you to Andrew Crawford, Anne Monoghan and particularly Simone Dudley at the WA Herbarium for showing me the ropes in the lab, the use of your space and equipment was crucial to this project. Thank you also to Matt McDonald for letting us adopt your surveying methods and Gaine Chiarenza from Curtin University for being a straight shooter about my blasphemous use of GAMS and R script.

Most importantly to Gill Craig, Nathan McQuoid and the Friends of the Fitzgerald River National Park. Thank you for entrusting me with your funding for this project, without you none of this would be possible. I hope this research is useful in the management of *B. media* heading into the future.

And lastly, thank you to my partner Yardley Smeaton for always being comedic relief through the process and reminding me that there is life after uni. I also can't forget Charlie

Bray, Isla Dunne, Kate Wilson, Claudia Carles, Matthew Clancy, Orla Roche, Paul Smeaton, High on 55, Cos Baby, The Buffalo Club and Ode to Sirens.

Thesis Structure

The structure of this thesis blends elements of a traditional thesis with conventions of a scholarly journal article. Chapter 1 consists of a literature review, aiming to offer readers a comprehensive insight into the broader topic and concepts that informed the research. Chapter 2 is presented as a draft manuscript targeting Annals of Botany, with abstract, introduction, extended methods, results, discussion and conclusion sections. The manuscript introduction contains summarised content from the literature review, with the intention that reading Chapter 1 is not required for the reader to understand the research context. Some conventions of the Annals of Botany journal are broken for improved readability and to uphold scientific rigour, such as reporting significance values, standard error and results of post hoc testing to satisfy the academic requirements of the honours programme.

Table of Continents

List of Figures

FIG 9. Viability of *B. media* seeds over TSLF (13, 19, 26, 35, 36, and 50 years; all seed age removed). Each data point represents the percentage germination of a subsample of full seeds (n = 3-129) from individual plants (n = 44*;* labelled means %). Grey shading represents 95% confidence intervals.

FIG 10. Mean time until germination over TSLF (13, 19, 26, 35, 36, and 50 years; n = 93). Age of seed (young and old) has been collapsed into the same data set. Reported with 95% Confidence interval bars.

FIG 11. Relative frequency distribution (%) of height (m), stem diameter (mm) and canopy volume (m^3) in *B. media* stands over TSLF (13, 17, 26, 36, and 50 years). Mean ± standard error is reported for canopy volume, height and stem diameter from density plots (n = 72 - 495). Canopy volume values were square root transformed for clearer interpretation of data.

FIG 12. Density of *B. media* (per ha) over TSLF (13, 17, 26, 36 and 50 years). Each data point represents a surveyed density plot (six per TSLF; n = 30). Grey shaded ribbon represents 95% confidence intervals.

FIG 13. Plant height as a predictor of seeds per plant (winning model). Each plant from the sample size (n = 44) is represented by full seed results regardless of seed age. Six individuals were not included as stem measurements were not included in data collection at the beginning of surveying. Shaded ribbons represent 95% confidence intervals.

FIG 14. Viable *B. media* seeds per ha over TSLF (13, 17, 26, 36 and 50 years since last fire). Each point represents accumulative viable seed data from density plots (n = 30) in west FRNP. Each TSLF received six plots, which surveyed a total of 1,486 *B. media* individuals. Grey shading represents 95% confidence intervals.

FIG S1. Short fire interval (<15 years) in the Fitzgerald River National Park (FRNP), orange scars represent where one or more fires have occurred at an interval of <15 years since 1972 (fire history accurate as of September 2025). Red dots and site numbers describe the locations of cone and density sampling. Fire interval history for sites outside the FRNP was not determined as they were improvised due to dieback

List of Tables

Chapter 1 – Literature Review

Introduction

The occurrence of fire in global ecosystems has shaped the diversity, traits and structure of ecosystems since the colonisation of terrestrial flora (Puasas and Keeley, 2009; Bowman et al., 2011; He et al., 2019; Keeley and Pausas, 2022). In fire-prone Mediterranean type climates such as southwestern Australia (SWA), persistent fire regimes have driven fire adaptations and shaped exaptations that increase plant fitness and therefore fire tolerance (Byrne et al., 2011; Lamont et al., 2020; Lamont, 2021; Pausas and Lamont, 2022; Pausas et al, 2022b). These reproductive and regenerative traits such as fire-smoke cued reproduction (seed release, germination, flowering), vegetative resprouting (basal, epicormic, rhyzomal) and the long-term storage of seed in arial (serotiny) or soil seed banks enhance either the survival of parent stands (resprouting) or seedling recruitment (non-resprouting) post-fire (Pausas and Keeley, 2014; Groom and Lamont, 2015; Causley et al., 2016; He et al., 2019; Lamont et al., 2020; Ottaviani et al., 2026).

The SWA region currently boasts over 8000 recorded plant taxa (Brundrett, 2021), shaped by the interaction between impoverished soils, topography, geographic isolation (semi-arid boundary) and high pyro-diversity (Pausas and Keeley, 2014; Lamont and He, 2017a). Both resprouting and non-resprouter species co-occur over the many vegetation types across SWA, however some climatic conditions constrain their distribution (Lamont and Markey, 1995). In the southern sandplains where rainfall, temperature and seasonality promote high intensity, canopy-scorching fire, vegetation communities are dominated by serotinous non-resprouting species (Lamont and Markey, 1995; Lamont, 2021; Ladd et al., 2022). These Proteaceae dominated shrublands and woodlands typically display strong serotiny, relying on long-term

seed dormancy and accumulation (average of five years) to replace stands following the onset of fire (Cowling and Lamont, 1985; Gill and McMahon, 1986; Meehan et al., 2015). Because reproductive processes in fire-prone flora are tied closely to landscape fire regimes, alteration of fire attributes such as interval, seasonality and severity can change plant community species composition (Puasas and Keeley, 2009; Bond, 2015). Climate driven modification of natural fire regimes and reduced plant resilience has already produced evidence of local and regional decline in short range endemic flora species in the SWA (Foster et al., 2018; Nolan et al., 2021; Santos et al., 2023; Lamont, 2023). Therefore, understanding requirements for maintaining reproductive processes from both a community and species level, is required to preserve the biodiversity of SWA in the face of climatic changes (Campbell et al., 2022; Williams et al., 2026).

Fire as an ecological process

Fire is an ecological disturbance that has shaped global biodiversity, ecosystem composition and distribution through time, producing regions reliant on fire for the facilitation of key plant life stages (Puasas and Keeley, 2009; He et al., 2019; Keeley and Pausas, 2022). The occurrence of fire itself is defined as the rapid oxidisation of carbon rich compounds, requiring oxygen (≥16% atmospheric O_2), fuel and ignition (Bowman et al., 2011). In climates where the occurrence of fire is supported, it aids fundamental geosphere and atmospheric cycling processes, such as nutrient decomposition (recalcitrant black carbon) and greenhouse gas release (CO_2) which influences climate (Bowman et al., 2011). Deposits of recalcitrant black carbon in the paleoclimatic record can be interpreted to reconstruct historic fire regimes that describe frequency, intensity, patchiness, seasonality and size of fire through time (Bowman et al., 2011; He and Lamont, 2019; Keeley and Pausas, 2022; Kelly et al., 2023).

Evidence of low intensity wildfires first appear during the Silurian period (440-420 Mya), coinciding with the origin of terrestrial flora (Bowman et al., 2009; Puasas and Keeley, 2009; Keeley and Pausas, 2022). The characteristics of global fire regimes during the Silurian change persistently over the proceeding 419 – 66 Mya, heavily influenced by atmospheric oxygen levels and fuel availability (Glasspool and Gastaldo, 2022; Keeley and Pausas, 2022). The Carboniferous (360-300 Mya) and Permian (300-250 Mya) were particularly active fire periods, where atmospheric oxygen of approximately 30% allowed for the ignition of moist fuel loads (Yan et al., 2019; Keeley and Pausas, 2022). The growing influence of fuel structure on fire regimes has been recorded for the Cretaceous (145–66 Mya), where the spread and diversification of angiosperms (flowering flora) produced the first instance of high-intensity crown-scorch regimes (Belcher and Hudspith, 2017). The increasing occurrence of fire due to aridification in the Cretaceous is determined as a casual agent in the

early diversification of angiosperms, producing primitive fire and drought tolerant plant species (Puasas and Keeley, 2009; He and Lamont, 2018; Keeley and Pausas, 2022). Declining atmospheric oxygen levels to current ambient conditions (20% atmospheric O_2) in the Cenozoic era (66 Mya – present) likely intensified the influence of climate and vegetation on fire regimes (Puasas and Keeley, 2009; Bond, 2015). This is observed in the emergence of stable Mediterranean and monsoonal type ecosystems in Australia during the Miocene period (23-5 Mya; Puasas and Keeley, 2009; Bond, 2015; He and Lamont, 2018; Keeley and Pausas, 2022). Increasingly fire-prone climate in the Miocene is ecident in the extensive coal deposits through south-eastern Australia, produced by recurrent fire in arid-adapted shrublands (Keeley and Pausas, 2022). Much contention surrounds the history of plant traits allowing flora to tolerate fire regimes in the Miocene and into the Quaternary (2.5 Mya - present), with their alternative origin as either fire adapted or fire related (exaptations) still divisive amongst authors (Bradshaw et al., 2011; Keeley et al., 2011; Midgley and Bond, 2013; Keeley and Pausas, 2022).

Mutch (1970) was the first author to identify that vegetation in fire-prone regions had developed traits to incite fire. However, the claim that these vegetation communities burn more readily due to traits naturally selected (fire adapted) for flammability is widely contentious (Bowman et al., 2011; Bradshaw et al., 2011; He et al., 2019; Keeley and Pausas, 2022). Fire adapted traits must be linked to an improvement in plant reproductive fitness through natural selection, otherwise a trait is likely fire exapted (Pausas and Keely, 2009; Keeley et al., 2011). Fire exaptations are traits that increase the fire tolerance of a species but were developed in response to other pressuring factors, such as drought, herbivory and poor soil nutrients (Bowman et al., 2011; Keely et al., 2011). For example, smoke cued flowering induced by the chemical ethylene is also produced in decomposing plant matter, indicating it

may be a trait developed under non-fire-prone conditions but has equal benefit in a fire-prone environment (Bradshaw et al., 2011; Keely et al., 2011; Midgley and Bond, 2013; Lamont and He, 2017b).

Fire driving the evolution of flora traits

The recognition of fire disturbance as a key driver of flora traits and biodiversity is a recent occurrence, challenging a long-term belief that diversity patterns were solely associated with climate, topography and impoverished soils (Bond and Keeley, 2005; Keely et al., 2011; Pausas and Schwilk, 2012; Midgley and Bond, 2013; He et al., 2019; Keeley and Pausas, 2022). This evolutionary pressure has produced two broad reproductive vegetation mechanisms promoting fitness in response to fire regime: fire-stimulated regeneration from surviving tissue (resprouting seeders) or regeneration purely from seed (fire killed non-resprouting seeders; Midgley and Bond, 2013; Pausas and Keeley, 2014; He et al., 2019). Fire-prone vegetation communities dominated by resprouting are often closely associated with frequent low-severity surface fire regimes, while non-resprouting becomes dominant in infrequent high-severity crown fire regimes (Murphy et al., 2013; Pausas and Keeley, 2014; He et al., 2019; Miller et al., 2024). Mixed severity and frequency fire regimes that benefit neither resprouting nor non-resprouting species exclusively, will often producing fine scale vegetation mosaics where they co-occur together (Miller et al., 2024).

Post-burn conditions produced from fire regimes are fundamental for seedling recruitment, providing reduced competition for nutrients, water and light (Keeley and Pausas, 2022; Lambers et al., 2022). However, success of post-fire recruitment is determined by plant traits either enhancing adult survivorship or seed bank accumulation (Miller et al., 2024). Traits such as insulating bark and storage of non-structural carbohydrates (via lignotubers and epicormic bunds) in resprouting species are vital to maintain existing stands due to typically low seed production (Groom and Lamont, 2015; Ottaviani et al., 2026). However, the long-term dormancy traits protecting seed banks in non-resprouters and resprouters from the properties of fire are most crucial for the persistence of species post-burn (Keely, 2012; Midgley and Bond, 2013; Lamont et al., 2019; He et al., 2019).

Fire-prone species enhance post-fire recruitment through either canopy or soil seed bank storage, dependant on the attributes of fire regime to which they are adapted (Lamont and Enright, 2000; Enright et al., 2007; Maikano et al., 2018; Pausas and Lamont, 2022a). Low severity, high frequency regimes will favour species with soil seed banks, where the heat properties of fire or chemicals released by smoke will break seed dormancy and allow germination (Makino et al., 2018; Pausas and Lamont, 2022b). Inversely, canopy stored seed banks often require fire at a less frequent, higher intensity for seed release en masse, tolerating temperatures of up to 500°C in some *Banksia* species as fruits are exposed to directly to fire (Lamont and Enright, 2000; Enright et al., 2007; Pausas and Lamont, 2022b). The subsequent germination of surviving seed will be cued by the first favourable period of rainfall, often after years of enforced dormancy in seed banks (Enright et al., 1996). Time spent in dormancy is dependent on individual plant traits and fire regime, with some species retaining seed for a minimum of one year, or up to 30 years observed in some *Pinus* genera (Lamont and Enright, 2000; Enright et al., 2007).

Fire and serotiny

Serotiny refers to the long-term enforced dormancy of seeds in canopy-held fruits or cones in woody plant taxa (Causley et al., 2016; Lamont et al., 2020; Lamont, 2021). This reproductive syndrome is generally recognised as a fire-adapted trait and is widespread in fire-prone Mediterranean ecosystems, particularly southwestern Australia (SWA) and to a lesser extent the Cape Floristic Region in South Africa (Causley et al., 2016; Lamont, 2021). Environmental conditions prone to Mediterranean climate such as fire, drought and prolonged weathering can cue seed release *en masse* or slowly over time from cones and fruits (Groom and Lamont, 2015; Causley et al., 2016; Lamont et al., 2020; Lamont, 2021). The central benefit of serotiny is the overlap of annual reproductive events, producing an accumulative seed bank beyond what is required for stand recovery (Groom and Lamont, 1997; Lamont et al., 2019; Lamont et al., 2020).

Serotiny is measured either non-temporally or temporally, quantifying the state of all cones/fruits as open or closed at a particular plant age (apparent serotiny or bulk assessment) or at the rate of which they open over time if fruit/cones can be aged (inherent, annual assessment; Lamont 1985; Lamont, 2021). Species range between the extremes of weakly and strongly serotinous, reflective of the fire regime to which they are adapted (Lamont, 2021; Ladd et al., 2022). Weakly serotinous species are widely regarded as 'bet-hedging', releasing low volumes of their annual seed crop to buffer against stand decline if fire intervals exceed plant longevity (Ladd et al., 2022; Pausas et al., 2022b). Although, success of inter-fire recruitment in bet-hedging species is reliant on high annual rainfall and opportunistic vegetation clearings at the time of seed release (Pausas et al., 2022b). Strongly serotinous species will slowly release seed from aging follicles or cones, although post-fire recruitment in these species is reportedly low due to high competition for resources in older fuel ages (Gill and McMahon, 1986; Cowling et al., 1987; Meehan et al., 2015).

Serotiny in species with large geographic distributions have been shown to display plasticity across their range, particularly when spanning climatic gradients or variable growing conditions (Cowling and Lamont, 1985; Gauthier et al., 1996; Lamont, 2021; Ladd et al., 2022). This was observed in three co-occuring *Banksia* species persisting along a 500 km climatic gradient in SWA, with degree/level of serotiny increasing with aridity (Cowling and Lamont, 1985). In these strongly serotinous species, seeds must be protected from environmental factors until the onset of fire (Lamont, 2021; Heyes et al., 2023). However, as seed housing structures age, the impact of predation (e.g. moths, weevils, beetles, cockatoos), fungal decay and spontaneous rupture increases (Witkowski et al., 1991b; Enright et al., 1996; Heyes et al., 2023). Many serotinous species display strategies to minimise seed loss through hiding or obscuring fruit in persistent flower structures or using seed decoys, although follicles and fruit escaping predation and fungal decay may remain closed for longer than seed is viable (Enright et al., 1996; Lamont, 2021; Heyes et al., 2023). This is evident in the seed bank dynamics of *Banksia cuneata,* where seed viability from cones one year old degraded from 97% to 50% after nine years of in-canopy aging (Lamont et al., 1991a).

In SWA four plant families are known to store their seed in canopy-held seed banks (Cupressaceae, Casuarinaceae, Myrtaceae and Proteaceae), with particularly high representation in the Proteaceae family (Lamont et al., 1991b; Groom and Lamont, 2015). Strongly serotinous Proteaceae genera typically retain their fruits from 5 to 15 years, releasing seed spontaneously from a combination of increasing fruit/cone age, extended exposure to sunlight, drought, repeated wet and dry cycles, limb senescence and fire (Lamont et al., 1991b; Enright et al., 1996; Groom and Lamont, 2015; Lamont, 2021)

Flora of southwestern Australia

Climatic and floristic evolutionary history

Southwestern Australia (SWA) is one of two globally recognised biodiversity hotspots in Australia, renowned for its exceptional species richness and endemism linked to infertile soils, complex habitats, stable climatic history and geographic isolation (Groom and Lamont, 2015; Brundrett, 2021; Gosper et al., 2021). Evidence of fire adaptions in SWA flora span back to the *Petrophile* clade (Proteaceae, 73.5 Mya), where fire prone climate persisted during a period when the Australian continent was dominated by temperate rain forest (Groom and Lamont, 2015). Key genera observed in contemporary SWA ecosystems such as *Banksia* (61 Mya) and *Eucalyptus* (62 Mya) first appear after the abrupt end to the Mesozoic era (66 Mya), marking the beginning of intensified speciation in SWA (Lamont and He, 2012; Groom and Lamont, 2015). Pollen records from the early-mid Eocene (45-56 Mya) indicate that SWA contained a mixture of temperate/sub-tropical rainforest (now mostly extinct) and sclerophyllous woodland and shrublands, dominated by the Proteaceae family (Groom and Lamont, 2015).

Between the Eocene period (56 Mya) and the beginning of the Miocene (23 Mya) the dominant genera *Nuytsia floribunda* (45 Mya), *Melaleuca* (34 Mya), *Allocasuarina* (27 Mya) and *Acacia* (26 Mya) emerge, indicating parts of SWA were under increasingly fire-prone Mediterranean-type climate. Although, the exact timing of this climatic change is highly debated (Christophel and Greenwood, 1989; Dodson et al., 2004; Hopper and Gioia, 2004; Byrne et al., 2011; Lamont and He, 2012). With the transition from the Miocene into the Pliocene (23-2.5 Mya), records indicate temperate woodlands and shrublands in SWA again underwent high speciation due to a major climatic drying period, with the evolution of serotiny and other fire-adapted traits at their peak (Byrne et al., 2011; Groom and Lamont,

2015; He et al., 2019). This is observed in the emergence of the fire-tolerant genera *Davesia* (21 Mya), *Hakea* (18 Mya), *Anigozanthos* (14 Mya) and *Grevillea* (11 Mya; Groom and Lamont, 2015). Approaching contemporary climate, the distribution of mesic zone ecosystems in the SWA retreat even further, replaced with Myrtaceous and Casuarinaceae dominated vegetation communities (Byrne et al., 2011; Groom and Lamont, 2015).

