Influence of fire history on reproductive traits in a congeneric obligate seeder and facultative resprouter tree species

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Abstract

In fire-prone regions globally, evolution of plant traits that confer resilience to historical fire regimes is widespread. However, many common plant species are currently declining due to a mismatch between historical and contemporary fire regimes. These changes threaten long term community trajectories of plants and the animal species relying on them for food or habitat. Understanding plant responses to fire at critical life stages is needed to improve conservation of plant-animal interactions. We investigated how fire history affected reproductive traits (i.e., proportion germination, time to 50% germination, reproductive output, population age structure) relevant to critical life history stages of *Allocasuarina littoralis* and *A. torulosa* (Casuarinaceae). In southeast Queensland, Australia, these species are primary food trees of the nationally vulnerable Glossy black-cockatoo (*Calyptorhynchus lathami*, Cacatuidae). For both species, fire-cues (heat and smoke) did not increase the proportion of seed germinated, but proportion germination increased with seed weight. Heavier seeds were associated with exposure to more extreme environments such as environments with higher fire frequencies and temperature variability. In *A. torulosa*, seed weight generally increased germination time, except when seeds were collected from frequently burned sites which could be linked to a trade-off between resprouting and seed production. Heat and smoke slowed germination of *A. torulosa* (recorded as time to 50% germination) but had no effect on *A. littoralis*. Fire history did not influence reproductive output or population age structure in either species, but reproductive output was greater in sites with more woody vegetation cover, potentially reflecting greater establishment success. For restoration, our results indicate that fire is not necessary for successful germination in *A. littoralis* or *A. torulosa*, but when collecting seeds the local fire history and seed weight should be considered, especially for *A. torulosa*. Our results can inform Glossy black-cockatoo conservation by guiding fire management practices associated with their food trees.

Introduction

The regeneration niche of plant species defines the climatic (e.g., temperature and precipitation) and environmental (e.g., nutrient availability, interspecific competition and allelopathy) conditions which control seed production, germination, establishment, and transitions from early life stages to adulthood (Grubb 1977; Pérez-Ramos *et al.* 2012; Poorter

2007; Smith *et al.* 2016). Given the close relationship between plant fitness and reproduction, the regeneration niche places reproductive traits under stronger selection pressure than vegetative traits (Campbell *et al.* 2022; Keeley *et al.* 2011; Villellas *et al.* 2021). This stronger selection on reproductive traits is reflected in fire-driven evolution of traits such as post-fire reproductive mode, fire-cued germination responses, and serotiny which increase plant species fitness for their historical fire regimes (Gill 1977; Gómez-González *et al.* 2011; Keeley and Pausas 2022; Pausas *et al.* 2004). However, contemporary fire regime changes are likely to shift the regeneration niche, potentially resulting in trait misalignments, due to changes in seasonality, frequencies, intensities, durations, and scales of fire (Dowdy *et al.* 2019; Le Page *et al.* 2017; Moritz *et al.* 2012). Contemporary fire regime changes are a key threatening process resulting in declining abundances and range sizes of plants, even for previously common and widespread species (Enright *et al.* 2015; Fairman *et al.* 2016; Gaston and Fuller 2007; Grau-Andrés *et al.* 2024; Le Breton *et al.* 2022). Thus, understanding plant responses to fire throughout their life cycle is critical, especially at early life stages and through transitions to adulthood (Smith *et al.* 2016).

In fire-prone ecosystems, post-fire reproductive modes can be divided broadly into resprouters, which survive through tissue structures below bark or soil (R+); or obligate seeders which are killed by fire but persist through propagules (i.e., seed) stored in soil or canopy seedbanks (P+) (Clarke *et al.* 2015; Pausas *et al.* 2004; Pausas and Keeley 2014). These strategies result in contrasting life histories: resprouters are long-lived with low population turnover, whereas obligate seeders are short-lived with high population turnover (Pausas *et al.* 2004; Pausas and Keeley 2014). Resprouters generally have lower seed production and seedling densities than seeders, and higher investment in resprouting tissue production may slow maturation rates (Bendall *et al.* 2022; Hunter 2003; Ojeda *et al.* 2016; Pausas *et al.* 2004; Pausas and Keeley 2014; Verdú 2000; Whelan *et al.* 2002). Thus, resprouters show a trade-off between seed investment and resprouting responses (Bendall *et al.* 2022; Hunter 2003; Ojeda *et al.* 2016; Pausas *et al.* 2004; Pausas and Keeley 2014; Verdú 2000; Whelan *et al.* 2002). Conversely, obligate seeders have high seed production and high seedling densities, with mass recruitment events post-fire (Hunter 2003; Keith *et al.* 2002; Ojeda *et al.* 2016; Pausas and Keeley 2014).

Population age structure, defined as the distribution of age classes within a population (hereafter ‘age class structure’) (Li and Barclay 2001; Taylor 2010), consequently varies across these contrasting post-fire reproductive modes. After fire, obligate seeders tend to form even aged-cohorts resulting from mass recruitment events, while resprouters tend to maintain their pre-fire age class structure and form multi-aged cohorts (McCarthy *et al.* 1999; Pausas and Keeley 2014; Taylor 2010). Consequently, short interval fires relative to the lifespan of obligate seeders can shift populations into younger states, a phenomenon observed in *Eucalyptus regnans* (Myrtaceae) (McCarthy *et al.* 1999). Such shifts can leave populations of obligate seeders more susceptible to an immaturity risk as frequent short interval fire can compromise their ability to reach reproductive maturity and increase the potential for localised extinctions (Agne *et al.* 2022; Keith 1996; McColl-Gausden *et al.* 2022; Pausas and Keeley 2014). In resprouters, shifts in age class structure can result from extremely short or long fire return intervals as these species require time to replenish bud banks and produce protective bark, but have reduced capacity to initiate shoots with age (Christensen *et al.* 1981; Clarke *et al.* 2015; Gill and Catling 2002). However, fire at appropriate intervals remains critical for obligate seeders and resprouters to cue regeneration, promote seedling establishment, and stimulate flowering (Agne *et al.* 2022; Enright *et al.* 2011; McCarthy *et al.* 1999; Taylor 2010; Thomsen and Ooi 2022; Zirondi *et al.* 2021). Thus, fire and post-fire reproductive mode act as strong drivers of age class structure but few studies examine these effects in closely related obligate seeders and resprouters (e.g., Ojeda *et al.* 2016; Schmidberger and Ladd 2020).

Regeneration from seed is a critical population process for obligate seeders; and also for resprouters to enable successful colonisation of new sites or recolonisation after local extinction (Bellingham and Sparrow 2000; Kennard *et al.* 2002; Pausas and Keeley 2014). Therefore, seeds must possess traits conferring resilience to fire and other environmental stressors (Bradshaw *et al.* 2011; Rosbakh *et al.* 2023; Tangney *et al.* 2020). Seed traits show substantial variability (Fenollosa *et al.* 2021; Helsen *et al.* 2017; Pausas *et al.* 2024); for example, seed size can vary widely between populations and species due to differential selection from dispersal mode (wind, water, or animal), growth form (tree, shrub or grass), and environmental attributes (climate and vegetation structure) (Moles *et al.* 2005; Sims 2012). Fire can drive selection on seed size due to its relation to heat tolerance with larger seeds providing greater insulation to embryos (Escudero *et al.* 2000; Gómez-González *et al.* 2011; Lamont *et al.* 2019; Pausas and Lamont 2022). Conversely, smaller seeds are associated with higher reproductive output in obligate seeders and might be selected under certain fire regimes (Verdú 2000). Therefore, exposure to more frequent or intense fire may result in development of larger seeds in these species (or populations) than close relatives in environments with lower fire activity, but this likely depends on post-fire reproductive mode (Escudero *et al.* 2000; Gómez-González *et al.* 2011; Lamont *et al.* 2019; Pausas and Lamont 2022; Verdú 2000). Studying closely related species with differing post-fire reproductive modes can help disentangle the role of fire in trait variation and germination because differences can be explained by environmental variation and trait variation rather than phylogeny (Cortés-Flores *et al.* 2020; Fenollosa *et al.* 2021; Seglias *et al.* 2018; Wang *et al.* 2016; Zhao *et al.* 2021). However, only a few studies have investigated the role of fire and post-fire reproductive mode in driving reproductive trait variability (e.g., Tangney *et al.* 2020), especially in phylogenetically related species (e.g., Ojeda *et al.* 2016; Schmidberger and Ladd 2020).

Contemporary changes in fire regimes are causing misalignments between plant trait variability and fire regime characteristics (Canadell *et al.* 2021; Day *et al.* 2020; Harvey and Enright 2022; Johnstone *et al.* 2016; Kelly *et al.* 2025; Moritz *et al.* 2012). For example, fires in sclerophyllous vegetation ecosystems have increased in severity, such that even species with well-established fire adaptations (i.e., resprouting or fire-cued germination) can fail to regenerate (Bennett *et al.* 2016; Etchells *et al.* 2020; Sano *et al.* 2025). These declines may impact plant-animal or trophic interactions, as plants are strong drivers of community structure and function (Ballarin *et al.* 2024; Carbone *et al.* 2019; Ellison 2019; Kelly *et al.* 2020; Rainsford *et al.* 2020; Smith 2018). Specialist interactions are most vulnerable to these declines; yet are drastically understudied in fire ecology (Charles *et al.* 2025). Whether trees can adapt in situ to fire regime changes is unclear, as more extreme climatic conditions have led to declining post-fire regeneration success (Kelly *et al.* 2025; Stevens-Rumann *et al.* 2018; Young *et al.* 2019). Therefore, understanding how plants respond to fire requires an understanding of species' responses to local and recent fire history. There has been much lab-based research on fire-cued germination responses (reviewed in Hodges *et al.* 2021; Moreira *et al.* 2010; Newton *et al.* 2021; Ooi *et al.* 2014; Younis and Kasel 2023). However, fire history from the seed collection site has infrequently been included in fire-cued germination analyses (e.g., Gómez-González *et al.* 2016; Gómez-González *et al.* 2011; Kasel *et al.* 2024; Plumanns-Pouton *et al.* 2024; Vandvik *et al.* 2014; Zaki *et al.* 2021) and often from only recent short term fire histories (e.g., <1 to 15 years post-fire, Amoako and Gambiza 2021; Dawe *et al.* 2022; Luo *et al.* 2022; Schmidberger and Ladd 2020; Zimmer *et al.* 2021; Zimmermann *et al.* 2008). To determine whether enough trait variability exists to allow species to respond to contemporary fire regime changes, we require more studies of critical regeneration stages (i.e., germination and transitions through seedlings and saplings to adults) where short-term (1-10 years) and multi-decadal (30 or more years) fire histories are known.