The SWA currently lists over 7000 flora taxa (52% endemic) as occurring within its boundary, split between 9 unique geographic bioregions bounded by a semi-arid zone (Brundrett, 2021; Lamont and He., 2017a). This entire region is considered under Mediterranean type climate, experiencing summer/autumn drought with low rainfall, and reliable annual winter rainfall with mild temperatures (Lamont and He., 2017a). The variability and interaction of these factors across the SWA supports a range of vegetation types, such as eucalypt woodlands and forests, mixed kwongan shrublands and coastal heathlands, of which all occasionally burn (Gosper et al., 2022). Serotinous species, particularly non-resprouters are strongly represented in the SWA, with the genera *Eucalyptus*, *Banksia* and *Hakea* dominating (Beard et al., 2000; Lamont and He., 2017). Threats to SWA floral biodiversity currently include modified fire regimes, vegetation clearing/fragmentation, long term decline in rainfall, weed invasion, feral fauna and *Phytophthora* dieback (Brundrett, 2021; Gosper et al., 2022).

Changing fire regimes

The occurrence of fire in contemporary SWA has been variable since geographic isolation from Antarctica approximately 85 Mya, with flora species modifying key reproductive processes to tolerate changing fire patterns (Causley et al., 2016; Lamont, 2021; Gosper et al., 2022; Kelly et al., 2023). Despite these regimes being a product of climate and vegetation dynamics, it's debated whether anthropic burning permanently modified natural fire regimes by changing species composition and habitat structure (Bowman, 2003; Mooney et al., 2011;

Morgan et al., 2020; Kelly et al., 2023). Late-Pleistocene colonization of SWA by humans produced fine scale fire-succession (mosaics) for subsistence, artificially modifying natural landscape fire regimes (Bowman, 2003; Enright and Thomas, 2008; Morgan et al., 2020; Adeleye et al., 2023). However, after mass indigenous displacement in SWA, the region experienced a return of high- intensity, homogenous wildfire regimes and associated changes in species composition and habitat structure (Bowman, 2003; Burrows et al., 2008; Mooney et al., 2011).

Prescribed burning was eventually developed in SWA in the 1960's, with the intention of managing fuel loads that were leading to frequent high-severity wildfire (Burrows et al., 2008; Boer et al., 2009; Bradshaw et al., 2018). Since its integration, prescribed burning has been hailed as one of few tools effective in suppressing wildfire risk on private and public assets, while also facilitating ecological fire requirements (Burrows, 2008; Boer et al., 2009; Bradshaw et al., 2018). Although, burns are typically prescribed as large homogenous landscape fires, occurring most frequently in peri-urban zones to reduce biomass between large blocks of remnant vegetation and human settlement (Penman et al., 2011; Lange and Gillespie, 2023). Ecological burns do occur on smaller scales, often with tangible outcomes such as facilitating germination of an at-risk species or assisting cultural burning for traditional owners (Penman et al., 2011).

While prescribed burning cannot stop the occurrence of wildfire, it's reported that burning fuel loads at short intervals can suppress the severity (Burrows et al., 2008; Bradshaw et al., 2018; Lange and Gillespie, 2023). However, the efficacy of prescribed burning is widely contentious, with many critics concerned that biodiversity outcomes are ill-informed and often secondary to fuel reduction (Burrows, 2008; Penman et al., 2011; Bradshaw et al., 2018; Tangney et al., 2019). Evidence shows modifying fire regimes on a regional scale has

the potential to change ecological composition in SWA, with short intervals decreasing the representation of non-resprouting species and replacing them with resprouting herbaceous communities (Lamont et al., 1991b; Lamont and Markey, 1995; Wooler et al., 2002; Penman et al., 2011; Muir et al., 2024). Similarly, long periods of fire absence favour mid-story shrubs, leading to the exclusion of understory species and exhausting the seed banks of short-lived serotinous species (Foster et al., 2018).

Land management in southwestern Australia

Current management of remnant vegetation by the Department of Biodiversity, Conservation and Attractions (DBCA) in SWA is based on the Boer et al. (2009) longitudinal fuel reduction study in SWA *Eucalyptus* Forest. This research implemented the concept of leverage into prescribed burning, which refers to the 'unit' of area protected from wildfire for every 'unit' treated by prescribed fire (Boer et al., 2009; Cannon and Clement, 2025). This ratio of 1:4 is now a feature of DBCA prescribed burning, translating to a burning target of approximately 200,000 ha annually (Boer et al., 2009; Burrows and McCaw, 2013; Campbell et al., 2022; Cannon and Clement, 2025). The locality, size and severity of fire prescribed by land managers to reach this target is dependent on the management zones of which they occur (Burrows and McCaw, 2013). These consist of a community protection zone (4-year fire interval), bushfire modification zone (5–7-year fire interval) and biodiversity management zone (heterogeneity of young, intermediate and old fuels; Burrows and McCaw, 2013). Specialised burning plans are implemented in vegetated regions of high value, such as the Fitzgerald River National Park (FRNP), although the broad scale burning programme for majority of SWA has been described as a disturbance regime driving biodiversity loss (Moore et al., 1991; Cannon and Clement, 2025).

Increasingly severe and recurrent wildfire from climate driven aridification, lengthening fire seasons and fire weather severity has sparked debate as to the changing balance of benefit

and risk in prescribed burning (Nolan et al., 2021; Santos et al., 2023; Lamont, 2023). The maintenance of short-interval PB regimes to combat wildfire risk is predicted by continue while vegetation is increasingly subject to climate stressors (Nolan et al., 2021). This scenario is projected to have devastating impacts on the resilience of post-fire recruitment in serotinous vegetation communities, particularly genera such as *Banksia* (Henzler et al., 2018). This is evident in the non-resprouting SWA species *Banksia hookerina*, which reports reduced seed production in years of below average rainfall (Henzler et al., 2018; Nolan et al., 2021). Species under climate stress subjected to short interval prescribed burning may result in local decline or extinction, bringing into question the environmental sustainability of the Boer et al. (2009) research that currently informs SWA prescribed burning (Wooller et al., 2002; Henzler et al., 2018; Nolan et al., 2021; Campbell et al., 2022).

Banksia media **(Southern Plains Banksia, Golden Stalk Banksia)**

Banksia media is a non-resprouting serotinous tree/shrub between 0.5-5 m tall, requiring fire to facilitate the dispersal of seed from reproductive follicles (Taylor and Hopper, 1998; Wooler & Wooler, 2002; Millar et al., 2020). The species occurs naturally along the fire-prone Esperance sandplains of SWA, from the eastern boundary of the Stirling Ranges to Israelite Bay, extending inland as far as 150 km north of the coast (Taylor and Hopper, 1998; Wooller and Wooller, 2002a; Millar et al., 2020). Soil substrate records indicate a preference for white infertile sand/loam and red clay/loam over limestone in Kwongan shrubland, heathland and open woodlands (Taylor and Hopper, 1998; Cochrane et al., 2014b; Millar et al., 2020). Its distribution spans a rainfall gradient between 300-600 mm year, with stands persisting in the eastern xeric range (300 mm) displaying drought tolerant traits (Cochrane et al., 2014b).

Flowering occurs in mature individuals between March – December, presenting as red/yellow/brown compound inflorescences between 6-16 cm high and 7-9 cm wide (Taylor and Hopper, 1998; Wooller and Wooller, 2002a; Millar et al., 2020;). *B. media* is self-compatible (selfing), however fruit set and outcrossing are enhanced by visits from invertebrate and vertebrate pollinators (Wooller and Wooller, 2002a; Millar et al., 2020). Successfully fertilised inflorescences develop into canopy-held cones, which produce woody seed-bearing follicles housing between one or two seeds (Wooller and Wooller, 2002a; Millar et al., 2020). Follicle opening in the absence of fire is reported as strongly serotinous, although this data comes from a single stand in the west of its distribution and is likely to display plasticity across its range (Wooller and Wooller, 2002a). Plasticity is observed in other plant demographics across *B. media's* distribution, with seed mass, leaf size and germination success increasing with aridity (Cochrane, 2014a; Cochrane et al., 2014b).

B. media is currently listed as not threatened under the Biodiversity Conservation Act (2016), however there is no literature describing the optimal fire regime for *B. media* (Florabase, 2026). The FRNP is currently under the management of the DBCA, which prescribes burns at an interval considering minimum fire requirements for the parks vegetation communities (Moore et al. 1991; Rathbone, 2013). As *B. media* persists in the park under current burning practises, they are deemed appropriate for stand maintenance. Although investigation into the optimal burning window (highest seed volume and viability) is important to aid in the continued conservation of *B. media* in the face of climate challenges (Williams et al., 2026).

Chapter 2 – Journal Article

Burn after growing: Investigating key life stages and seed bank development with age and height in *Banksia media* to inform fire interval

Matthew Marschall

School of Arts and Sciences, University of Notre Dame Australia, Corner Cliff and High Streets, Fremantle, WA, 6160, Australia

*For correspondence. E-mail mattpm99@gmail.com

ABSTRACT

- **Background and Aims** Prescribed burning aims to reduce the risk of high-severity wildfire in Mediterranean-type ecosystems such as south-western Australia (SWA), through modifying fuel loads with short-interval burning. Landscapes in SWA dominated by long-lived serotinous non-resprouting plants such as *Banksia media,* require long inter-fire periods, which if undermined by short interval-fire can prevent canopy seed bank maturation. This study aimed to determine when *B. media* reaches a seed bank size sufficient for post-fire stand regeneration by investigating critical life events: juvenile period and the dynamics of seed production, storage, loss and viability over time and with plant size.
- **Methods** *B. media* cones from three age classes were collected from 50 plants over the chrono-sequence: 13, 19, 26, 35/36 and 50 years since last fire. Seeds were extracted, tested for viability and the relationship with time since last fire (TSLF), plant height, stem width and canopy volume analysed to determine the best predictor of seed volume. Height (winning predictor) data from 1,550 individuals in density plots across 13, 17, 26, 36 and 50 years since

last fire were allocated a seed volume using this seed predictor to determine time until optimal seed bank size.

- **Key Results** Juvenile period was estimated to end between 4-18 years, variable dependent on burn season and post-fire rainfall. Cone, follicle and seed accumulation generally increased between 13 to 50 years since last fire, however seed viability significantly reduced to 82% at 50 years since last fire regardless of seed age. TSLF was a poor predictor of optimal seed bank size due to plant variability at sites burnt the same year. Instead, height was the winning predictor of optimal seed bank size, occurring in plants between 2.6 and 3.2 meters tall.
- **Conclusion** Optimal fire interval for *B. media* is determined as any plant age where mean stand plant height is between 2.6 and 3.2 m tall.

Keywords: serotiny, non-resprouter, seed bank, *Banksia media*

INTRODUCTION

Since the establishment of terrestrial flora, fire has been a natural driver of plant diversity and endemism in fire-prone regions (Puasas and Keeley, 2009; He et al., 2019; He and Lamont, 2019; Keeley and Pausas, 2022). In these regions, the attributes describing fire regime such as severity, interval, size, patchiness and season, influence the dominant plant traits observed in vegetation communities (Bowman et al., 2011; Keely et al., 2011 He and Lamont, 2019; Keeley and Pausas, 2022). Plant species adapted to different fire regimes will observe contrasting traits that either enhance survival of adult plants (resprouters) or seedling-recruitment in post-fire conditions (non-resprouters) (Midgley and Bond, 2013; Pausas and Keeley, 2014; He et al., 2019). Traits associated with non-resprouting seeders can be linked to infrequent, high-severity crown fire regimes, and resprouting seeders with frequent, low-severity surface regimes (Murphy et al., 2013; Pausas and Keeley, 2014; He et al., 2019; Miller et al., 2024). However, fundamental to the persistence of species in fire prone climate is the survival of seeds from the

properties of fire itself, through in-canopy (serotiny) or soil-stored seed banks (Causley et al., 2016; Lamont et al., 2020; Lamont, 2021).

Serotinous non-resprouting seeders are reliant on the overlap of reproductive events for the accumulation of a seed bank large enough to replace parent stands post-burn (Enright et al., 1996; Groom and Lamont, 1997; Lamont et al., 2019; Lamont et al., 2020). However, seed bearing cones and fruits can spontaneously rupture in the absence of fire from in-canopy aging factors, such as prolonged environmental weathering. The probability of successful seedling recruitment due to inter-fire seed dispersal is dependent on timing of seed release coinciding with vegetation clearings and high moisture availability (Pausas et al., 2022). The degree or level of serotiny in plant species ranges from weak (bet-hedging), where plants release low volumes of their annual seed crop to buffer against stand decline (Ladd et al., 2022; Pausas et al., 2022), to strongly serotinous, where seeds are retained for many years, sometimes remaining closed for longer than seed is viable (Enright et al., 1996; Lamont, 2021; Heyes et al., 2023). Although, degree of serotiny is not always consistent within a species; for example, serotiny is reported to increase in strength with aridity (Cowling and Lamont, 1985; Gauthier et al., 1996; Lamont, 2021; Ladd et al., 2022).

The dynamics of seed production, storage and loss in relation to seed and plant age determines the interval in which serotinous non-respouting species can tolerate fire (Enright et al., 1996 Lamont, 2021; Heyes et al., 2023). If the minimum tolerable period (juvenile period) or time until sufficient seed bank accumulation is undermined by fire, serotinous species may be at risk of decline or local extinction (Lamont et al., 1991; Lamont and Markey, 1995; Wooler et al., 2002; Penman et al., 2011; Muir et al., 2024). However, seed banks may also perish in prolonged periods of fire absence (Enright et al., 1996; Foster et al., 2017). In genera of serotinous Proteaceae, species will typically reach maturity between 4-9 years (under optimal

climatic and growing conditions) and on average retain their fruits for five or more years (Lamont et al., 1991; Cowling and Lamont, 1985; Enright et al., 1996; Groom and Lamont, 2015; Lamont, 2021).

In Mediterranean-type ecosystems, serotinous non-resprouters are particularly well represented where high-severity crown fire regimes prevail (Beard et al., 2000; Causley et al., 2016; Lamont and He., 2017; Lamont, 2021). Due to the hazard of high-severity wildfire to human health and assets, prescribed burning – the deliberate modification of the fire regime – is implemented to suppress wildfire and facilitate ecological requirements (Boer et al., 2009). Prescribed burning is effective in reducing the intensity and impact of wildfires in peri-urban areas, where risk to human health and assets is greatest (Burrows, 2008; Boer et al., 2009; Bradshaw et al., 2018). Although, the efficacy of prescribed burning to facilitate ecological requirements at modified fire intervals is contentious (Burrows, 2008; Penman et al., 2011; Bradshaw et al., 2018; Tagney et al., 2018). Shortening fire-interval in vegetation types adapted to long-unburnt periods is known to modify vegetation structure and species composition, limiting the representation of serotinous non-resprouter species and increasing the representation of herbaceous resprouters (Lamont et al., 1991; Lamont and Markey, 1995; Wooler et al., 2002b; Penman et al., 2011; Muir et al., 2024).

In the Mediterranean-type climate of southwestern Australia (SWA), the frequency of dangerous fire weather and therefore wildfire risk is increasing due to climate-driven changes (Nolan et al., 2021). Prescribed burning is anticipated to continue as a tool for reducing wildfire under these conditions, projected to cause the potential loss of approximately 2000 SWA flora species in the coming century (Wooller et al., 2002b; Henzler et al., 2018; Nolan et al., 2021; Campbell et al., 2022). Due to this, local stakeholders and government departments are researching high value serotinous non-resprouting genera, such as *Eucalyptus* and *Banksia*, to

ensure reproductive processes can be facilitated when prescribing fire (e.g. Friends of the Fitzgerald River National Park, 2024; Department of Biodiversity, Conservation and Attractions, 2026). Current burning regimes prescribed by land managers for fuel reduction are dependent on the management zones of which they occur, collectively aiming to retain 45% of remnant vegetation in SWA at a fuel age of ≤ 6 years (Burrows and McCaw, 2013; Department of Biodiversity, Conservation and Attractions, 2023). Specialised burning plans are implemented in regions of high ecological value such as the Fitzgerald River National Park (FRNP), although investigation into the optimal burning window (highest seed volume and viability) of individual species such as *Banksia media* is important to aid in species-level conservation in the face of climate-driven challenges (Moore et al., 1991; Williams et al., 2026; Cannon and Clement, 2025).

B. media (Proteaceae) is a serotinous non-resprouting tree/shrub widely distributed along the Esperance sandplains of SWA, ranging between the eastern boundary of the Stirling Ranges to Israelite Bay (Taylor and Hopper, 1988; Wooler and Wooler, 2002a; Millar et al., 2020). Flowering occurs in mature individuals between March and December, presenting as red/yellow/brown compound inflorescences with a mixed mating strategy of selfing and outcrossing from invertebrate and vertebrate pollinators (Taylor and Hopper, 1988; Wooller and Wooller, 2002a). Successfully pollinated inflorescences develop into woody cones with seed bearing follicles (two seeds per follicle), of which infrequent high intensity crown scorches typically facilitate their opening (Wooller and Wooller, 2002a). Although, climate variability is modifying the interval at which these fires occur, as well as the growing conditions (e.g. temperature and rainfall) in which they develop (Supplementary Fig S1, Appendix S1; Cochrane et al., 2014a; Cochrane et al., 2014b). Little is published on the development of seed banks in *B. media*, particularly time until maximum size and viability

(Wooller and Wooller, 2002 Cochrane et al., 2014a; Cochrane et al., 2014b). Therefore, an understanding of the species key reproductive and life stages are crucial to inform current risk and future conservation in the face of climatic challenges.

This research aimed to investigate the critical reproductive stages of *B. media*, with the ultimate goal of determining when optimal seed bank size is achieved during its lifecycle. This aim was driven by questions focusing on fruit production (1, 2 and 3), seed viability (3 and 5) and stand density (4 and 5):

1. At what plant age does *B. media reach* reproductive maturity?
2. How does the production and accumulation of cones and follicles change with plant age?
3. How does seed availability, viability and vigour change with both seed and plant age?
4. How does inter-fire recruitment and plant mortality impact stand density and stand structure with time since fire?
5. Are plant size measures or time since last fire the best predictor of optimal seed bank size?

MATERIALS AND METHODS

Study site

The research was conducted within the Fitzgerald River National Park (FRNP) and nearby outskirts on the south coast of SWA between Bremer Bay (119° E) and Hopetoun (120° E) (Rathbone, 2013; Fig. 1). Climate in the FRNP is seasonally dry Mediterranean with mild winters and hot summers, with a mean minimum and maximum temperature between 8°C (July) and 26°C (February; Moore et al, 1991; Gill, 2010; Rathbone, 2013). Average annual rainfall for the park ranges between 500 – 400 mm, typically depreciating with distance from the coast (Gill, 2010; Rathbone, 2013). Majority of rainfall occurs between May-October;

however, occasional rains and thunderstorms (a natural source of ignition) occur in summer (Moore et al, 1991; Gill, 2010; Rathbone, 2013; Bureau of Meteorology, 2025).

The unique geological composition of the FRNP supports an array of vegetation types high in biodiversity and endemism, with approximately 1,693 flora taxa persisting in the park alone (Rathbone, 2013). In the FRNP, *B. media* is found in either aeolian sands overlying phyllitic schist or shallow sand over spongolite bedrock throughout open-mallee woodland and kowangan heath/shrubland (Rathbone, 2013). These vegetation communities supporting *B. media* stands are dominated by serotinous non-resprouting Myrtaceous and Proteaceous genera, of which fire is the main reproductive facilitator through lightning strikes or prescribed burning (Moore et al., 1991). However, local stakeholders have identified the potential risk of decline in these serotinous communities due to impacts of changing fire regime under increasing aridification (Gill, 2010; Rathbone, 2013).

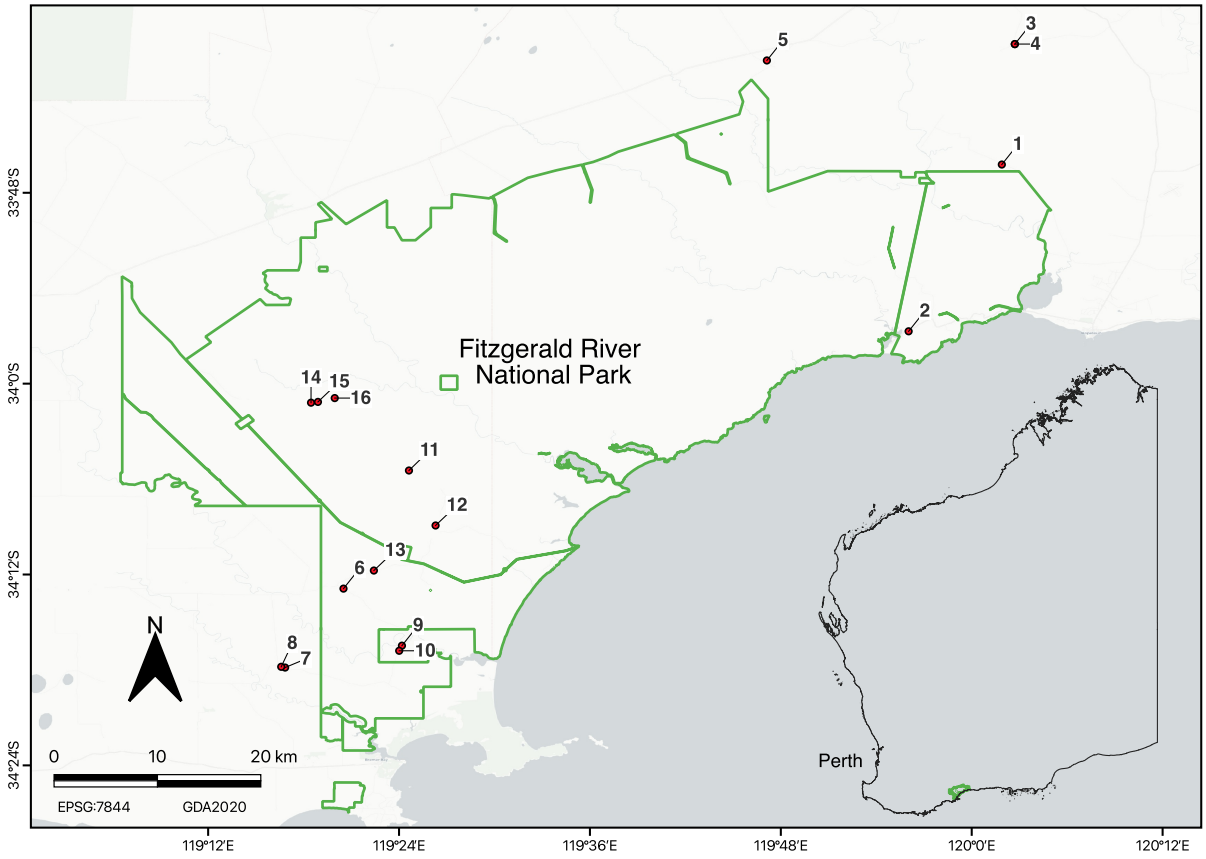

FIG 1. Site map for the Fitzgerald River National Park (FRNP) and the surrounding biosphere. Red dots and associated numbers represent the location of sites visited for cone sampling, density surveying or both. Red outline describes the boundary of the FRNP.

Study design and site selection

A space-for-time approach (landscape chrono-sequence; Walker et al., 2010) was used to sample cones (to estimate cones, follicles and seed per plant) and conduct density surveying (changes in stand density and age structure) over different life stages in *B. media*. As *B. media* is a fire-killed non-resporuter, it was assumed stands could be aged using the year of the last known fire. Therefore, historic fire data for the FRNP and surrounding biosphere produced by the Department of Biodiversity, Conservation and Attractions (DBCA) was investigated and mapped beneath the distribution of *B. media* to determine a desired target chrono-sequence (Atlas of living Australia, 2025; DataWA, 2025; QGIS, 2025). For site

selection, accessibility by 2WD, proximity to tracks/roads and dieback restrictions were considered, and any landscapes with potentially modified plant density from short-interval fire (i.e. one or two fire-intervals <15 yrs) were removed (Supplementary Fig S1, Appendix S1). Using this approach, 16 sites were identified over the following fire chrono-sequence: 13, 17/19, 26, 35/36 and 50 years since last fire (Fig 1; Table 1).

Data was collected for closely aged sites (*B. media* stands) 35/36 and 17/19 years since last fire, as large stands could not be located for the target ages of 36 and 19 years exclusively. Therefore, data for these plant ages were combined as they were deemed close enough not to introduce significant within-age variability. When possible, replicate sampling of cone and stand density at time since last fire (TSLF) was conducted between independent fire scars separated by 21- 80 km. The placement of density plots and selection of plants for cone sampling was randomised with a number generator, giving the location for stand entry point (parallel to the access road) and the perpendicular interior distance to travel. Density plots were established at the exact final coordinate, or if cone sampling, the nearest neighbour method was used to identify the closest individual. This process was repeated when establishing the location of the next plot or plant with the addition of a random compass bearing for direction.

We sampled 50 *B. media* plants between the 18th-22nd of September 2025 and surveyed stand density using 30 plots between the 5-10th of January 2026. During field work we collected cones, measured plant size metrics, vegetation dynamics and topographical features of the surrounding landscape. Seed was extracted from collected cones and germinated between November 2025 and February 2026.

TABLE 1. Site description of fuel age, location, topographical features, sampling (cone harvesting or density sampling) and population height conducted on *B. media* in the FRNP. Fire history (TSLF) accurate as of January 10th 2026.

TSLF (years)	Site	Location	Sampling type	Plot (n)	Plot size (m^2)	Elevation (m)	Aspect/slope	Mean height (m)	Latitude	Longitude
13	7	Doubtful Island Rd.	Cone/Density	3	400	54	Flat	0.9 / 0.7	-34.29748	119.280643
13	8	Doubtful Island Rd.	Cone/Density	3	400	69	Flat	0.8 / 0.7	-34.296691	119.276573
17	14	Twertup track	Density	2	400	45	NE, gentle slope	0.8	-34.019901	119.307824
17	15	Twertup track	Density	2	400	47	SE, medium slope	0.8	-34.0191	119.315059
17	16	Twertup track	Density	2	400	49	N, gentle slope	0.8	-34.015093	119.33265
19	3	Desmond Rd.	Cone	-	-	265	SW, gentle slope	1.7	-33.6442	120.045241
19	4	Desmond Rd.	Cone	-	-	237	SW, gentle slope	1.7	-33.644107	120.045221
26	9	Gairdner Rd.	Cone/Density	6	400	45	Flat	1.6 / 1	-34.27455	119.40306
26	10	Gairdner Rd.	Cone	-	-	47	Flat	1.4	-34.279901	119.40019
35	1	No Tree Hill	Cone	-	-	143	E, gentle slope	2.2	-33.770349	120.031619
36	2	West Beach Rd.	Cone	-	-	46	N, gentle slope	2.2	-33.945112	119.933961
36	12	Pabelup Rd south	Density	6	400	36	N, gentle slope	1.2	-34.148612	119.43831
50	5	South coast Highway	Cone	-	-	323	Flat	3.6	-33.661288	119.785454
50	6	Gairdner Rd.	Cone/Density	2	2904, 866	83	S, gentle slope	3.2 / 2.3	-34.214765	119.341818
50	11	Pabelup Rd south	Density	1	929	35	W, gentle slope	3.2	-34.090985	119.410425
50	13	Pebelup Rd north	Density	3	929-7698	40	S, gentle slope	3.2	-34.19582	119.373665

Mean height (m) of plants sampled for cones from different sites were averaged together when reported. The symbol '/' separates mean height between plants sampled for cones or density when both types of sampling were conducted at the same site.

Estimating plant age

The use of TSLF as a surrogate for plant age was the appropriate measure due to project time constraints (Jenkins et al., 2005). However, to confirm *B. media* stands germinated after the previous fire, annual growth nodes (years) from the apex of the plant to the lowest distinguishable increment were counted (Lamont, 1985). As nodes are absorbed by secondary thickening in older stems, stem diameter (mm) was also recorded as a second indicator of plant age. These measures were effective in excluding any potential inter-fire recruits from plants selected for cone sampling or identifying older individuals that had escaped the last fire (Jenkins et al., 2005). For density plots, stem diameter was the single plant age identifier, as node counting was too time-consuming for the high number of *B. media* plants in each plot (Jenkins et al., 2005).

Estimating cone age

The aging of *B. media* cones could not be determined purely by stem node counting, as current season inflorescences were observed on both new stems and within the crown on old stems (Lamont, 1985). Consequently, a visual assessment of follicle/cone colour and condition was also used to separate cones into the categories; young, ≤ 3 years (follicles purple, floral remnants brown); moderate, 4-6 years (follicles purple/brown, floral remnants grey with many persistent) and old, ≥ 7 years (exposed follicles brown/grey, floral remnants grey with few persistent, cones showing signs of weathering; Fig 2; Crawford et al., 2011). As some individuals had a large seed bank of old (≥ 7 years) qualifying cones, a range was selected at varying degrees of weathering.

FIG 2. Division of *B. media* cones into the three age categories based on node counting and visual condition (from top to bottom); young (≤ 3 years), moderate (4-6 years) and old (≥ 7 years). Cones in the image were sampled from a plant 36 years since last fire in east FRNP. The code on the bags from left to right describes site, plant ID and cone age category.

Density and plant size surveying

Changes in *B. media* stand density and age structure over time were measured from six plots per TSLF (30 total), established across the chrono-sequence 13, 17, 26, 36 and 50 years old (Figure 1, Table 1). Plot size ranged from 400-7695 m^2, with plot shape (square, circle or semi-circle) modified and size increased when less than eight *B. media* plants were present in the plot area (Environmental Protection Authority, 2016). As previously mentioned, when possible, plots were used to sample independent stands and fire scars to better account for between-stand differences. Otherwise, separation of plots in the same fire scar and stand

ranged from 41 m to 14 km. Each plot received a 20 m minimum buffer from tracks and roads to avoid edge effects and were consistently no closer than 2.8 km from the coast. Reducing the potential influence of abiotic coastal factors (e.g. high wind speed, salt spray) on some stands and not others.

Plot data included size metrics of *B. media*, topographical features and vegetation community type, condition and structure. Canopy volume (m^3) per plant was calculated using plant height (*h*; subtracting ground to canopy height) and two perpendicular measurements of width (*w1* and *w2*) in the following ellipsoid form (e.g. as used by Miller et al., 2024):

$$V = \frac{4}{3} \times \pi \times \frac{h}{2} \times \frac{w1}{2} \times \frac{w2}{2}$$

Cone sampling

To estimate cone, follicle and canopy seed bank size and describe changes through time, cones were collected from ten sites 13, 19, 26, 35, 36 and 50 years since last fire (Fig, 1; Table 1). A total of 50 individuals were sampled, with five plants sampled per site (Table 1). Young, moderate and old cones were harvested until each age class was represented by a minimum of 25 intact follicles (approximately 50 seeds). For reproductive plants unable to reach the follicle minimum, all cones were harvested (Crawford et al., 2011). To estimate cone density per plant, a cone sub-sample (young, moderate and old) from one main limb was recorded and multiplied by a main limb count (n). This measure also allowed for follicle and seed per plant to be estimated. Plant size metrics such as height, stem width and canopy dimensions were also recorded.

Seed processing and germination trials

Prior to seed extraction, cones were stored at 15% relative humidity (RH) and 15ºC for nine days at the Western Australian Herbarium. During this period, persistent styles were removed with a wire brush, exposing follicles for counting and scoring as either open, closed or predated. Seed was removed from follicles by rupturing them with a gas flame, soaking in water for 24 hours then drying (15% RH and 15ºC) for 28 days (Crawford, 2011). Due to inexperience in working with *B. media*, some harvested young cones had immature follicles that failed to rupture from burning. Seeds from ruptured follicles were cleaned from ejected reproductive material (i.e. divider and chaff) in a seed aspirator, then counted as predated, aborted and full before packaging for storage (15% RH and 15ºC) for three months (Nov-Jan).

For germination, full seeds were treated in Plant Preservative Mixture (Plant Cell Technology, AUSTRATEC) at a 10% dilution for 15 minutes before being plated directly onto agar (90 mm diameter plates). Number of seeds per agar plate ranged from 2- 30 and were incubated at 15ºC on a 12 hour/12 hour day and night cycle in air-tight containers to prevent moisture loss (Cochrane, 2014a). Germination scoring of plates was repeated every seven days for 35 days; some seeds may have germinated beyond 35 days, however time constraints prevented continued incubation. Successful germination was classified when radical length had reached 3 mm, and any seed failing to germinate were subjected to a cut test and determined as; full non-viable (seed hard with white interior), predated (empty seed casing), or aborted (soft with discoloured interior; Crawford et al., 2011).

Statistical analysis

Non-linear relationships for over-dispersed count data were analysed using both Generalized Linear Models (GLMs; log link) and negative binomial (NB) Generalised Additive Models (GAMs; log link), using the *mgcv* and *ggplot2* packages in *R* (Wickham, 2016; Wood, 2017;

R Core Team, 2025). Any data sets dealing with proportions were fitted with quasi binomial GLMs (logit link), and data with continuous time variables (e.g. mean time until germination) with gamma GAMs (log link) with the *R* packages previously mentioned. For each GAM, *k* (wigglyness) was set at three ($k = 3$) to prevent overfitting and ensure environmental logic (Miller et al., 2025). After fitting either a GAM or GLM, assumptions were checked using residuals, Quantile-Quantile plots, effective degrees of freedom (EDF) and if numerous models were viable, Akaike's Information Criterion (AICc) to rank best fit (Miller et al., 2025).

Significance between the relationship of count, proportion and continuous data over TSLF and reproductive age (cone, follicle and seed) was determined in *R* with Shapiro-Wilks testing for normality, one-way ANOVA testing (post-hoc pairwise comparisons with Turkey HSD) for parametric data and Kruskal-Wallis (post-hoc pairwise comparisons with Dunn's test) for non-parametric data. Two-way testing for non-parametric data was conducted using Aligned Rank Transform (ART) ANOVA.

The seed ages young and moderate were combined into a single group ("young") for viability and vigour testing, as sample size in the original young category was too small for two-way ART ANOVA testing. Changes in plant size with time (canopy volume, stem diameter and height), for each TSLF over the chrono-sequence, was separated into a three-panel histogram. All response variables remained at their original scale except canopy volume, which was square-root transformed to improve the interpretation of data in stands (Miller et al., 2025). The Gini coefficient (a measure of evenness) was determined for each size metric over TSLF to identify possible inter-fire recruitment. The Gini coefficient ranges from 0 and 1, with 0 indicating all plant sizes occur at the same frequency and a value of 1 indicating every

individual falls within the same size class. Mulitcohort stands (inter-fire recruiting) are evident when the Gini coefficient score starts high and depreciates over time (e.g. 1 to 0).

RESULTS

Juvenile period

Juvenile period (time until 50% fruiting) for *B. media* could not be established because of constraints imposed on site availability. However, plants 13-years since last fire were consistent with early-stage maturity. From the 10 individuals sampled, 80% had flowered and 60% averaged 1.5 ±0.4 (mean ± SE) cones and 15 ± 7 follicles per plant (Fig 3, Fig 4). The condition of cones sampled were assessed as moderate in age (4-6 years) and old (≤7 years), suggesting first fruiting may have occurred as early as 6-years since last fire. At the time of sampling there were no inflorescences from the current season.

Cone and follicle production

Total cones per plant increased non-linearly from 13 (1.5 ± 0.4; mean ± SE) to 50 (352 ± 73) years since last fire ($p \leq 0.01$, Kruskal-Wallis, Fig 3).

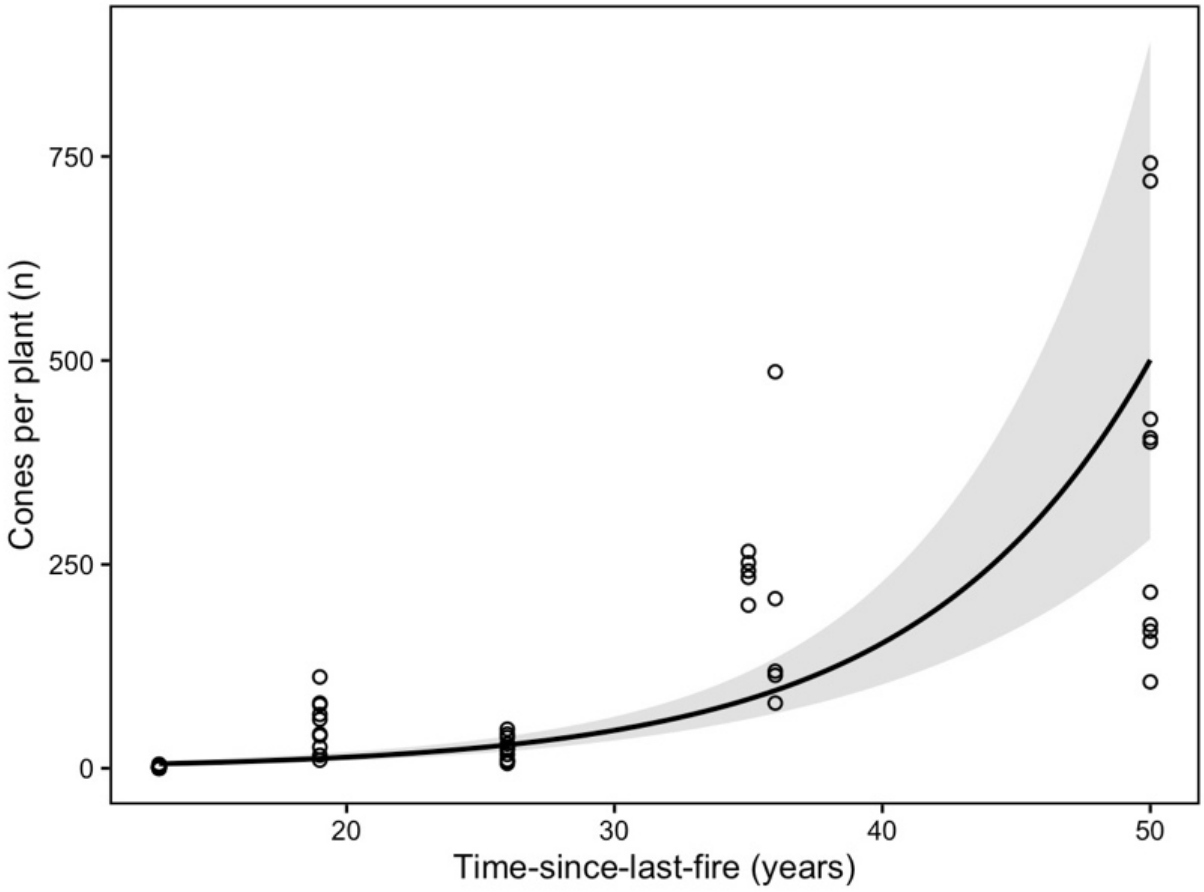

FIG 3. Cones per plant (n = 5-10 per fire age) over TSLF (13, 19, 26, 35, 36 and 50 years). Grey shaded ribbon represents 95% confidence intervals.