I investigated the influence of fire on reproductive trait variation in two congeneric species with differing post-fire reproductive modes: the obligate seeder *Allocasuarina littoralis* and the facultative resprouter *Allocasuarina torulosa* (Casuarinaceae). These *Allocasuarina* species are common across eastern Australia, where they form mixed stands with *Eucalyptus spp*.. *Allocasuarina littoralis* typically occurs in swamps and eucalypt woodlands and forests, and *A. torulosa* in wet eucalypt forests (Atlas of Living Australia 2021a; Atlas of Living Australia 2021b; Neldner *et al.* 2019). The distributions of these species overlap, extending from the coast to *ca.* 300 km inland. *Allocasuarina torulosa* extends from Cairns to Sydney with a small population in Cape York Peninsula in far-north Queensland. *Allocasuarina littoralis* has a broader range, from far-north Queensland to the Fleurieu Peninsula in South Australia (Atlas of Living Australia 2021a; Atlas of Living Australia 2021b). Fire management guidelines are often based on the *Eucalyptus* species which co-occur with Casuarinaceae, but eucalypts require different fire regime conditions than she-oaks (Kellman 1986; Moss *et al.* 2011; Neldner *et al.* 2019; Stewart and Moss 2015). Although these *Allocasuarina* species are common and widespread, their seeds are primary food resources for the dietary specialist Glossy black-cockatoos, *Calyptorhynchus lathami* (Cacatuidae) (listed nationally as Vulnerable, *EPBC* Act 1999), which has one of the most specialised diets of all Australian birds (Chapman 2007; Menkhorst *et al.* 2024). Thus, understanding the fire ecology of *Allocasuarina spp.* is fundamental to effective conservation for these cockatoos.

Reproductive traits investigated were: germination rates in response to heat and smoke treatments (i.e., proportion germination, time to 50% germination); age class structure (i.e., ratio of seedlings and/or saplings to adults); seed size (i.e., seed weight); and female reproductive output. Proportion of seeds that germinated was used as a measure of an individual trees resilience to seed treatments, with higher proportions of germinated seeds indicating higher resilience. Time to 50% germination was used as a measure of an individual's competitiveness, such that less time to reach 50% germination indicated faster establishment, and thus, a higher competitiveness. Seed weight was used as a measure of seed size and related to an individuals' investment in sexual reproduction. These traits were analysed in relation to fire regime variables, at the site where seeds were collected, that could drive short-term ecological responses (e.g., time since last fire), and longer-term evolutionary responses (e.g., responses to multiple fire events – fire frequency) (Fig. 1).

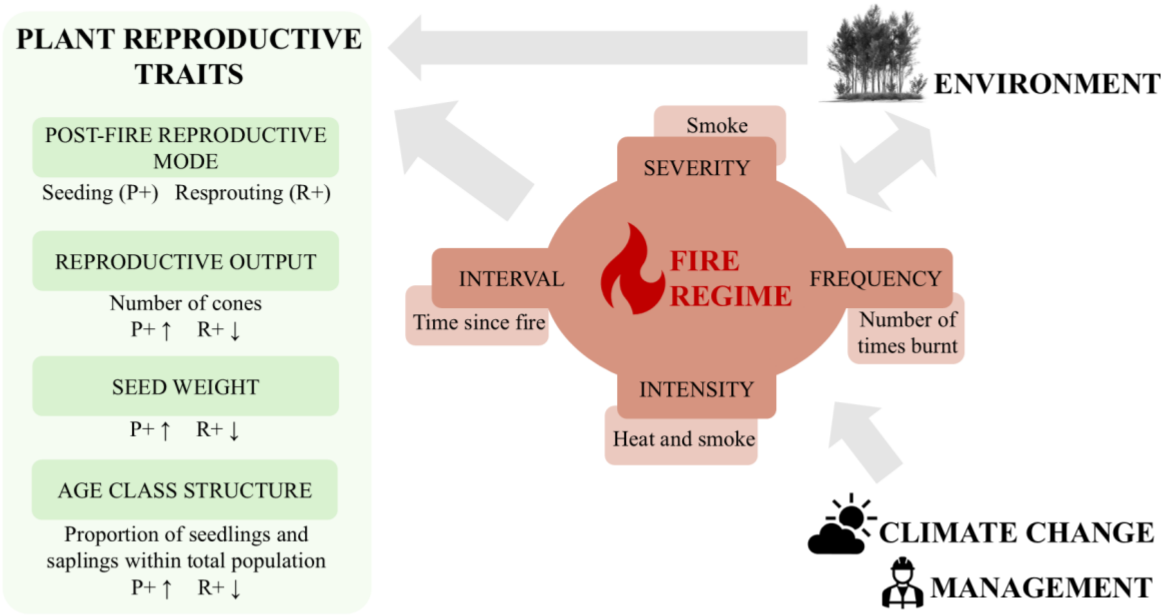

Figure 1 Conceptual diagram showing the relationship between plant reproductive traits, fire regime attributes, environmental attributes, climate change, and management. Plant-reproductive trait arrows relate to my hypotheses regarding plant trait responses between differing post-fire reproductive modes to increasing fire frequency. I expected reproductive output, seed weight, and age class structure to increase with fire frequency in the obligate seeder and decrease in the facultative resprouter.

I first aimed to determine how contemporary fire frequency, and post-fire reproductive mode, affected fire-cued germination responses and seed size. (**H1**) I expected that post-fire reproductive mode would shape fire-cued germination responses and seed investment, with higher seed investment and tolerances in *A. littoralis* (obligate seeder) than *A. torulosa* (facultative resprouter). *Allocasuarina littoralis* was expected to have higher seed investment with a larger quantity of smaller seeds, which would increase in environments with increasing fire frequencies, high germination rates in response to heat and smoke, and a higher lethal temperature threshold (Paula and Pausas 2008; Pausas and Keeley 2014). *Allocasuarina torulosa* was expected to have lower seed investment, which would reduce with increasing fire frequency, lower germination rates in response to heat and smoke, and a lower lethal temperature threshold (Paula and Pausas 2008; Staden *et al.* 2000). Exposure to frequent fire was expected to correspond with an increase in seed weight for *A. littoralis*, but an decrease in seed weight in *A. torulosa* due to a trade-off between seed production and resprouting capacity (Bellingham and Sparrow 2000; Pausas and Keeley 2014).

Second, I aimed to determine how fire frequency, time since fire, and post-fire reproductive mode influenced age class structure and reproductive output (i.e., number of cones). (**H2**) I expected that longer times since fire and low fire frequencies would reduce the proportions of plants in younger age classes (i.e., seedling and sapling age classes) but increase reproductive output. (**H2a**) Due to the immaturity risk of the obligate seeding mode of reproduction, I expected high fire frequencies and short times since fire would result in fewer plants in younger age classes in *A. littoralis* than *A. torulosa*. (**H2b**) I also expected that higher fire frequencies and short times since fire would reduce reproductive output due to stem or cone consumption by fire and reduced capacity to reach reproductive maturity during inter-fire periods (Enright and Lamont 1989; Pausas and Keeley 2014).

Third, I aimed to investigate how environmental attributes relating to site productivity (topographic wetness, quantifying water availability (Gallant and Austin 2012); foliage projective cover, quantifying the percentage of the ground covered by woody vegetation; thus, photosynthetic potential (Fisher *et al.* 2018)) and climatic attributes (latitude; precipitation seasonality and temperature seasonality, quantifying annual range trends (Noce *et al.* 2020; Wang *et al.* 2024)) interacted with fire regimes to influence reproductive trait variation. (**H3**) I expected environments with low site productivity and increasing climatic variability would be associated with more stressful environments, reducing reproductive output, seed weights, and proportions of younger age classes (Enright *et al.* 2015; McColl-Gausden *et al.* 2022). Additionally, as lower latitudes are associated with increased temperatures, promoting photosynthesis, growth and reproductive processes, I expected these sampling locations to have higher reproductive outputs, seed weights and proportions of younger age classes (Chamorro *et al.* 2018; Käber *et al.* 2021; Moles and Westoby 2003; Wang *et al.* 2023).

Methods

Study region

This study took place in southeast Queensland, Australia, within the distributions of *Allocasuarina littoralis* and *A. torulosa*. The Glossy black-cockatoo is a dietary specialist in eastern Australia, listed as vulnerable (*EPBC* Act 1999) (Department of Climate Change 2022). These cockatoos feed exclusively on a subset of species (12 of 78 species) in the Casuarinaceae family (Chapman 2007) including the two examined here. Glossy black-cockatoos are notoriously cryptic, shifting their feeding locations in response to a range of unknown environmental cues (similar to other nomadic bird species, Webb et al. 2014).

Sampling locations included public land (i.e., national parks and state forests) and private properties such as Hidden Vale Nature Refuge, Dwyers Scrub Conservation Park, Gillies Ridge Nature Refuge, Bartopia Nature Refuge, and Bulimbah Nature Refuge (Fig. 2). The region has a temperate climate with mean maximum temperatures in summer ranging from 25 °C to 32 °C, and winter from 17 °C to 21 °C. The mean annual rainfall in the region ranges from 688 mm to 1584 mm. In my inland study region in southeast Queensland, *A. torulosa* is more common than *A. littoralis* (Atlas of Living Australia 2021a; Atlas of Living Australia 2021b). Dominant vegetation included eucalypt woodland to open forests for *A. littoralis* and *A. torulosa* sampling locations, and wet eucalypt forests for *A. torulosa* sampling locations (Neldner *et al.* 2019). At these sampling locations, the dominant soil orders included tenosols, sodosols and dermosols and soil types included volcanics; red soils; sandstone; and igneous, Cainozoic and sedimentary rocks (Neldner *et al.* 2019).