Despite an apparent increasing trend in mean *B. media* cone production across sites 13-26 years since fire, there was no significant difference between them (13-19 TSLF $p = 0.08$ and 19-26 TSLF $p = 0.91$, Dunn's test). From 26 to 36 years, cone production increased significantly (20 ± 5 to 220 ± 36 cones per plant; $p = 0.04$, Dunn's test; Fig 3) then remained constant from 36 to 50 years since fire despite an exponential trend ($p = 1$, Dunn's test, Fig 3). The large confidence intervals at 50 years since last fire reflects variability between plants sampled in the east ($n = 5$) and west ($n = 5$) FRNP, with *B. media* in the east on average 32% taller with 67% more cones (Fig 3, Table 1).

Intact follicles per plant were tied closely to cone production, although 13-year-old plants were significantly less productive than all other plant ages (i.e. p <0.05, pairwise testing, Dunn's test). Follicle variability between 19-26 years since last fire was again not significant (p = 1, Dunn's test), although the intensification of follicles per plant from 26 (367 ± 86) to 36 (7001 ± 1162) years since last fire marked a significant increase and peak follicle accumulation (p <0.01, Dunn's test; Fig 4). No difference in follicles per plant occurred between 36-50 years; however, an average decrease of 19% was observed (p = 1, Dunn's test, Fig 4).

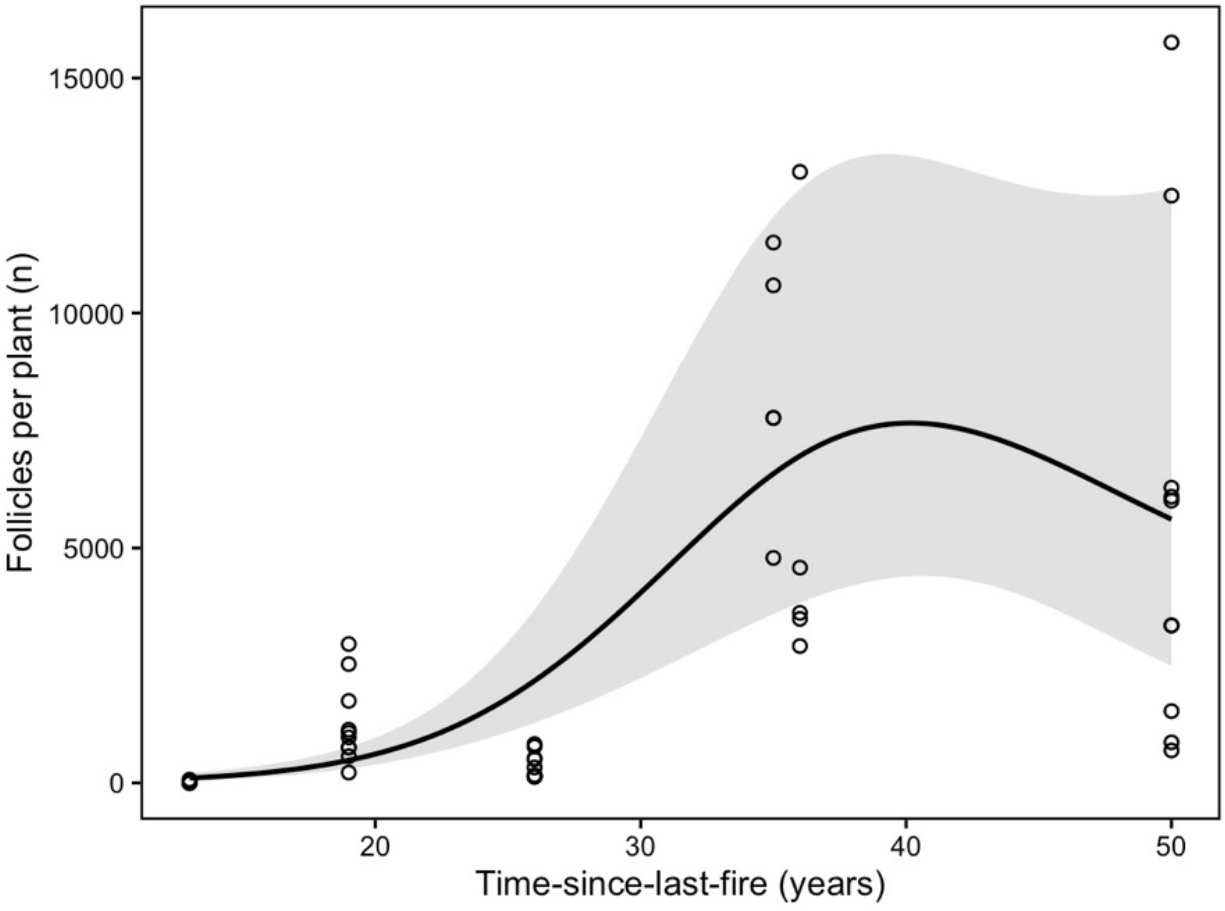

FIG 4. Intact follicles per plant (n = 5-10 per age class) over TSLF (13, 19, 26, 35, 36 and 50 years). Grey shaded ribbon represents 95% confidence intervals.

Follicle production per cone increased significantly between plants from sites 13 (14 ± 2; mean ± SE; Fig 5) and 36 (29 ± 3; Fig 5) years since last fire ($p = 0.03$, one-way ANOVA; $p = 0.01$, Turkey HSD). However, for all other plant ages between 19-50 years since last fire, follicle production per cone was constant (i.e. $p \geq 0.07$, pairwise testing, Turkey HSD).

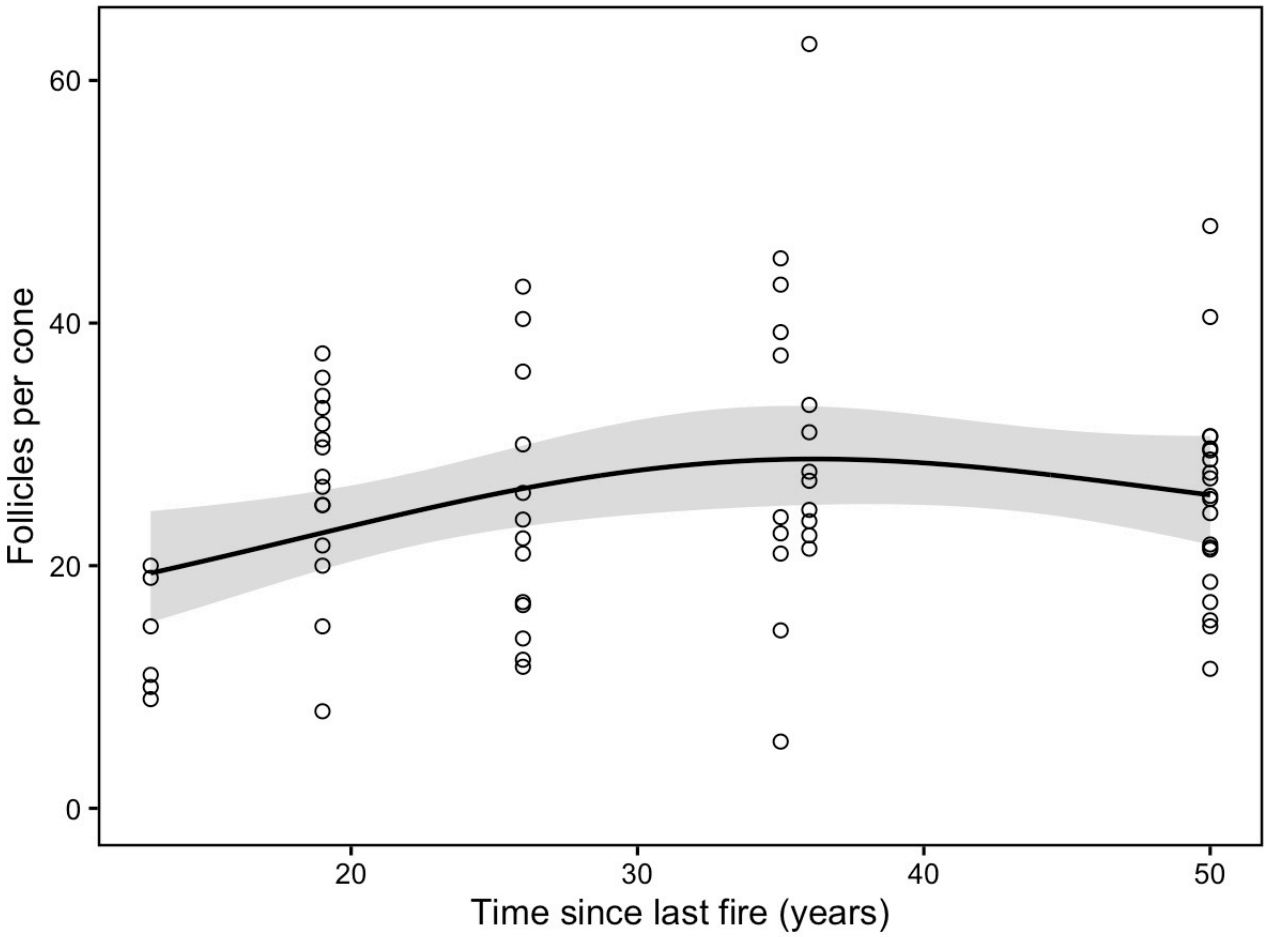

FIG 5. A measure of current (in the last 6 years) follicle production vigour over TSLF (13, 19, 26, 35, 36 and 50 years). Data are follicles per cone (irrespective of condition, i.e. intact, predated and damaged) from cones ≤6 years old ($n = 74$). Grey shaded ribbon represents 95% confidence intervals.

Seed loss, viability and vigour

Full seeds per plant for *B. media* (young, moderate and old cone ages combined) follows the non-linear relationship with TSLF as seen in follicle counts (p <0.01, Kruskal Wallis; Fig 6). Production peaks significantly between 26 to 36 years since last fire (p <0.01, Dunn's test) before reducing by 68% between 36 and 50 years since last fire, although this change in follicle counts was only significant at the level of p = 0.1 (Dunn's test; Fig 6).

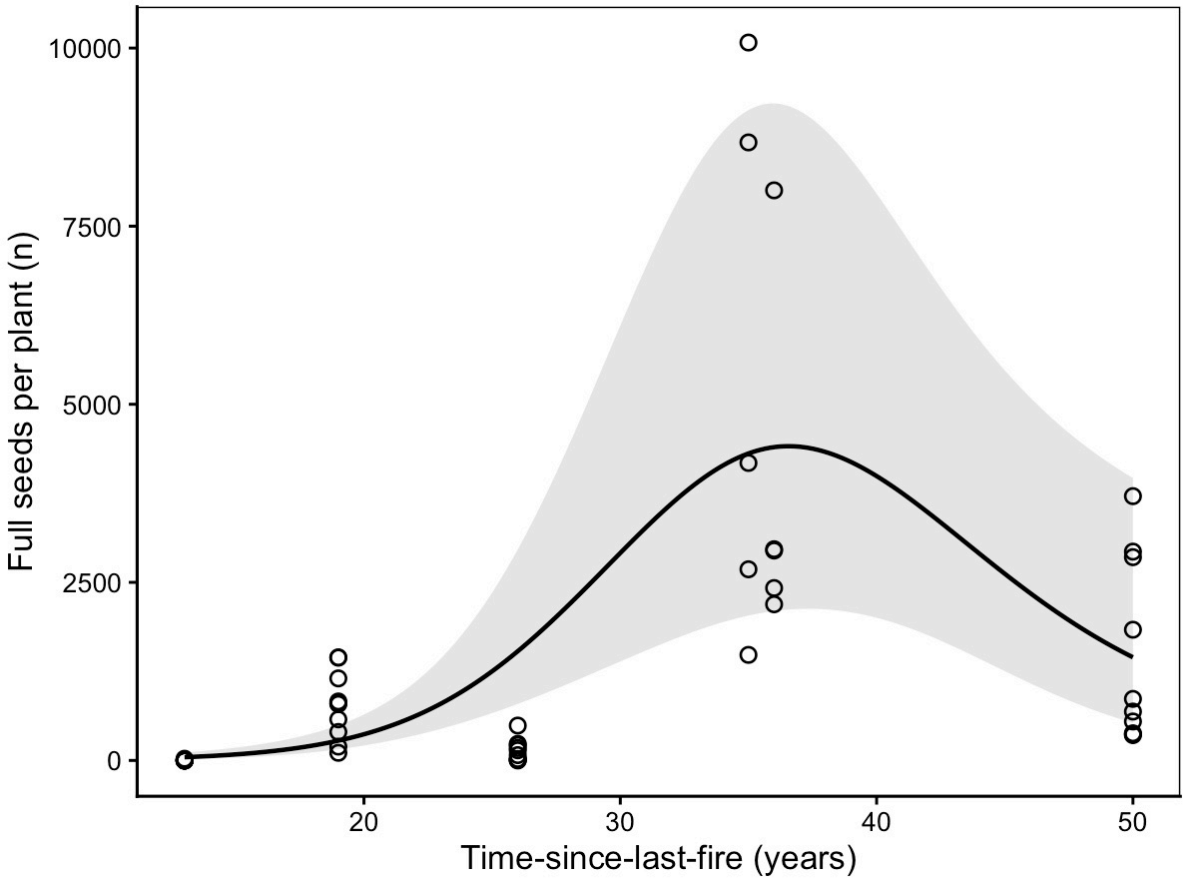

FIG 6. Full seeds per plant (n = 5-10 per age class) for all seed age classes over TSLF (13, 19, 26, 35, 36, and 50 years). Grey shaded ribbon represents 95% confidence intervals.

The number of aborted and predated seeds per plant appears to increase continuously with TSLF (p <0.01 respectively, Kruskal-Wallis; Fig 7), although significance is only reported in comparison with 13-year-old *B. media* plants (i.e. p >0.04, pairwise testing, Dunns test; Fig 7). Changes in both seed abortion and predation were therefore non-significant across the chrono-

sequence, despite the highest levels being observed for *B. media* at sites 50 years since last fire, translating to averages of 617 ± 362 and 1451 ± 362 for aborted and predated seeds, respectively (Fig 7).

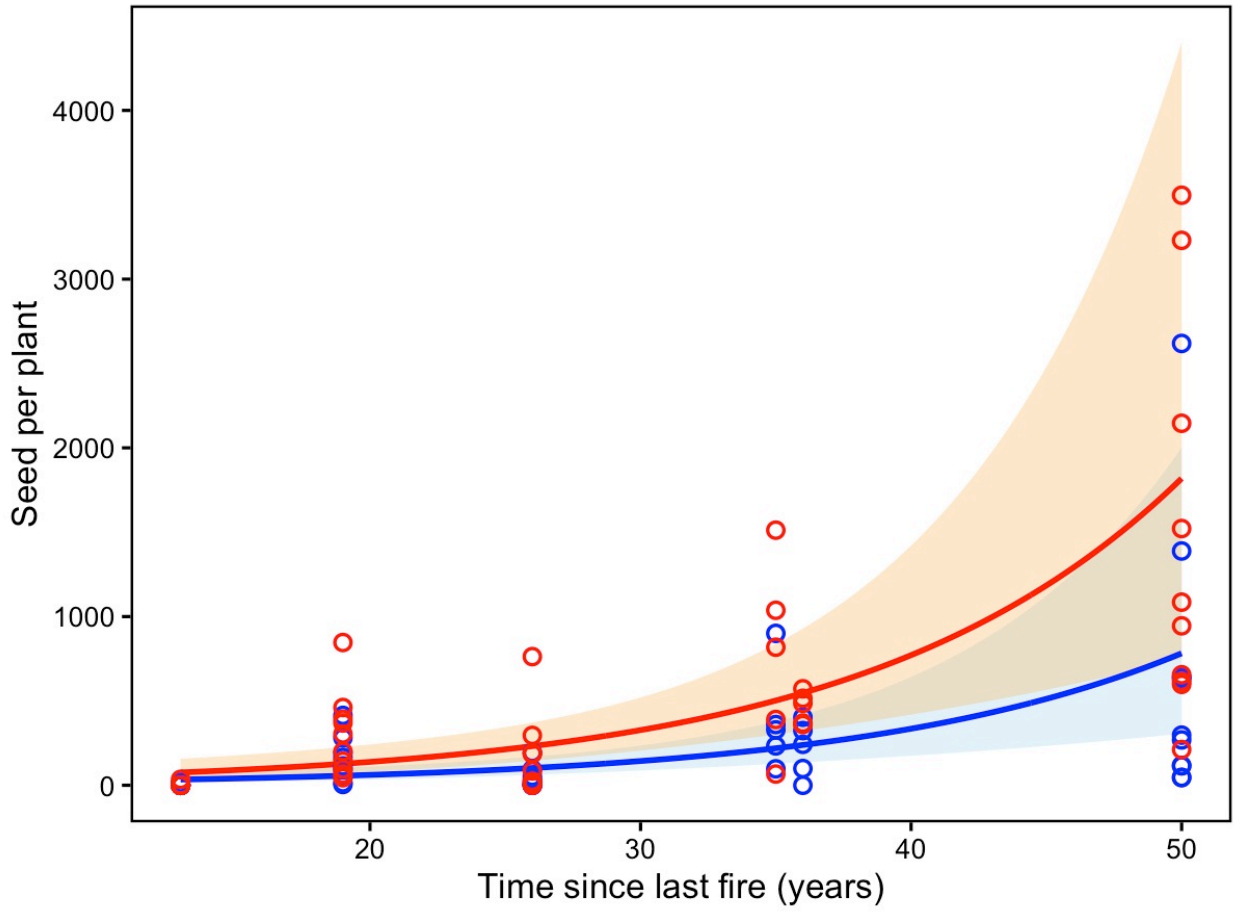

FIG 7. Aborted (blue) and predated (red) seeds per plant (n = 5-10 per age class and category) over TSLF (13, 19, 26, 35, 36, and 50 years). Blue and red shading represents 95% confidence intervals.

Viability of seed (measured through germination) from all age classes was high across the chrono-sequence (Fig 8). However, because the youngest cone age class produced few ripe follicles, statistical testing against other age classes was not possible. Consequently, to test for a seed age effect on viability, the two youngest categories of seed (i.e. ≤3 years and 4-6 years)

were combined. Viability for the combined "young" age class (≤6 years; blue) decreased by 11% and old seed (≥ 7 years; red) by 21% across the TSLF chrono-sequence (Fig 8).