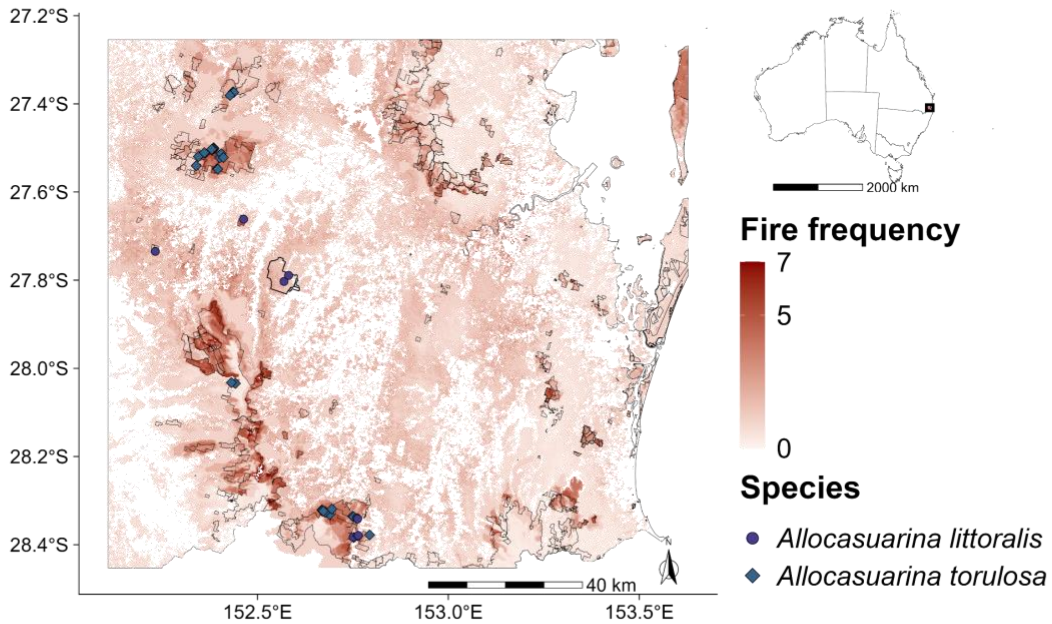

Figure 2 Sampling locations of two *Allocasuarina* species in southeast Queensland, Australia. Protected areas are displayed with black outlines including public land (state forests and national parks) and privately managed nature refuges. Fire frequency between 1987-2023 is shown in red shading (see Charles *et al.* 2025 under review) and ranged from 0 to 11 fires in the past 36 years for the study region, with white representing areas mapped as unburnt. To aid visualisation of fire frequency variation between my sampling transects, fire frequency was rescaled so areas burnt 7 or more times are represented by the darkest shade of red.

Allocasuarina littoralis and *A. torulosa* are dioecious trees growing 5 to 15 m and 5 to 30 m tall, respectively (Australian Biological Resources Study. Advisory Committee 1989; Spencer 1995). *Allocasuarina littoralis* has a more coastal distribution on sandy, heavy clay, or stony soils (Australian Biological Resources Study. Advisory Committee 1989; Foreman and Walsh 1993) while *Allocasuarina torulosa* may be found in coastal regions but is also common in forests on fertile soils (Australian Biological Resources Study. Advisory Committee 1989; Stanley *et al.* 1983). *Allocasuarina littoralis* has an average longevity of 50-70 years but may live for >500 years, while *A. torulosa* has a longevity of 500 years (Falster *et al.* 2021; Kattge *et al.* 2020). Reproductive maturity is usually reached in five years for both species, but *A. littoralis* may take 10 years (Falster *et al.* 2021; Kattge *et al.* 2020). Both species gradually release seed from serotinous cones as they dry, allowing recruitment in the absence of fire (Crowley 1986; Falster *et al.* 2021; Kattge *et al.* 2020). *Allocasuarina littoralis* is commonly described as an obligate seeder (R-P+) which is fire killed and germinates from canopy-stored seed (Falster *et al.* 2021). However, intermediate post-fire resprouting capacity from basal lignotubers has also been reported in *A. littoralis* but is likely linked to low severity fires which do not kill stems or result in 100% scorch (Falster *et al.* 2021; Kattge *et al.* 2020) (a condition required for categorisation as R+, Pausas *et al.* 2004). *Allocasuarina torulosa* is a strong basal and epicormic facultative resprouter, also displaying fire-cued seeding responses when canopy seedbanks are available (R+P+) (Kattge *et al.* 2020).

Both tree species lack seed dormancy beyond the physical dormancy imposed by storage in serotinous cones (Crowley 1986; Turnbull and Martensz 1982). Germination occurs across a range of incubation temperatures between 17-37 °C (Turnbull and Martensz 1982). There has been limited research on fire-cued germination in *A. littoralis* and *A. torulosa* (but see, Clarke *et al.* 2000; Crowley 1986). In other Casuarinaceae, seeds have been reported to survive heat shock of up to 120 °C (Callister *et al.* 2018; Hanley and Lamont 2000). *Allocasuarina* leaf litter burns at high temperatures (e.g., 60 ° to 111 °C at 1 cm soil depth, Tangney *et al.* 2020), likely exposing canopy seedbanks to temperatures above 100 °C.

Field age class structure surveys and cone collection

I established 40 sampling points to cover a range of fire histories within the distribution of the Glossy black-cockatoo, *A. littoralis*, and *A. torulosa*. Age class structure surveys investigated the hypotheses that (**H2**) fire history and (**H3**) environmental attributes influenced proportions of plants in younger age classes and reproductive output. Identification of sampling point was assisted using occurrence records from Atlas of Living Australia. From these records, I randomly selected sampling points across a range of fire frequencies. In the field at these sampling points, I then located a stand of *Allocasuarina* but where no *Allocasuarina* were found, further scouting was performed to locate a stand of *Allocasuarina* with a similar fire frequency. More sampling points were able to be established at low fire frequencies (1-3 fires from 1987-2023; 32 transects), the majority (n = 26) of which were *A. torulosa* transects, than high fire frequencies (4-7 fires from 1987-2023; six transects), all of which were *A. torulosa* transects. Once the stand of *Allocasuarina* was identified at the sampling point, a 50 m × 4 m transect was established at an individual tree and age class structure was measured, with transects spaced at least 140 m apart (range within sampling locations 140 m – 14 km). Measurements from each individual *Allocasuarina* along the transect included: age class; diameter at breast height (DBH), recruitment type (e.g., basal resprout, trunk resprout, seedling or none); condition (e.g., dead or alive); and height (using a

Suunto PM5/360 PC Clinometer (Vantaa, Finland) or Nikon Forestry Pro II Laser Rangefinder (Tokyo, Japan)). Age classes were defined as: adult = height >1 m, DBH >3 cm; sapling = height >1 m, DBH <3 cm; and seedling = height <1 m (see Schmidberger and Ladd 2020). For female plants, the number of cones were counted to measure reproductive output, with counts over 100 recorded as the average estimates from two observers.