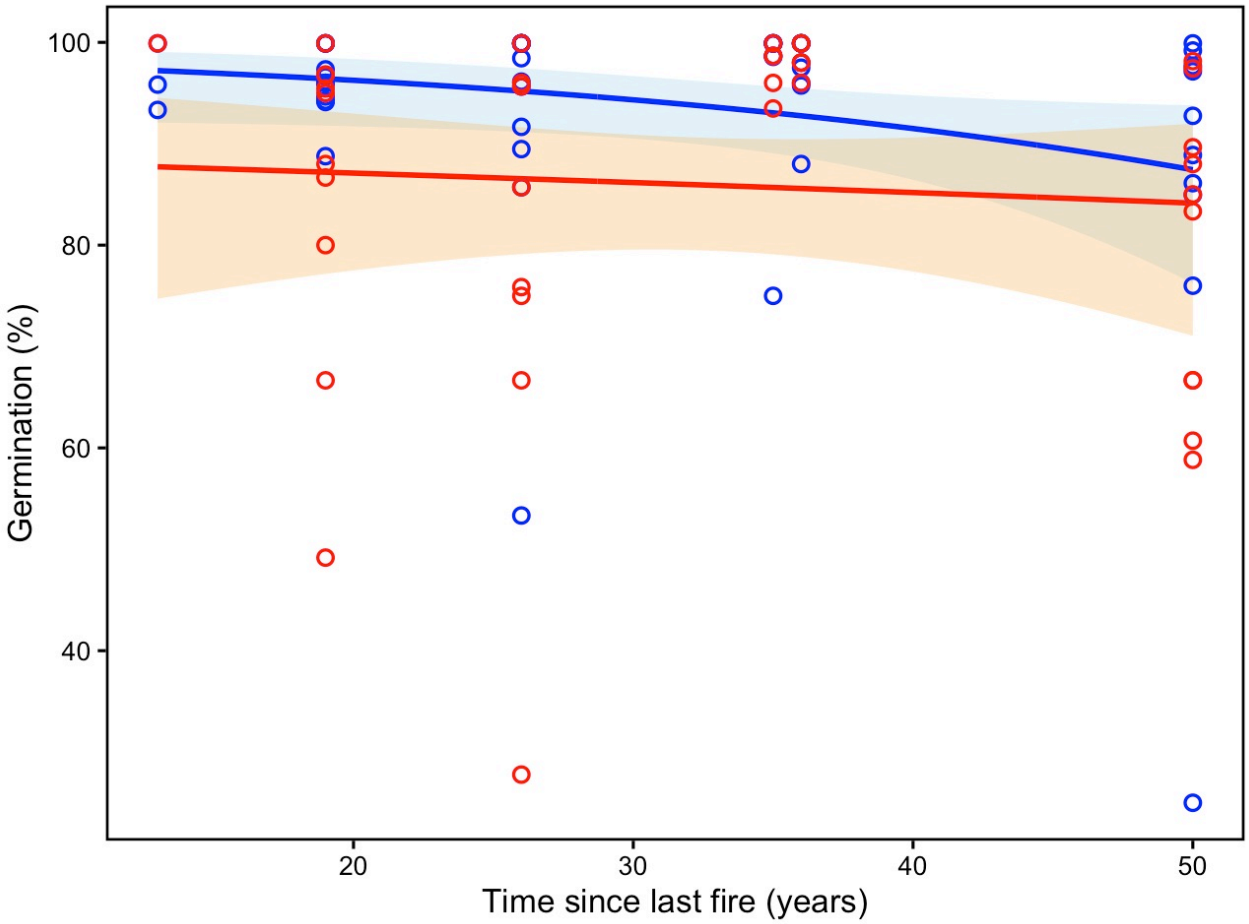

FIG 8. Viability of young (≤ 6 years; blue) and old (≥7 years; red) *B. media* seeds over TSLF (13, 19, 26, 35, 36, and 50 years). Each data point represents the percentage germination of a subsample of full seeds (young, n = 4-129; old, n = 3-75) from individual plants (n = 44). Blue and red shading represents 95% confidence intervals.

However, because there was no difference in seed viability between seed ages (young and old) over TSLF (marginal, p = 0.6, ART ANOVA; Fig 8), seed age cohorts were combined to test for change in viability with TSLF. This revealed a period of high viability (93 ± 1%) occurring in *B. media* between 13-36 years since last fire (i.e. p ≥0.1, pairwise testing, Dunn's test; Fig

9) which then significantly reduced by 11% (82 ± 4%) at 50 years since last fire (36-50 TSLF, p <0.01, Dunn's test; Fig 9).

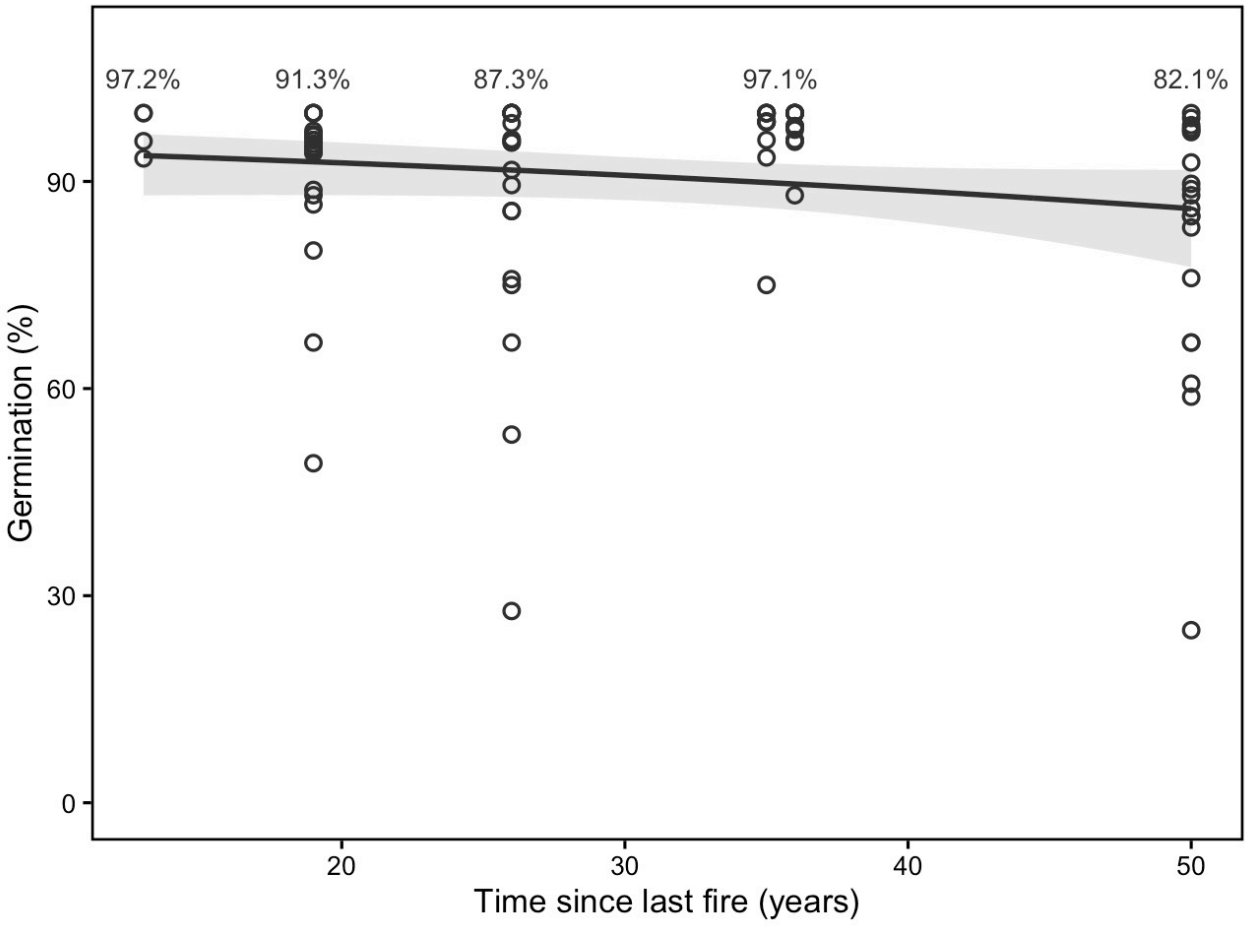

FIG 9. Viability of *B. media* seeds over TSLF (13, 19, 26, 35, 36, and 50 years; all seed age removed). Each data point represents the percentage germination of a subsample of full seeds (n = 3-129) from individual plants (n = 44*;* labelled means %). Grey shading represents 95% confidence intervals.

Mean time until germination (MTG), measuring the delay in germination across *B. media* stands revealed no significance between young and old seed over TSLF, as shown in seed viability (marginal, p = 0.6, ART ANOVA; Table 2).

TABLE 2. Mean time until germination (MTG) reported in days for *B. media* over TSLF (13, 19, 26, 35, 36, and 50 years).

TSLF	*Seed class*	*MTG (Seed age and TSLF)*	*MTG (TSLF)*
13	Young*	16.30	15.70[a]
	Old**	14	
19	Young	20.30	20.9[b]
	Old	21.80	
26	Young	16.90	16.80[a]
	Old	16.50	
36	Young	18.90	19.60[ab]
	Old	20.70	
50	Young	21.10	21.10[b]
	Old	21.00	

*Indicates three seed samples, **indicates one seed sample. The youngest cone age class (≤ 3 years) was combined with moderate seed (4-6 years) due to small sample size in see aged ≤ 3 years. MTG (TSLF) values that don't share a letter ([a] or [b]) represents significant difference between them (p >0.05). Standard error (SE) calculated but not reported to improve readability.

Therefore, regardless of seed age, MTG across TSLF showed a significant non-linear pattern (p >0.01, Kruskal-Wallis; Fig 10) with MTG generally increasing from 15.7 ± 1 days to 21± 1 days. However, seeds 19 years since last fire (21 ± 1 days; Table 2) germinated at the same rate as 50-year-old seeds (p = 0.8, Dunn's test; Table 2).

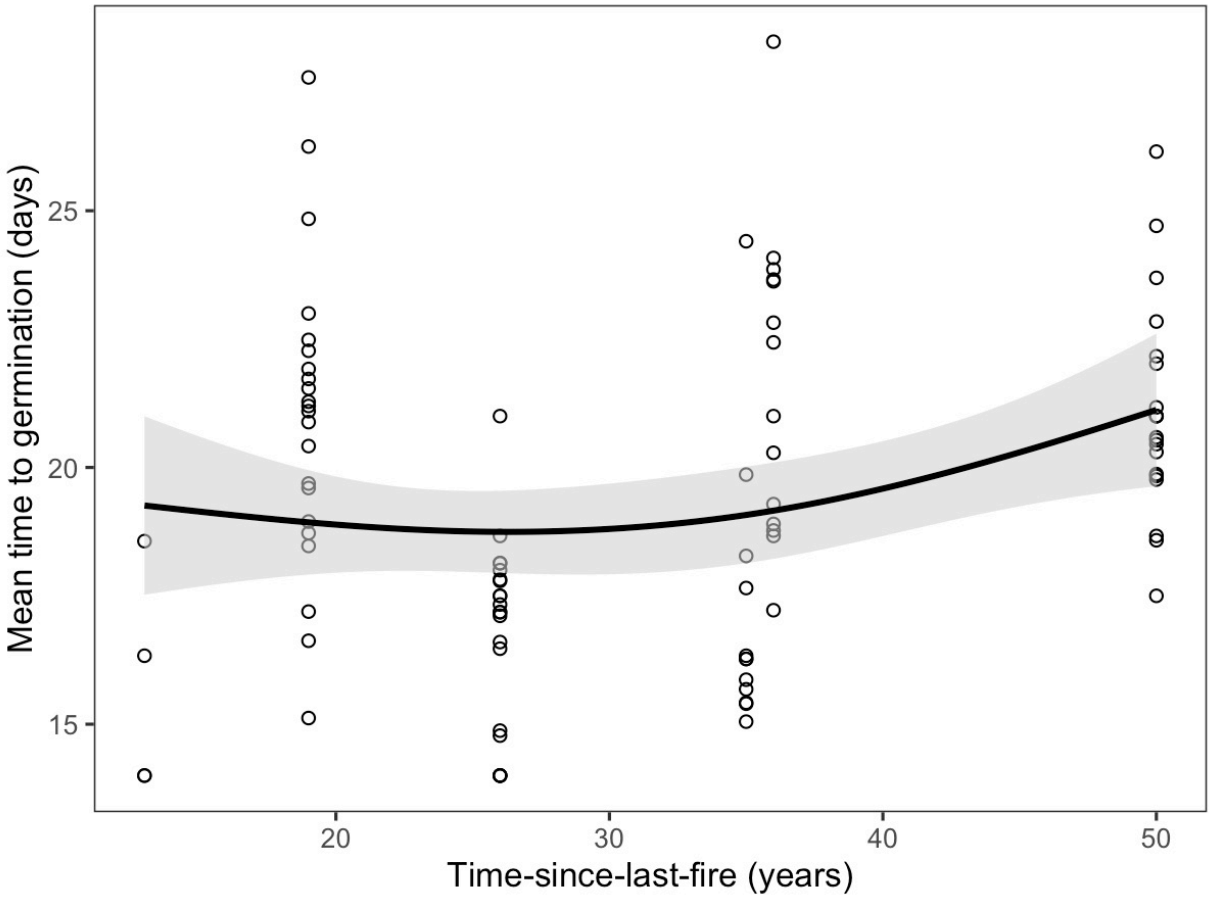

FIG 10. Mean time until germination over TSLF (13, 19, 26, 35, 36, and 50 years; n = 93). Age of seed (young and old) has been collapsed into the same data set. Reported with 95% Confidence interval bars.

Serotiny and inter-fire recruitment

Counts of open and closed follicles from each cone age class indicate that *B. media* is strongly serotinous (Lamont, 2021), with 86 ± 3% of follicles closed in cones ≥7 years old (Table 3).

TABLE 3. Proportion of *B. media* follicles remaining closed and open for cone age categories irrespective of plant age over TSLF (13, 19, 26, 35, 36, and 50 years).

Follicle age (years)	Follicles assessed (n)	Follicles closed (%)	Follicles open (%)
≤3 (Young)	1684	99.5	0.5
4-6 (Moderate)	4366	98.6	1.48
≥7 (Old)	5970	85.7	14.3

Predated and damaged follicles were removed from the serotiny assessment.

To identify changes in stand age structure in *B. media*, including inter-fire recruitment associated with follicle opening, changes in evenness (Gini coefficient) for canopy volume, stem width and height across TSLF was analysed. Sample size of the chrono-sequence was too small (n = 5) to confidently report significance of Gini results, however trends were still considered.

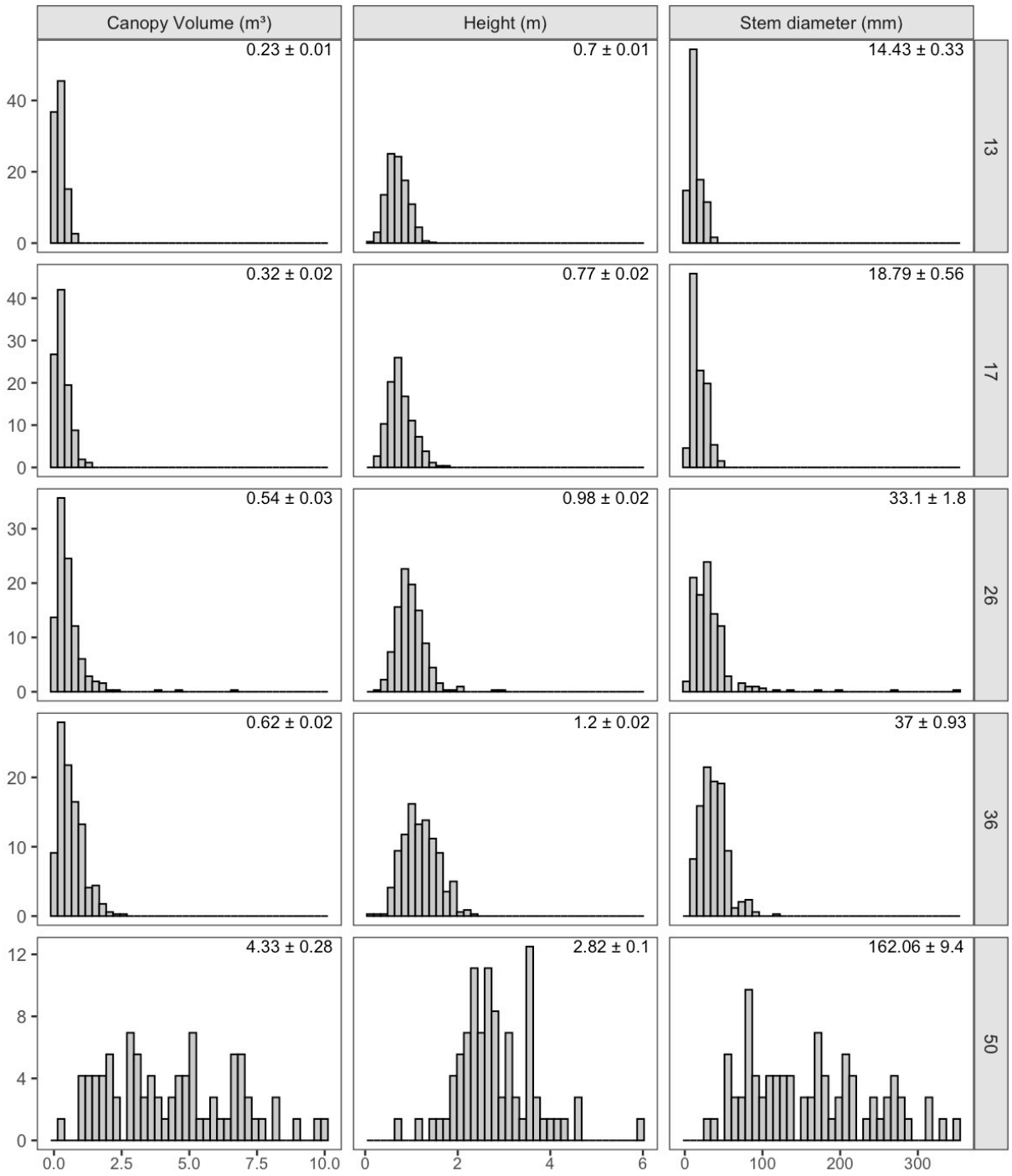

FIG 11. Relative frequency distribution (%) of height (m), stem diameter (mm) and canopy volume (m³) in *B. media* stands over TSLF (13, 17, 26, 36, and 50 years). Mean ± standard error is reported for canopy volume, height and stem diameter from density plots (n = 72 - 495). Canopy volume values were square root transformed for clearer interpretation of data.

The greatest decrease in evenness was observed in canopy volume across TSLF (i.e. *Gini* = 0.8 and 0.6, for 19 and 50 years respectively; Supplementary Fig S2, Appendix S1) and gives the best indication of potential inter-fire recruitment. On the inverse, flat frequency distributions are reported for stem width and height across the whole chrono-sequence (consistently flat; *Gini* = 0.2 and 0.3 over TSLF, respectively; Fig 11). This indicates size variability is potentially typical of single cohort stands and not due to inter-fire recruitment.

The density of these stands significantly decreased from 13 (2067 ± 401 plant/ha; mean ±SD) to 50 (113 ± 36) years since last fire (p <0.01, Kruskal-Wallis; Fig 12). Although, post-hoc comparisons show that significance was only evident at 50 years since last fire when compared to all stands along the chrono-sequence (i.e. $p \leq 0.05$, pairwise comparisons, Dunn's test).