Females bearing cones were randomly selected along and nearby to transects for cone collection, with at least 20 m spacing between individuals (range within sampling locations 20 m – 130 m). Cones were collected from up to six individuals per transect, with fewer individuals sampled if no cones were available or cones were not within *ca.* 5 m of the ground. On each individual tree, I collected a minimum of two mature cones (i.e., brown to grey-brown in colour with closed valves) to ensure seed had not been released but were fully developed. More cones were collected where possible (up to 73 cones with an average of 12 cones per individual) to increase sample sizes for the germination experiment. Cones were stored in paper bags in a warm, dry environment until seeds were shed and any unshed seeds were manually extracted from cones using tweezers. Seeds were stored for eight to 24 months in an air-conditioned laboratory inside an airtight container to minimise ambient temperature fluctuations prior to the germination experiment.

Germination experiment

<u>Germination experimental overview</u>

I conducted a full factorial germination experiment with a replicated design, to test the hypothesis (**H1**) that post-fire reproductive mode variation and fire frequency influenced fire-cued germination responses. The full factorial experiment was conducted with a replicated design such that three separate rounds of seed germination were conducted, with individuals exposed to the same treatment(s) in each replicate. Before conducting this experiment, I ran a series of optimisation trials to determine incubation temperatures, heat shock temperatures and durations, aerosol exposure duration and material. Incubation temperature tests were run to determine the optimal germination temperatures for each species and the baseline germination rate for *Allocasuarina littoralis* and *Allocasuarina torulosa* using thermal gradient bars (Fig. S1). Heat shock and smoke trials were conducted to determine (1) upper thresholds for heat tolerance and (2) the level at which seeds would show germination variability, thus, indicating heat and smoke levels that could drive selection. The following seed traits were measured to examine the influence of variation in post-fire reproductive mode, fire history, and environment on seed investment (**H1, H3**): seed weight and number of seeds. Seed lots (i.e., all seeds for an individual) were weighed, both as the whole seed lot and as a 10 seed fraction to estimate the total number of seeds in the seed lot and average seed weight per seed for the seed lot.

For all germination experiments, 20 seeds from an individual tree (hereafter 'individual seed lot') were placed in plastic 90 mm petri dishes lined with Whatman no. 1 filter paper moistened with distilled water and sealed with parafilm to reduce water loss. Seeds exposed to aerosol smoke were plated on sterile petri dishes prior to germination to reduce exposure to accumulated smoke residues. Seeds exposed to a combination of heat shock and smoke treatments were heat shocked prior to aerosol smoke exposure. Seeds in all experiments (excluding incubation temperature optimisation) were germinated in illuminated refrigerated incubators (TRIL495-1-SD,Thermoline Scientific, Wetherhill Park, New South Wales, Australia) with a 12-hour photoperiod provided by Grolux fluorescent lighting (36W) and temperatures set to 17 °C for *Allocasuarina littoralis* and 20 °C for *Allocasuarina torulosa* (see Fig. S1 and Turnbull and Martensz 1982). Seeds were germinated for at least 21 days, with germination considered to have occurred upon emergence of the radicle from the testa. After emergence, the germinant was recorded and removed from the dish to allow space for other seeds to germinate. If no new seeds germinated between 21-28 days, then germination was considered to have ceased and the trial ended. If seeds continued to germinate up to 28 days, the germination trial was continued until no new seeds germinated over a 7-day period.

Seed viability measurements

Seed viability was measured using two methods: (1) x-ray prior to germination experiments to estimate pre-treatment viability without reducing the number of seeds for the experiment, and (2) post-experiment tetrazolium tests to determine whether seeds which remained ungerminated at the end of the trial were viable (Peters 2000). X-rays were taken on a Faxitron MX-20 Imaging system (Lincolnshire, IL, USA), on *ca*. 100 seeds per individual seed lot with four replicates of 25 seeds at 28 kV for 6.55 seconds. X-ray images were examined to determine seed fill; a metric related to the amount of seed embryo and endosperm which is correlated with viability (Gagliardi and Marcos-Filho 2011; Tausch *et al.* 2024). Unfilled seeds were considered unviable but seeds with partial filling were classed as viable as there was potential seed mass from which germination could occur. The x-ray viability data were summarised as the proportion of viable seeds in the individual seed lot for analysis. Tetrazolium tests used a 1% 2,3-5 triphenyl tetrazolium chloride (TTC) solution with seeds cut laterally through the distal end of cotyledons and incubated in solution for 18 hours at 30 °C in darkness (Peters 2000). After incubation in TTC solution, seeds were observed under a dissection microscope with seeds classed as viable if the radicle and cotyledons were completely stained pink (Peters 2000). Any lack or inconsistencies in TTC staining was considered to indicate unviable seeds (Peters 2000).

<u>Incubation temperature optimisation</u>

Water in a thermal gradient bar (CSK Model CSK-TGB, Serial 3310; CSK Group, Wacol, Queensland, Australia) was heated to temperatures ranging between 4 °C to 41 °C, with the ambient temperature in five chambers monitored on an hourly basis for two weeks using data loggers (Tinytag, TGP 4500; Hastings data loggers, Port Macquarie, New South Wales, Australia). Ambient temperatures ranged from *ca*. 6 °C to 36 °C across 10 insulated chambers, with chambers differing by *ca.* 3 °C to 4 °C along the gradient (Fig. S1). During incubation, seeds were exposed to a 12-hour photoperiod (Callister *et al.* 2018) of cool white fluorescent LED light (1200 lumens, 12W). For each species, three individual seed lots, representing three different individuals, were used with 20 seeds per petri dish, giving 600 seeds across the thermal gradient bar for incubation temperature optimisation. Incubation temperature optimisation tests were ceased on day 28 as previous studies considered this sufficient time for viable seeds to germinate (Crowley and Jackes 1990; Turnbull and Martensz 1982). Ungerminated, viable seed was considered to be exposed to an unsuitable germination temperature, with germination likely having been slowed by exposure to low temperatures. Optimal incubation temperatures for germination were determined to be 17 °C for *A. littoralis* and 20 °C for *A. torulosa* (Fig. S1).

Heat shock and smoke exposure optimisation

Preliminary heat shock tests were conducted using a dehydrating oven (Thermoline Scientific, Wetherhill Park, New South Wales, Australia) to determine the lethal temperature threshold. Heat shocks tests were conducted at 80 °C, 95 °C, 110 °C, 125 °C, and 150 °C for durations of 0.5, 1, 2, 5 and 10 minutes. Three individual seed lots from both species with a large quantity of seeds were used for these tests, with cones from two *A. torulosa* individuals collected only for optimisation tests. These tests indicated that temperatures over 100 °C were, in most cases, sufficient to kill loose seeds (Fig. S2). Thus, 80 °C and 95 °C were selected for heat shock temperatures in the full factorial experiment as they were below the lethal temperature threshold but still produced variability in germination rates (Fig. S2).

Allocasuarina species produce dense leaf litter, which has an allelopathic effect on other plants (Ahmed *et al.* 2019; Buehler 2010). As such, I expected smoke responses in my study species could be strongly tied to smoke from their own leaf litter, rather than smoke more generally. Therefore, aerosol smoke tests were conducted to compare germination responses to smoke from *Allocasuarina torulosa* leaf litter material and to pine sawdust, which promotes germination across a range of species (Keeley and Bond 1997). Leaf litter from *A. torulosa* was collected from a private property in Seventeen Mile, Queensland, Australia (one of the main sampling locations) and compared to commercially available pine sawdust.

Aerosol smoking was implemented in a modified 54 L rectangular plastic container (65 cm × 28 cm × 41 cm) used as a smoke chamber. The chamber included a 40 cm × 25 cm door on the long edge, attached with hinges and sealed with weatherproof tape to minimise smoke escape while enabling access to samples. A 50 cm PVC pipe with 1 cm holes along its length (spaced *ca.* 4 cm – 4.5 cm apart) spanned the full length of the container. The pipe passed through a 4.5 cm diameter hole in the bottom of the short side of the container, enabling even smoke dispersal. A beekeepers' smoker was held at the end of this pipe, with a 20 cm extension pipe extending outside the container to minimise heat transfer into the main chamber. A cluster of small holes were drilled in the opposite corner of the chamber lid from the smoke entry point to create air flow. During smoke exposure, regular smoke flow was maintained by pumping smoke from the beekeepers' smoker through the PVC pipe and into the chamber to maintain an approximately even amount of smoke in the chamber. Seeds from three *A. littoralis* and three *A. torulosa* individuals were used for the smoke optimisation trials. Each individual seed lot of 20 seeds was placed in petri dishes on an approximately 10 cm high shelf inside the smoke chamber. All smoke was released from the chamber between petri dishes with new individual seed lots to maintain a similar amount of smoke across individuals. I tested smoke exposures of 5, 10, and 20 minutes for each individual. To minimise cross contamination between smoke material types, the beekeepers' smoker was thoroughly cleaned with acetone and the smoke chamber wiped with ethanol between trials. *Allocasuarina torulosa* leaf litter produced a similar effect to pine sawdust and was most consistent at a 20-minute exposure time in both species (Fig. S3).

<u>Full factorial germination experiment</u>

The full factorial experiment included six treatments: (1) control; (2) 80 °C heat shock for 5 min; (3) 95 °C heat shock for 5 min; (4) 20 min smoke exposure; (5) 80 °C heat shock for 5 min + 20 min smoke exposure; and (6) 95 °C heat shock for 5 min + 20 min smoke exposure. Three replicates for each treatment combination were conducted, with the start time for each replicate staggered by 14 days to minimise bias related to starting conditions. Seed germination was recorded on the first day after plating then every second to third day until day 29 (i.e., day 1, 3, 6, 8, 10, 13, 15, 17, 20, 22, 24, 27 and 29) or until germination ceased. Cessation of germination was 35 days, 36 days and 46 days post-commencement of the germination experiment for each replicate, respectively. Therefore, for replicates one and two, I assigned values of zero germination for all seeds up to 46 days to standardise test periods across replicates, a step required for calculating germination metrics.

To test the hypothesis (**H1**) that variation in post-fire reproductive mode affected fire-cued germination responses and seed size, species were considered separately. Individual seed lots for *A. torulosa* were also divided based on the fire frequency at the collection site (i.e., low fire frequency individual seed lots and high fire frequency individual seed lots). Due to limited seed available, I was unable to assign each individual to all six treatments (e.g., an individual with only 120 seeds could only be assigned to 3 treatments). Thus, I used `arrangements` package version 1.1.9 (Lai 2019) in R version 4.3.1 (R Core Team 2018) to randomly assign the six treatments to individuals, with six separate rounds of assignment. I subsequently reduced treatment assignments on a case-by-case basis such that only three treatments were assigned to an individual with 120 seeds. During this case-by-case treatment assignment reduction, I ensured 15 individual seed lots were included for all six treatments. Thus, each germination experiment replicate included six treatments with 300 seeds from 15 individual seeds lots, totalling 1800 seeds for *A. littoralis*, 1800 seeds for *A. torulosa* low fire frequency, and 1800 seeds for *A. torulosa* high fire frequency.