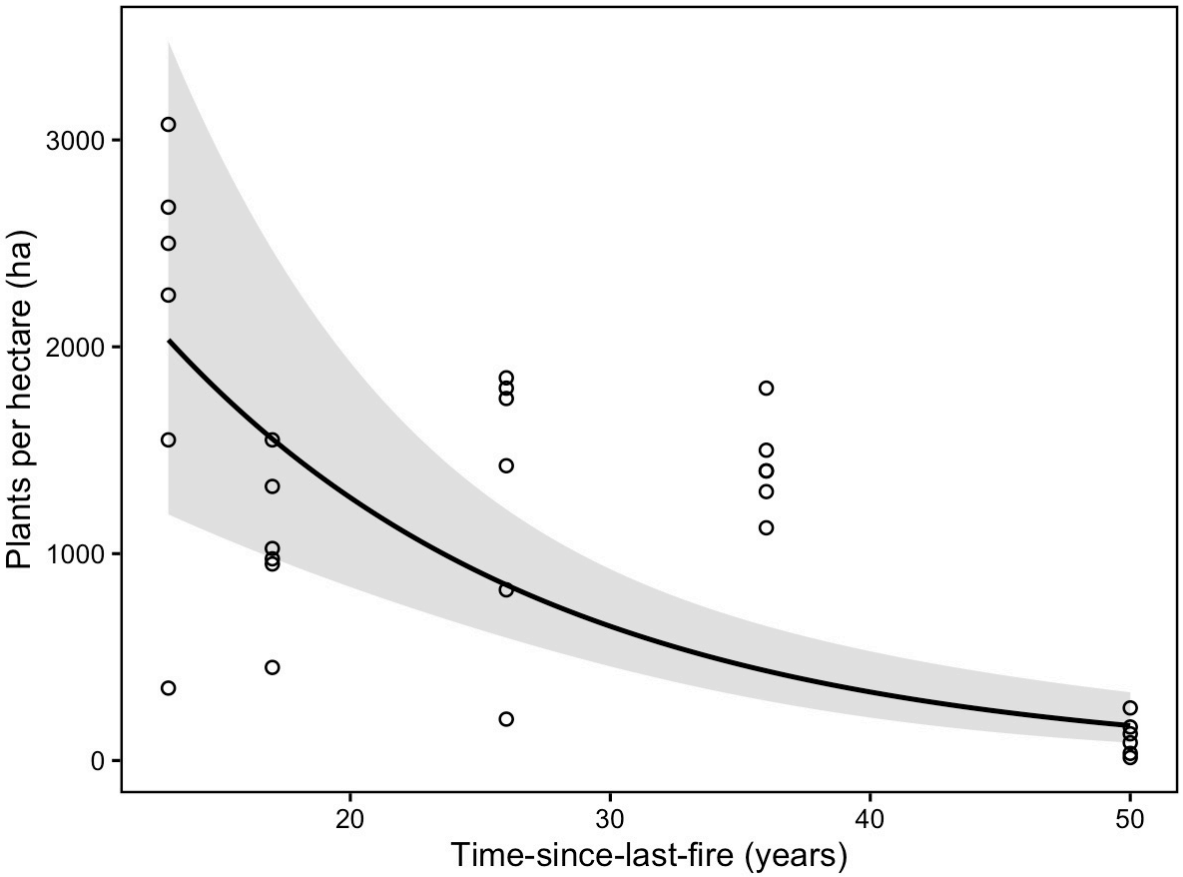

FIG 12. Density of *B. media* (per ha) over TSLF (13, 17, 26, 36 and 50 years). Each data point represents a surveyed density plot (six per TSLF; $n = 30$). Grey shaded ribbon represents 95% confidence intervals.

Predicting optimal seed bank size: Time since last fire versus plant size

While TSLF is an obvious predictor of reproductive output for single cohort stands of non-resprouting seeders, stands of *B. media* displayed considerable variation in plant height, and reproductive output within and between sites, particularly at 36 and 50 years since last fire (Table 1, Fig 11). To account for this variability, the use of TSLF as a factor for predicting seeds per plant was compared with plant size measures (stem width, height and canopy volume) to identify a better predictor. The goal therefore was to determine which plant metric best described reproductive output: a more accurate predictor of available seed than TSLF. From all plant size measures that were modelled, height was the best predictor of full seed per plant (Fig 13; ΔAIC = 0; Supplementary Table S1, Appendix S1).

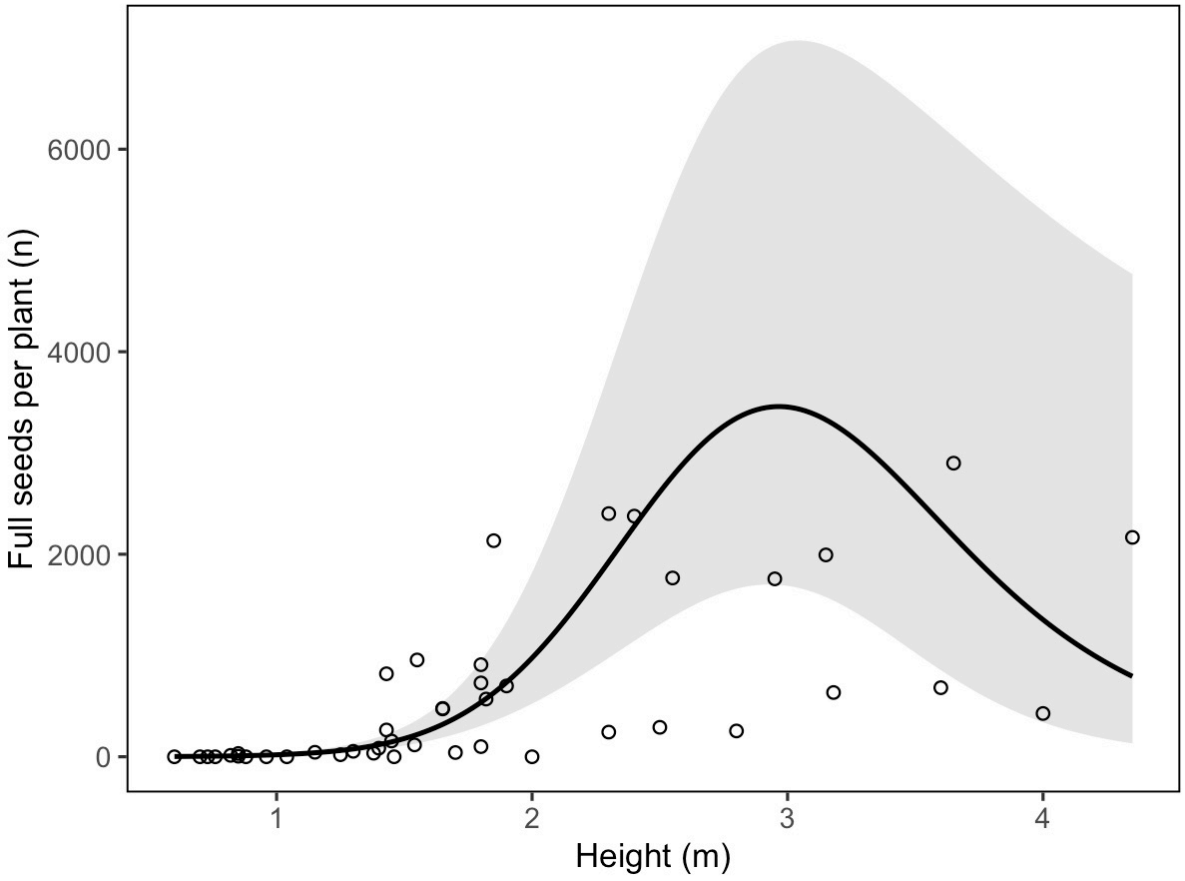

FIG 13. Plant height as a predictor of seeds per plant (winning model). Each plant from the sample size (n = 44) is represented by full seed results regardless of seed age. Six individuals were not included as stem measurements were not included in data collection at the beginning of surveying. Shaded ribbons represent 95% confidence intervals.

The relationship between height and seed shows peak reproductive output occurs at the plant height of 2.6 m and decreases at 3.2 m (the mean height of plants 50 years since last fire) when seed viability declines by 11% (Fig 13, Fig 9; Ranstom and Cook, 2022;). This height-seed predictor estimated viable seed volume per ha was greatest in stands 50 years since last fire (Fig 14). Although, viable seed volume was not significantly different between the plant ages 26-50 years since last fire (i.e. p <0.42, Dunn's test; Fig 14).

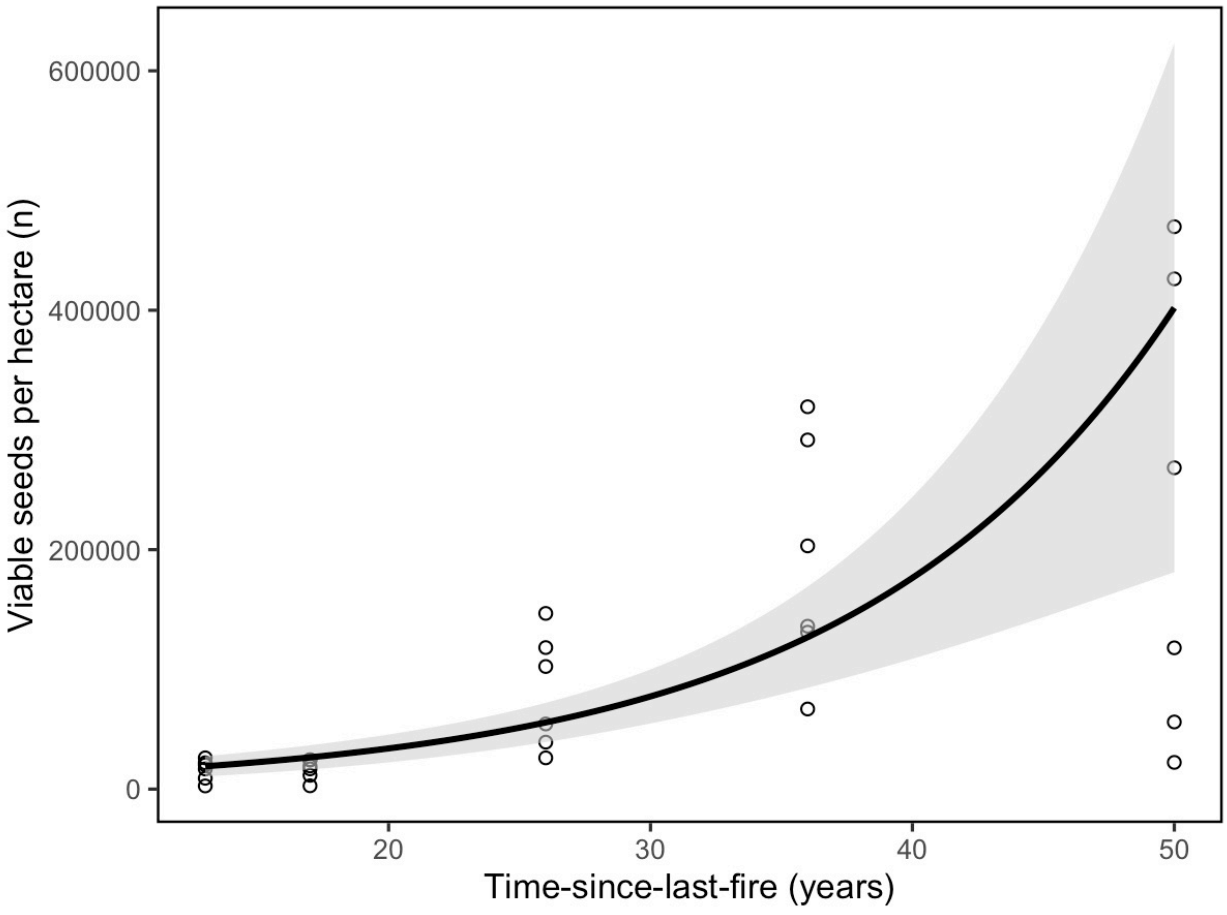

FIG 14. Viable *B. media* seeds per ha over TSLF (13, 17, 26, 36 and 50 years since last fire). Each point represents accumulative viable seed data from density plots (n = 30) in west FRNP. Each TSLF received six plots, which surveyed a total of 1,486 *B. media* individuals. Grey shading represents 95% confidence intervals.

DISCUSSION

Juvenile period

Juvenile period in fire prone ecosystems is the measure of the minimum time before species reach reproductive maturity, which for the purpose of this research was defined as 50% fruiting (Gosper et al., 2022; Enright and Ange, 2025). Although the juvenile period for *B. media* could not be accurately identified, it was estimated to be between 12-18 years using a regional environmental productivity metric model developed by Gosper et al. (2022). However, this model does not consider post-burn seasonality, which in cohorts of *Banksia Baxteri* and *Banksia coccinea* east of the Stirling Range National Park (and close to FRNP) delayed juvenile periods of 4 years (Autumn burn) to 7.5 years (*B. Baxteri)* and 12 years (*B. coccinea)* when burnt in spring (McCaw, 2008). The influence of long-term moisture stress was also influential in increasing juvenile period from 6 to 15 years in *Banksia ornata* between stands burnt in 1990 (wetter) and 2017 (dry), respectively (Enright and Ange., 2025). Therefore, juvenile period for *B. media* is likely to be between 4-18-years dependent on the timing of fire and post-fire rainfall (Wooller et al., 2002; McCaw, 2008; Burrows et al., 2008).

Cone and follicle production and loss

Cones per plant over the *B. media* chrono-sequence was defined by a period of low (13 to 26 years since fire) and high productivity (35/36 to 50 years since fire) after reaching maturity (Fig 3). This increase in productivity at older plant ages was also evident in the non-resprouting *Banksia nutans, Banksia baxteri* and *Banksia Baueri* co-occurring in west FRNP (Wooller et al., 2002b). These species report an intensification in seed production between 30 to 40 years

since last fire, attributed to the limitations of nutrient poor sands preventing high seed-production until plants were established (Wooller et al., 2002b). Cones per plant peaking in *B. media* at 50 years since last fire was expected due to the retention of cones in *Banksia* species over time (Fig 3; Wooller et al., 2002b). However, due to in-canopy cone ageing processes, intact follicles per plant (typically two seeds per follicle) reduced 19.4% from the plant ages 36 to 50 years since fire (Fig 4). Follicle vigour per cone (intact, predated and damaged) was constant at 27 ± 1 follicles per cone over TSLF (excluding plants 13 years since fire; 14 ± 2) indicating this reduction was not due to decreasing reproductive vigour in aging plants (Fig 5). Wooller and Wooller (2002a) demonstrated that due to resource delivery limitation in *B. media*, the only factor influencing follicle set per cone was the success of cross-pollination from Honey possums (*Tarsipes rostratus*), New Holland honeyeaters (*Phylidonyris novaehollandiae*) and the White-cheeked (*Phylidonyris niger*) honeyeater. As larger plants generally attract more pollinators, the reduction of intact follicles per plant at 50 years since last fire is instead likely due to increasing predation (Fig 7) and spontaneous follicle rupture with follicle and seed age (Table 3; Cowling et al., 1987; Middleton et al., 1996; Wooller and Wooller, 2002a).

Evidence of predation on *B. media* follicles and seed was found during sampling, as bore holes and frass; however, the predatory larvae and invertebrates were not seen. Predation data from six *Banksia* species published by Scott (1982) indicated invertebrates are likely from the genera *Arotrophora* (Totrix moths), *Xyloryctis* (Rhinoceros beetles), *Peraglyphis* (Moths) and *Myositta* (Weevils), typical in *Banksia* herbivory. Scott (1982) suggests boring only occurs during the inflorescence stage before increasing woodiness in cone development. Although, here we found that *B. media* predation was highest in the oldest plants (although not significant; Fig 7). This is consistent with observations of predation in older cones of *Banksia menziesii*, confirming predation is not exclusive to young cones (Cowling et al., 1987). Predation from Carnaby's Black Cockatoo (*Zanda latirostris*) is also expected, as FRNP is a foraging location

during the non-breeding season (Witkowksi et al., 1991; Saunders et al., 2024). The proportion of follicles and cones removed by Carnaby's, and at what plant age in *B. media* cannot be described, as cones are often destroyed in the process (Saunders et al., 2024). Although, as food availability for Carnaby's peaked on the Swan coastal plain in fuel ages between 25 and 30 years since last fire, it's likely that bird predation may be contributing to cone and follicle loss in older *B. media* stands (36 to 50 years).

Serotiny, stand density and *structure*

Proportion of follicles remaining closed in *B. media* was high (Table 3; strongly serotinous), with 86 ± 3% of follicles remaining closed on ≥7-year-old cones over the chrono-sequence (excluding predated or damaged follicles). This is higher than, but generally consistent with, Wooller and Wooller's (2002a) findings for a 28-year-old *B. media* stand, where 73% of follicles aged 6-10 years remained closed. The proportion of follicles open on *B. media* cones were likely facilitated by the persistence of weathering processes, drought and random limb senescence over plant age (Gill and McMahon, 1986; Wooller et al., 2002b; Lamont, 2020; Morgan et al., 2021). The rate at which these processes occur has been shown by Lamont (2020) to be highly variable both within and between stands, dependent on follicle exposure to the sun, microclimate (arid sites supporting longer follicle closure) and fire regime.

Despite little evidence for inter- fire recruitment (Fig 11), conversion of spontaneous follicle rupture into seedling recruits is most evident in stands 50 years since last fire (Fig 11). Demographic measurements at these sites were indicative of a multi-cohort stand, although its unknown if smaller individuals were new recruits or slow growing plants from the original post-fire cohort constrained by microsite factors (i.e. moisture, nutrients and competition). Anecdotal evidence from Wooller and Wooller (2002a) reports that no successful recruits had been observed in *B. media* stands during 20-years of research in the FRNP, other than after fire. However, gradual increase in seed release as stands age may represent an opportunity for

successful recruitment if a vegetation clearing coincides with high moisture availability (Wooller and Wooller, 2002a). If smaller *B. media* individuals in stands 50 years since last fire are inter-fire recruits (Fig 11), the decrease in plants per hectare between 36 and 50 years (Fig 12) indicates that inter-fire recruitment is not sufficient to replace stands in the absence of fire.

Canopy seed bank development over time

In non-resprouting *Banksia* species, optimal canopy seed bank size at the time of fire is crucial for ensuring maximum recruitment (Lamont and Markey, 1995; Muir et al., 2024). Full seed (i.e. excluding damaged and aborted seeds) estimates determined this occurs at approximately 36 years since last fire in *B. media* (Fig 6). Beyond this plant age, increasing seed predation, abortion and reducing plant density begins to offset the annual accumulation of new seed (Fig 7). This was comparable to *B. ornata* in Australia's south-east, which reports the largest viable seed bank at 34-39 years since last fire despite plants living beyond 50 years of age (Gill and McMahon, 1986; McCarthy et al., 2001; Morgan et al., 2021).

Differences in viability between young (≤6 years) and old (≥ 7 years) seed ages were variable in *B. media* over TSLF, although these differences were ultimately insignificant (Fig 8). This is also reported in the obligate seeding *Banksia hookerina*, with the age of a seed having no impact on its ability to germinate (Enright et al., 1996). Seed viability in *B. media* instead decreased between ≤ 36 and 50 years since last fire (no seed age), reducing from an average of 94% to 82% respectively (Fig 9). Seeds were also impacted by a five-day increase in mean time until germination (MTG) over TSLF (Table 2). However, germination trails conducted by Cochrane et al. (2014b) on *B. media* determined a MTG of less than 23 days was quick when incubated at 15°C. Therefore, as all plant ages were below this, differences in MTG over TSLF were considered negligible (Table 3). Consequently, despite seed viability declining to 82% at 50 years since last fire, viability of intact seed at this plant age remains highly viable in comparisons to other long-lived *Banksia sp* in the FRNP such as *Banksia speciosa;* which

observed a seed viability reduction from 47 % to 35 % between stands 10 and 21 years since last fire (Witowski et al., 1991).

Predicting optimal seed bank size: Plant height as a reproductive predictor

The use of plant size metrics to predict reproductive output has been deemed a more accurate measure over TSLF for some species persisting in fire-prone climate (von Takach Dukai et al., 2018; Andruset et al., 2020; Miller et al., 2025). This is evident in stands of *Allocasuriana humilis*, *Banksia prionotes* and *Banksia attenuata* on the Swan Coastal Plain (Western Australia), where within-site size variability led to diameter at breast height (DBH) and canopy volume being the best predictors of cone counts (Miller et al., 2025). While TSLF was a good indicator of seeds per plant in *B. media*, plant height was deemed a stronger measure (Fig 13, Table S1, Appendix S1). This was likely due to variability in environmental site conditions causing plants to mature at different rates despite being burnt in the same year. This was evident in mean plant height between *B. media* stands 36 years since last fire, where site 1 and 2 (Table 1) were on average 50% taller the same aged stand at site 12 (Table 1, Fig 11).

Allocating seed volume based on plant height (Fig 13) was therefore able to accurately allocate seed volume per plant, with the minimum mean burn height determined at 1.4 m (100 viable seeds per plant) and optimal reproductive height window between 2.6 – 3.2 m (Fig 13). As we could not determine an appropriate minimum burn period from our data, the 100 viable seeds estimated for parent replacement in *B. ornata* and *B. hookerina* was applied to the height – seed predictor (Gill and McMahon, 1986; Enright et al., 1996). Seeds per hectare over TSLF (calculated using the height – seed predictor) peaked at sites 50 years since last fire (Fig 14), despite plants of this age having less viable seed and a lower plant density than *B. media* at 36 years since last fire (Fig 6, Fig 9, Fig 12). The stands ≤36 years since last fire implicated in density surveying were all yet to reach a mean height of ≥ 1.4 m, where at cone sampling sites mean plant height had reached ≥ 1.4 m at 19 years, 36 years and 50 years since last fire (Table

1). The role of micro-climate and soil nutrient in producing these differences across our sites burnt in the same year (and sometimes the same wildfire) is important, although variability between fire interval at each site may also be a contributor (Agne et al., 2022). It's reported that burning plants with underdeveloped seed banks could undermine genetic diversity and therefore tolerance for sub-optimal climatic and soil conditions in the following plant generations (Ayre, et al 2010; Cochrane et al., 2014; Agne et al., 2022). Although, the extent to which this contributed to the 50% height reduction between stands 36 year since last fire is uncertain due to limitations in accessing fire data beyond 1972 (DataWA, 2025). With the current fire history data available, the inter-fire period for all sites 36 years since last fire (1989 wildfires) was determined as 17 years (Table 1, Fig S1, Appendix S1; DataWA, 2025)

CONCLUSIONS

Although *B. media* is listed as a 'non-threatened' species, the current gaps in understanding of the species seed bank development puts it at risk of short-interval fire causing long-term stand decline (Wooller et al., 2002b). It is also projected that changing post-fire rainfall patterns and narrowing germination windows (shortening winter) due to progressive aridification in SWA will increase post-burn seedling mortality (Henzler et al., 2018). It's likely that *B. media* may maintain pre-fire stand numbers when burnt at a mean stand height of 1.4 m (approx. 100 seed per plant). However, to account for potential delays in canopy seed bank maturation and changes in post-burn weather conditions, it's recommended that *B. media* stands in the FRNP are burnt when seed banks are largest and seeds most viable at a mean stand height between 2.6 and 3.2 m. As a word of caution, it's unknown if the time taken to reach this optimal plant height may cause seed bank exhaustion in co-occurring species, such as *Banksia cirsiodes.* Although, as *B. media* was the largest and likely slowest maturing non-respouter within its vegetation community, the time interval taken to reach 1.4 m may be a suitable fire interval for its vegetation community (Gosper et al., 2022). Future research opportunities may include

studying the role of soil nutrients and micro-climate on the development of *B. media* mean stand height and canopy seed banks to the optimal size, or quantifying the pre- and post-seedling density after the first summer at the recently burnt density plots at site 12, 13, 14, 15 and 16. Assuming that seedlings surviving the first summer will reach maturity, this would help determine the conversion rate of seed to mature plants, and close our understanding of the *B. media* life cycle.

FUNDING

This work was supported by the Friends of the Fitzgerald River National Park, who provided $5000 in support of this project.

ACKNOWLEDGEMENTS

Thanks to Gill Craig, Nathan McQuoid and the Friends of the Fitzgerald River National Park for the selection of this project and support throughout. Thankyou also to Andrew Crawford, Simone Dudley and Anne Monoghan from the WA Herbarium for the use of lab space and equipment crucial to the project. Special thanks to Matt McDonald for guidance in surveying methods and Gaine Chiarenza from Curtin University for assistance with R script. Finally, thanks to Dylan Korczynskj, Meredith Korczynskj and Bevan Grant for volunteering their time in the field for cone sampling and density surveying. All sampling of reproductive material was conducted with appropriate licensing approved by the Department of Biodiversity, Conservation and Attractions Albany Office.

LITERATURE CITED

Adeleye MA, Andrew SC, Gallagher R, *et al*. Haberle SG. 2023. On the timing of megafaunal extinction and associated floristic consequences in Australia through the lens of functional palaeoecology. *Quaternary Science Reviews* **316**: 1-11. DOI: 10.1016/j.quascirev.2023.108263

Agne MC, Fontaine JB, Enright NJ. Harvey BJ. 2022. Fire interval and post-fire climate effects on serotinous forest resilience. *Fire Ecology* **18**: 1-20. DOI: 10.1186/s42408-022-00145-4

Andrus RA, Harvey BJ, Hoffman A, Veblen TT. 2020. Reproductive maturity and cone abundance vary with tree size and stand basal area for two widely distributed conifers. *Ecosphere* **11**: 1-16. DOI: 10.1002/ecs2.3092

Atlas of Living Australia, 2026. *Banksia media R.Br.* https://bie.ala.org.au/species/https://id.biodiversity.org.au/node/apni/2912703#overview. Accessed 12 May. 2026.

Ayre D, O'Brien E, Ottewell K, Whelan R. 2010. The accumulation of genetic diversity within a canopy-stored seed bank. *Molecular Ecology* **19**: 2640–2650. DOI: 10.1111/j.1365-294X.2010.04677.x

Beard JS, Chapman AR, Gioia P. 2000. Species richness and endemism in the Western Australian flora. *Journal of Biogeography* **27**: 1257–1268. DOI: 10.1046/j.1365-2699.2000.00509.x

Belcher CM, Hudspith VA. 2017. Changes to Cretaceous surface fire behaviour influenced the spread of the early angiosperms. *New Phytologist* **213**: 1521–1532. DOI: 10.1111/nph.14264

Boer M, Sadler R, Wittkuhn RS, McCaw L, Grierson P. 2009. Long-term impacts of prescribed burning on regional extent and incidence of wildfires. *Forest Ecology and Management* **259**: 132–142. DOI: 10.1016/j.foreco.2009.10.005

Bond WJ, Keeley JE. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**: 387–394. DOI: 10.1016/j.tree.2005.04.025

Bond WJ. 2015. Fires in the Cenozoic: a late flowering of flammable ecosystems. *Frontiers in Plant Science* **5**: 1-11. DOI: 10.3389/fpls.2014.00749

Bowman DM. 2003. Australian landscape burning: a continental and evolutionary perspective. In: Abbott I, Burrows N, eds. *Fire in ecosystems of south-west Western Australia: impacts and management*. Leiden: Backhuys Publishers, 107–118.

Bowman DM, Balch JK, Artaxo P, *et al.* Pyne SJ. 2009. Fire in the Earth system. *Science* **324**: 481-484. DOI: 10.1126/science.1163886

Bowman DM, Murphy BP, Burrows GE, Crisp MD. 2011. Fire regimes and the evolution of the Australian flora. In: Bradstock RA, Gill AM, Williams RJ, eds. *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World.* CSIRO Publishing, 27–48.

Bradshaw SD, Dixon KW, Hopper SD, Lambers H, Turner SR. 2011. Little evidence for fire adapted plant traits in Mediterranean climate regions. *Trends in Plant Science* **16**: 69–76. DOI:10.1093/biolinnean/blaa170

Bradshaw SD, Dixon KW, Lambers H, Cross AT, Bailey J, Hopper SD. 2018. Understanding the long-term impact of prescribed burning in mediterranean-climate biodiversity hotspots. *International Journal of Wildland Fire* **27**: 643–657. DOI: 10.1071/WF18067

Brundrett MC. 2021. One biodiversity hotspot to rule them all: southwestern Australia—an extraordinary evolutionary centre for plant functional and taxonomic diversity. *Journal of the Royal Society of Western Australia* **104**: 1–14. DOI: 10.70880/001c.129578

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

Burrows N, McCaw L. 2013. Prescribed burning in southwestern Australian forests. *Frontiers in Ecology and the Environment* **11**: 25-34 DOI:10.1890/120356

Byrne M, Steane DA, Joseph L, *et al*. 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* **38**: 1635-1656. DOI: 10.1111/j.1365-2699.2011.02535.x

Campbell T, Bradshaw SD, Dixon KW, Zylstra P. 2022. Wildfire risk management across diverse bioregions in a changing climate. *Geomatics, Natural Hazards and Risk* **13**: 2405–2424. DOI: 10.1080/19475705.2022.2119891

Cannon PJ, Clement S. 2025. Why do we burn? Examining arguments underpinning the use of prescribed burning to manage wildfire risk. *People and Nature* **1**: 1-19. DOI: 10.1002/pan3.70146

Causley CL, Fowler WM, Lamont BB, He T. 2016. Fitness benefits of serotiny in fire- and drought-prone environments. *Plant Ecology* **217**: 773–779. DOI: 10.1007/s11258-015-0552-y

Christophel DC, Greenwood, DR. 1989. Changes in climate and vegetation in Australia during the Tertiary. *Review of Palaeobotany and Palynology* **58**: 95-109. DOI: 10.1016/0034-6667(89)90079-1

Cochrane JA, Hoyle GL, Yates CJ, Wood J, Nicotra AB. 2014a. Predicting the impact of increasing temperatures on seed germination among stands of Western Australian Banksia (Proteaceae). *Seed Science Research* **24**: 195–205. DOI: 10.1017/S0960258514000067

Cochrane JA, Hoyle GL, Yates CJ, Wood J, Nicotra AB. 2014b. Evidence of stand variation in drought tolerance during seed germination in four Banksia (Proteaceae) species from Western Australia. *Australian Journal of Botany* **62**: 481–489. DOI: 10.1071/BT14108

Cowling RM, Lamont BB. 1985. Variation in serotiny of three *Banksia* species along a climatic gradient. *Australian Journal of Ecology* **10**: 345–350. DOI: 10.1111/j.1442-9993.1985.tb00899.x

Cowling RM, Lamont BB, Pierce SM. 1987. Seed bank dynamics of four co-occurring *Banksia* species. *Journal of Ecology* **75**: 289–302. DOI: 10.2307/2260419

Craig, GF. 2010. *Fitzgerald River National Park improvement project Culham inlet to Hamersley inlet.* Unpublished report. Main Roads Western Australia. https://www.epa.wa.gov.au/sites/default/files/API_documents/Att%2013%20-%20FloraSurvey_HamersleyDriveRecSites_Craig2010-web.pdf

Crawford AD, Plummer JA, Probert RJ, Steadman KJ. 2011. The influence of cone age on the relative longevity of *Banksia* seeds. *Annals of Botany* **107**: 303–309. DOI: 10.1093/aob/mcq236

DataWA. 2025. *DBCA Fire History (DBCA-060).* https://catalogue.data.wa.gov.au/dataset/dbca-fire-history. Accessed 12th May. 2026.

Davis RA, Valentine LE, Craig MD. 2022. Do bird communities differ with post fire age in Banksia woodlands of southwestern Australia? *International Journal of Wildland Fire* **31**: 621–633. DOI: 10.1071/WF22005

Department of Biodiversity, Conservations and Attractions. 2023. *Fire Management Strategy.* Unpublished report. https://www.dbca.wa.gov.au/media/871/download. Accessed 20th May. 2026.

Department of Biodiversity, Conservation and Attractions. 2026. *Fire ecology of obligate-seeder Eucalypt woodlands in the Great Western Woodlands.* https://www.dbca.wa.gov.au/science/research-projects/fire-ecology-obligate-seeder-eucalypt-woodlands-great-western-woodlands. Accessed 9th May. 2026

Dodson JR, Robinson M, Tardy C. 2005. Two fine-resolution Pliocene charcoal records and their bearing on pre-human fire frequency in south-western Australia. *Austral Ecology* **30**: 592–599. DOI: 10.1111/j.1442-9993.2005.01490.x

Enright NJ, Lamont BB, Marsula R. 1996. Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub Banksia hookeriana. *Journal of Ecology* **84**: 9–17. DOI: 10.2307/2261695

Enright NJ, Mosner E, Miller BP, Johnson N, Lamont BB. 2007. Soil vs. canopy seed storage and plant species coexistence in species-rich Australian shrublands. *Ecology* **88**: 2292–2304. DOI: 10.1890/06-1343.1

Enright NJ, Thomas I. 2008. Pre-European fire regimes in Australian ecosystems. *Geography Compass* **2**: 979–1011. DOI: 10.1111/j.1749-8198.2008.00126.x

Enright NJ, Agne MC. 2025. Climate drying reduces serotinous seed banks and threatens persistence in two fire killed shrubs. *International Journal of Wildland Fire* **34**: 1-14. DOI: 10.1071/WF24046

Environmental Protection Authority. 2016. *Technical guidance: Flora and Vegetation Surveys for Environmental impact assessment.* Technical report. Government of Western Australia. https://www.epa.wa.gov.au/sites/default/files/Policies_and_Guidance/EPA%20Technical%20Guidance%20-%20Flora%20and%20Vegetation%20survey_Dec13.pdf. Accessed 18th May. 2026.

Florabase. 2026. *Banksia media R.Br.* https://florabase.dbca.wa.gov.au/. Accessed 28th Apr. 2026.

Foster CN, Barton PS, MacGregor CI, Catford JA, Blanchard W, Lindenmayer DB. 2018. Effects of fire regime on plant species richness and composition. *Applied Vegetation Science* **21**: 132–143. DOI: 10.1111/avsc.12345

Friends of the Fitzgerald River National Park. 2024. *Botanist Brief: Fitzgerald Biosphere vegetation research for appropriate fire regimes.* Technical report. Government of Western Australia.

https://www.fitzgeraldfriends.org.au/_files/ugd/a8231b_d3ecc2871c2a47caaa567e994cc079dc.pdf. Accessed 12th May. 2026.

Gauthier S, Bergeron Y, Simon JP. 1996. Effects of fire regime on the serotiny level of jack pine. *Journal of Ecology* **84**: 539–548. DOI: 10.2307/2261476

Gill A, McMahon A. 1986. A postfire chrono-sequence of cone, follicle and seed production in Banksia ornata. *Australian Journal of Botany* **34**: 425–433. DOI: 10.1071/BT9860425

Glasspool IJ, Gastaldo RA. 2022. Silurian wildfire proxies and atmospheric oxygen. *Geology* **50**: 1048–1052. DOI: 10.1130/G50193.1

Gosper CR, Kinloch J, Coates DJ, Byrne M, Pitt G, Yates CJ. 2021. Differential exposure and susceptibility to threats based on evolutionary history. *Biological Journal of the Linnean Society* **133**: 373–393. DOI: 10.1093/biolinnean/blab073

Gosper CR, Miller BP, Gallagher RV, *et al*. Yates CJ. 2022. Mapping risk to plant stands from short fire intervals via relationships between maturation period and environmental productivity. *Plant Ecology* **223**: 769–787. DOI: 10.1007/s11258-022-01229-6

Groom PK, Lamont BB. 1997. Fruit–seed relations in *Hakea*: serotinous species invest more dry matter in pre-dispersal seed production. *Australian Journal of Ecology* **22**: 352–355. DOI: 10.1111/j.1442-9993.1997.tb00684.x

Groom PK, Lamont BB. 2015. *Plant life of southwestern Australia: Adaptations for survival,* 1st edn. Berlin: De Gruyter Brill. DOI: 10.1515/9783110370195

He T, Lamont BB. 2018. Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth's flora. *National Science Review* **5**: 237-254. DOI: 10.1093/nsr/nwx041

He T, Lamont BB, Pausas JG. 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews* **94**: 1983–2010. DOI: 10.1111/brv.12544

Henzler J, Weise H, Enright NJ, Zander S, Tietjen B. 2018. A squeeze in the suitable fire interval. *Ecological Modelling* **389**: 41–59. DOI: 10.1016/j.ecolmodel.2018.10.006

Heyes SD, Morgan JW, Sinclair SJ, Walker ZC, Hoebee SE. 2023. Pre-dispersal seed predation affects fruit crop and seed fitness. *Australian Journal of Botany* **71**: 434–442. DOI: 10.1071/BT23011

Hopper SD. 1979. Biogeographical aspects of speciation in the southwest Australian flora. *Annual Review of Ecology and Systematics* **10**: 399–422. DOI: 10.1146/annurev.es.10.110179.002151

Hopper S, Gioia P. 2004. The Southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology, Evolution and Systematics* **35**, 623-650. DOI: 10.1146/annurev.ecolsys.35.112202.130201

Jenkins ME, Morrison DA, Auld TD. 2005. Use of growth characteristics for predicting plant age of three obligate-seeder Proteaceae species. *Australian Journal of Botany* **53**: 101–108. DOI: 10.1071/BT04067

Kelly LT, Fletcher M-S, Oliveras Menor I, *et al*. Bowman DS. 2023. Understanding fire regimes for a better Anthropocene. *Annual Review of Environment and Resources* **48**: 207–235. DOI: 10.1146/annurev-environ-120220-055357

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* **16**: 406–411. DOI: 10.1016/j.tplants.2011.04.002

Keeley JE. 2012. Fire in Mediterranean climate ecosystems. *Israel Journal of Ecology and Evolution* **58**: 123–135. DOI: 10.1560/IJEE.58.2-3.123

Keeley JE, Pausas JG. 2022. Evolutionary ecology of fire. *Annual Review of Ecology, Evolution, and Systematics* **53**: 203–225. DOI: 10.1146/annurev-ecolsys-112921-101402

Ladd PG, Zhao X, Enright NJ. 2022. Fire regime and climate determine spatial variation in level of serotiny and stand structure in a fire-killed conifer. *Plant Ecology* **223**: 849–862. DOI: 10.1007/s11258-022-01243-8

Lambers H, de Britto Costa P, Cawthray GR, *et al*. Zhong H. 2022. Strategies to acquire and use phosphorus in phosphorus-impoverished environments. *Plant and Soil* **476**: 133–160. DOI: 10.1007/s11104-022-05464-8

Lamont BB. 1985. Fire responses of sclerophyll shrublands – a stand ecology approach with particular reference to the genus Banksia. In: Ford JR, eds. *Fire ecology and management in Western Australian ecosystems.* Perth: Curtin University, 41-46.

Lamont BB, Connell SW, Bergl SM. 1991a. Seed Bank and Stand Dynamics of Banksia cuneata: The Role of Time, Fire, and Moisture. *Botanical Gazette* **152**: 114–122. DOI: 10.1086/337870

Lamont BB, Le Maitre DC, Cowling RM, Enright NJ. 1991b. Canopy seed storage in woody plants. *Botanical Review* **57**: 277–317. DOI: 10.1007/BF02858770

Lamont BB, Markey A. 1995. Biogeography of fire-killed and resprouting *Banksia* species. *Australian Journal of Botany* **43**: 283–303. DOI: 10.1071/BT9950283

Lamont BB, Enright NJ. 2000. Adaptive advantages of aerial seed banks. *Plant Species Biology* **15**: 157–166. DOI: 10.1046/j.1442-1984.2000.00036.x

Lamont BB, He T. 2012. Fire adapted Gondwanan angiosperm floras evolved in the Cretaceous. *BMC Evolutionary Biology* **12**: 1-10. DOI: 10.1186/1471 2148 12 223

Lamont BB, He T. 2017a. When did a Mediterranean-type climate originate in southwestern Australia? *Global and Planetary Change* **156**: 46–58. DOI: 10.1016/j.gloplacha.2017.08.004.

Lamont BB, He T. 2017b. Fire proneness as a prerequisite for the evolution of fire adapted traits. *Trends in Plant Science* **22**: 278–288. DOI: 10.1016/j.tplants.2016.11.004

Lamont BB, He T, Yan Z. 2019. Evolutionary history of fire-stimulated resprouting, flowering, seed release and germination. *Biological Reviews* **94**: 903–928. DOI: 10.1111/brv.12483

Lamont BB, Pausas JG, He T, Witkowski ETF, Hanley ME. 2020. Fire as a selective agent for both serotiny and nonserotiny over space and time. *Critical Reviews in Plant Sciences* **39**: 140–172. DOI: 10.1080/07352689.2020.1768465

Lamont BB. 2021. Evaluation of seven indices of on plant seed storage (serotiny) shows that the linear slope is best. *Journal of Ecology* **109**: 4–18. DOI: 10.1111/1365 2745.13436

Lamont BB. 2023. To burn, or not to burn: That is the question. *Trends in Ecology & Evolution* **38**: 1119–1121. DOI: 10.1016/j.tree.2023.09.010

Lange J, Gillespie J. 2023. Bushfire, prescribed burning, and non-human protection. *Geographical Research* **61**: 169–192. DOI: 10.1111/1745-5871.12558

Maikano GN, Cohn J, Di Stefano J. 2018. Are germination cues for soil-stored seed banks different in structurally different fire-prone communities? *Austral Ecology* **43**: 89–101. DOI: 10.1111/aec.12546

McCarthy MA, Possingham HP, Gill AM. 2001. Using stochastic dynamic programming to determine optimal fire management for *Banksia ornata*. *Journal of Applied Ecology* **38**: 585–592. DOI: 10.1046/j.1365-2664.2001.00617.x

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

Meehan M, Keirsten-Wakefield A, Cowan M, Atkinson J. 2015. Premature opening and dimorphism in *Hakea decurrens* follicles. *The Victorian Naturalist* **132**: 139–146. DOI: NA

Middleton ND, Ladiges PY, Enright NJ. 1996. Stand ecology of *Banksia saxicola* (Proteaceae). *Proceedings of the Royal Society of Victoria* **108**: 43–56. DOI: NA

Midgley JJ, Bond WJ. 2013. Plant adaptations to fire. In: Belcher CM, eds. *Fire phenomena and the Earth system*. Wiley. DOI: 10.1002/9781118529539.ch7

Millar MA, Coates DJ, Byrne M, Krauss SL, Jonson J, Hopper SD. 2020. Evaluating restoration outcomes through assessment of pollen dispersal, mating system and genetic diversity. *Restoration Ecology* **29**: 1-13. DOI: 10.1111/rec.13335

Miller RG, Enright NJ, Fontaine JB, Merritt DJ, Miller BP. 2024. Plant life history data as evidence of an historical mixed severity fire regime in Banksia woodlands. *Australian Journal of Botany* **72**: DOI: 10.1071/BT23098

Miller RG, Enright NJ, Merritt DJ, Miller BP, Fontaine JB. 2025. Using patterns of post fire plant reproduction to inform minimum fire intervals for conservation management in a fire prone woodland. *Austral Ecology* **50**: 1-21. DOI: 10.1111/aec.70023

Mooney SD, Harrison SP, Bartlein PJ, *et al*. Williams N. 2011. Late Quaternary fire regimes of Australasia. *Quaternary Science Reviews* **30**: 28–46. DOI: 10.1016/j.quascirev.2010.10.010

Moore S, Cavana M, Gillen K, *et al*. Schmidt W. 1991. *Fitzgerald River National Park: management plan 1991–2001*. Perth: Department of Conservation and Land Management, Australia. https://researchportal.murdoch.edu.au/esploro/outputs/report/Fitzgerald-River-

National-Park-management-plan/99100554220480789 1#file-0. Accessed 13th May 2026.

Morgan JW, McCarthy MA, Willocks E. 2020. Does intraspecific variation in demography have implications for fire management of an obligate seeder shrub across its geographic range? *Austral Ecology* **46**: 315–323. DOI: 10.1111/aec.12981

Muir AM, Amos NN, Moloney PD. 2024. High fire severity and frequency threaten a widespread obligate-seeder *Banksia*. *Australian Journal of Botany* **72**: 1-12. DOI: 10.1071/BT24048

Mutch RW. 1970. Wildland fires and ecosystems – a hypothesis. *Ecology* **51**: 1046-1051. DOI: 10.2307/1933631

Murphy BP, Bradstock RA, Boer MM, *et al.* Bowman DJ 2013. Fire regimes of Australia: a pyrogeographic model system. *Journal of Biogeography* **40**: 1048–1058. DOI: 10.1111/jbi.12065

Nolan RH, Collins L, Leigh A, *et al*. Bradstock R. 2021. Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment* **44**: 3471–3489. DOI: 10.1111/pce.14176

Ottaviani G, Beckett H, Costa-Saura JM, *et al*. Millan M. 2026. Not only reseeder or resprouter plants: trait syndromes and post-fire responses. *Plant Biology Journal*. 1-12. DOI: 10.1111/plb.70213

Pausas JG, Keeley JE. 2009. A burning story: the role of fire in the history of life. *BioScience* **59**: 593–601. DOI: 10.1525/bio.2009.59.7.10

Pausas JG, Schwilk D. 2012. Fire and plant evolution. *New Phytologist* **193**: 301–303. DOI: 10.1111/j.1469-8137.2011.03957.x

Pausas JG, Keeley JE. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol* **204**: 55-65. DOI: 10.1111/nph.12921

Pausas JG, Lamont BB. 2022a. Fire-released seed dormancy: a global synthesis. *Biological Reviews* **97**: 1612–1639. DOI: 10.1111/brv.12855

Pausas JG, Lamont BB, Keeley JE, Bond WJ. 2022b. Bet-hedging and best-bet strategies shape seed dormancy. *New Phytologist* **236**: 1232–1236. DOI: 10.1111/nph.18436

Penman TD, Christie FJ, Andersen AN, *et al*. York A. 2011. Prescribed burning: how can it work to conserve the things we value? *International Journal of Wildland Fire,* **20** 721-733. DOI: 10.1071/WF09131

QGIS. 2025. *QGIS Geographic Information System.* QGIS Association. http://www.qgis.org

R Core Team. 2025. *R: A Language and Environment for statistical computing*. R Foundation for Statistical Computing

Ranstam J, Cook JA. 2022. Quantiles. *British Journal of Surgery* **109**: 783-783. DOI: 10.1093/bjs/znac030

Rathbone, D. 2013. *Flora Survey of the Coastal Catchments and Ranges of the Fitzgerald River National Park*. Unpublished report. Department of Environment and Conservation, Western Australia. https://library.dbca.wa.gov.au/FullTextFiles/627702.pdf

Walker LR, Wardle DA, Bardgett RD, Clarkson BD. 2010. The use of chrono-sequences in studies of ecological succession and soil development. *Journal of Ecology* **98**: 725–736. DOI: 10.1111/j.1365-2745.2010.01664.x

Wickham H. 2016. *ggplot2: Elegant graphics for data analysis,* 2nd edn. New York: Springer. DOI 10.1007/978-3-319-24277-4

Williams LJ, Gallagher RV, Rifai SW, *et al*. Medlyn BE. 2026. Detecting and attributing climate change effects on vegetation: Australia as a test case. *Plants, People, Planet* **8**: 461–485. DOI: 10.1002/ppp3.70090

Witkowski ETF, Lamont BB, Connell SJ. 1991. Seed bank dynamics of three co-occurring banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and inter-fire establishment. *Australian Journal of Botany* **39**, 385–397. DOI: 10.1071/ BT9910385

Wood SN. 2017. *Generalized Additive Models: An Introduction with R*, 2nd edn. New York: Chapman and Hall/CRC. DOI: 10.1201/9781315370279

Wooller SJ, Wooller RD. 2002a. Mixed mating in Banksia media. *Australian Journal of Botany* **50**: 627-631. DOI: 10.1071/BT01075

Wooller SJ, Wooller RD, Brown KL. 2002b. Regeneration by three species of Banksia on the south coast of Western Australia in relation to fire interval. *Australian Journal of Botany* **50**: 311–317. DOI: 10.1071/BT01078

Santos F, Bailey JK, Schweitzer JA. 2023. The eco-evolutionary role of fire in shaping terrestrial ecosystems. *Funct Ecol* **37**: 2090-2095. DOI: 10.1111/1365-2435.14387

Saunders DA, Mawson PR, Dawson R, Beswick H, Pickup G, Usher K. 2024. Movements of adult and fledgling Carnaby's cockatoos (Zanda latirostris Carnaby, 1948) from eleven breeding areas throughout their range. *Pacific Conservation Biology* **30**: 1-15. DOI: 10.1071/PC24042

Scott J. 1982. The impact of destructive insects on reproduction in six species of *Banksia L.f.* (Proteaceae). *Australian Journal of Zoology* **30**: 901–921. DOI: 10.1071/ZO9820901

Tangney R, Merritt DJ, Fontaine JB, Miller BP. 2019. Seed moisture content as a primary trait regulating the lethal temperature thresholds of seeds. *J Ecol* **107**: 1093–1105. DOI: 10.1111/1365-2745.13095

Taylor A, Hopper S. 1988. *The Banksia Atlas,* 8th edn. Canberra: AGPS Canberra.

von Takach Dukai B, Lindenmayer DB, Banks SC. 2018. Environmental Influences on Growth and Reproductive Maturation of a Keystone Forest Tree: Implications for Obligate Seeder Susceptibility to Frequent Fire. *Forest Ecology and Management* **411**: 108–119. DOI: 10.1016/j.foreco.2018.01.014.

Yan Z, Shao L, Glasspool IJ, Wang J, Wang X, Wang H. 2019. Frequent and intense fires in the final coals of the Paleozoic indicate elevated atmospheric oxygen levels at the

onset of the End-Permian Mass Extinction Event. *International Journal of Coal Geology* **207**: 75–83. DOI: 10.1016/j.coal.2019.03.016

APPENDIX S1

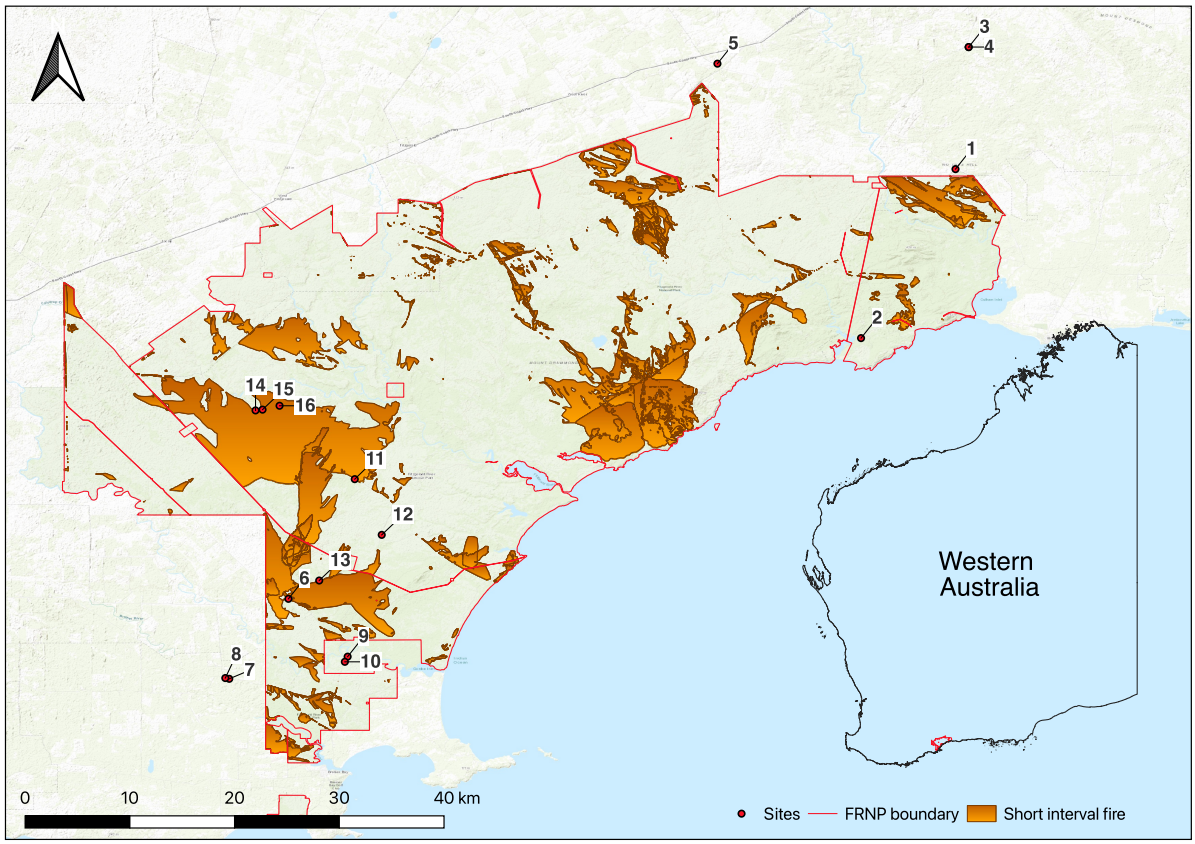

FIG S1. Short fire interval (<15 years) in the Fitzgerald River National Park (FRNP), orange scars represent where one or more fires have occurred at an interval of <15 years since 1972 (fire history accurate as of September 2025). Red dots and site numbers describe the locations of cone and density sampling. Fire interval history for sites outside the FRNP was not determined as they were improvised due to dieback restrictions in place at the first field trip. Produced following the methodology from Wittkuhn & Hamilton (2010).

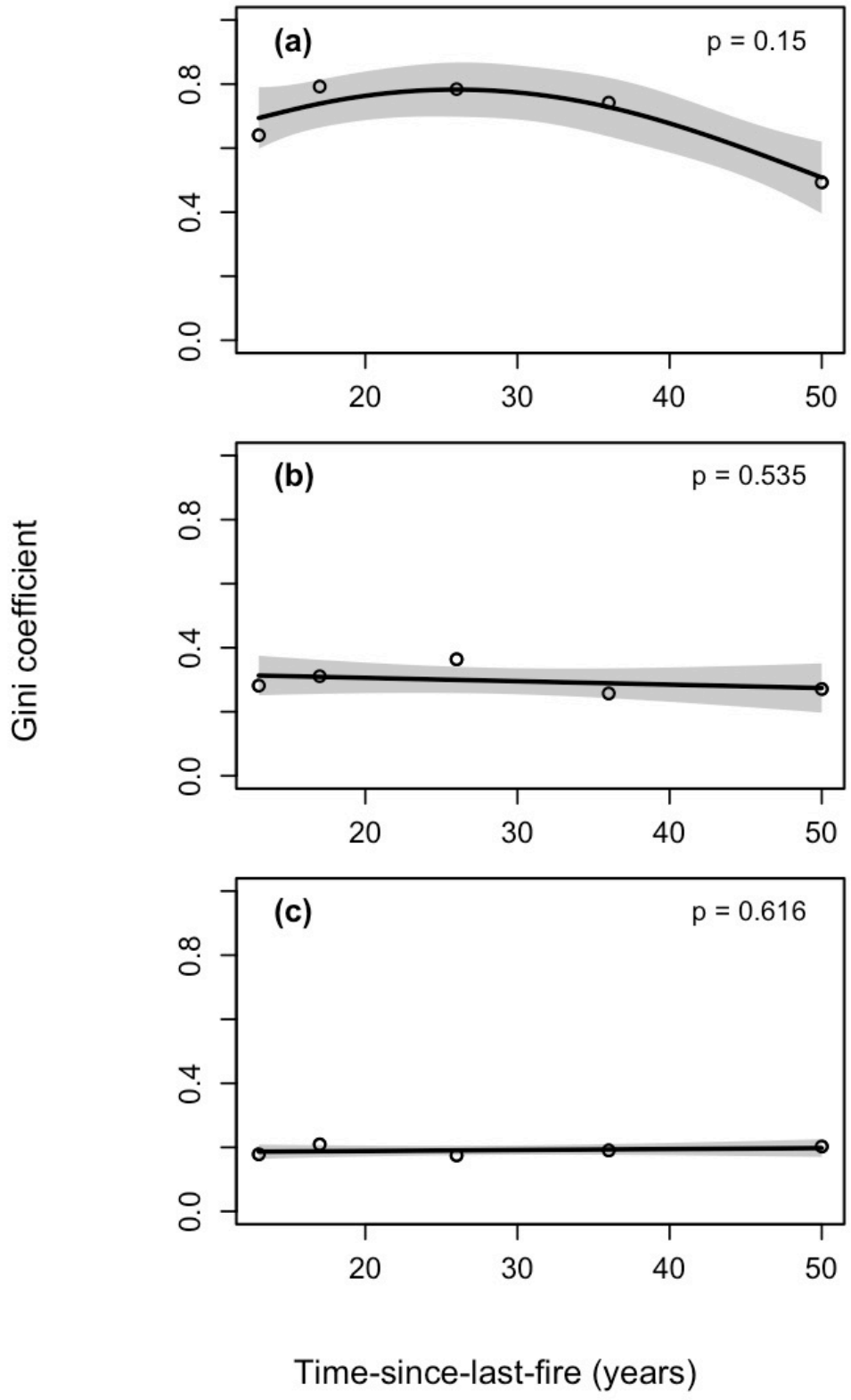

FIG S2. Gini coefficient values for (a) canopy volume, (b) stem width and (c) height. Permutation index (PI) not reported as values were identical to Gini. *P* values are reported within plots and sample size for each plot is n = 5.

TABLE S1. Top-ranking negative binomial generalised additive models (GAMs) for predicting viable seed volume per plant with height, stem diameter, time since last fire (TSLF) and canopy volume).

Size metric	AIC	Dev	EDF	P	ΔAIC	Rank
Height	559	0.46	1.94	>0.01	0	1
Stem	566	0.38	1.99	>0.01	7	2
TSLF	578	0.21	1.99	>0.01	19	3
Canopy volume	582	0.15	1.99	>0.01	23	4