Analysis

Fire frequency data from was obtained from Queensland Parks and Wildlife Service (Table 1) and subset temporally (i.e., 1987-2023) to match the temporal resolution of generalised additive modelled satellite fire frequency estimates used to supplement data for areas outside of public estates (see Charles *et al.* 2025 under review). Year of last fire was obtained from Queensland Parks and Wildlife fire history data and satellite fire history data, with areas of no fire data between 1987-2023 assigned 1986. Time since fire was then calculated by subtracting year of last fire from sampling year. Temperature and precipitation seasonality data (Fick and Hijmans 2017), Topographic Wetness Index (TWI) (Gallant and Austin 2012), and Foliage Projective Cover (FPC) (Department of Environment 2020; Department of Environment 2022; Department of Environment 2024a; Department of Environment 2024b; Department of Environment 2024c) data are summarised in Table 1. Spatial data requiring resolution adjustments were rescaled to 30 m resolution (see Table 1) using `gdalUtilities` version 1.2.5 nearest neighbour resampling. Foliage projective cover data was provided as 0-100% foliage cover, but data from 2014 were on a different scale. Therefore, 2014 FPC data were reclassified to align with other years. Foliage projective cover was then rescaled to 30 m, prior to calculation of the average FPC (Table 1).

Table 1 Spatial fire, climate, and environment variables used to investigate reproductive trait variability in *Allocasuarina littoralis* and *A. torulosa* in southeast Queensland, Australia.

Variable	**Raw resolution**	**Resampled resolution**	**Temporal resolution**	**Data source**
Fire history – Queensland Parks and Wildlife Service	1 m	30 m	1930-2023	(Queensland Parks and Wildlife Service 2023)
Annual Fire Scars – Landsat, QLD DES algorithm	30 m	Unchanged	1987-2016	(Collett 2021)
Sentinel-2 fire scars – QLD DES algorithm, annual	10 m	30 m	2017-2023	(van den Berg 2021)
Temperature seasonality	1 km	30 m	1970-2000	(Fick and Hijmans 2017)
Precipitation seasonality	1 km	30 m	1970-2000	(Fick and Hijmans 2017)
Topographic wetness index	30 m	Unchanged	2000	(Gallant and Austin 2012)
Foliage projective cover				
- Landsat 2014	30 m	Unchanged	1998-2014	(Department of Environment 2020)
- Statewide Landcover and Trees Study Sentinel-2 2018	30 m	Unchanged	2018	(Department of Environment 2022)
- Statewide Landcover and Trees Study Sentinel-2	10 m	30 m	2019, 2020, 2021	(Department of Environment 2024c)

Analyses of reproductive trait data were conducted in R version 4.3.1 (R Core Team 2023) using generalised linear mixed models in `lme4` R package version 1.1-34 (Bates *et al.* 2015). I used the same model structure for each response variable but modified the model family (error structure) as appropriate for each type of response variable. Models were fit separately for each species to account for biological differences related to their post-fire reproductive modes and other biological factors. Prior to modelling, continuous numeric predictors were scaled by dividing values by the series-wide standard deviation. I fit models with and without a main effect for fire to investigate the influence of environmental variation on reproductive trait variation (**H3**). For each response variable a null model was fit with no variation, against which to compare the other models. Model selection was performed by ranking models based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) in `AICcmodavg` R package version 2.3-3 (Mazerolle 2020). The best model was chosen as the model with the lowest AIC_c in the candidate set which improved model fit over the null model by $\Delta AIC_c > 2$ (Arnold 2010; Leroux 2019). Where additional models were ranked within 2 AIC_c units of the top model and included one additional parameter, I considered the additional parameter to be supported by the data if (1) the additional parameter improved log likelihood over that of the top-ranked model; (2) confidence intervals did not overlap zero (Fig. S7, S9) (Arnold 2010; Leroux 2019). For top-ranked models including factorial predictors with multiple levels, I calculated least-squares means comparisons to determine differences between levels within the factor (Fig. S8). For example, if the top-ranked model included germination treatment, I used least-squares means comparisons to determine if 95 °C heat shocked seed germination was different to control seed germination (Fig. S8).

<u>Germination experiment</u>

Cumulative proportion germination for each individual was calculated by dividing the cumulative sum of germination by the total number of seeds germinated at the end of the period. First and last germination day and time to 50% germination were calculated by adapting functions from `germinationmetrics` R package version 0.1.8 (Aaravind *et al.* 2022). To analyse the effect of seed treatment and fire frequency on fire-cued germination (**H1**) I fit seven models each for proportion of seeds germinated and time to 50% germination: a null model; three univariate models with main effects for treatment, fire frequency, and seed weight; and three multivariate models investigating interactions between treatment, fire frequency and seed weight. To account for individual-level similarities in responses and potential effects of replicates, I included a random effect for replicate and individual in each model. To analyse the effect of fire frequency and environment on seed weight (**H1, H3**), I used the average weight of a singular seed (hereafter 'seed weight') as the response variable as a proxy measure of seed size as these measures are strongly correlated (Eriksson 1999; Gnan *et al.* 2014). I fit twelve models with a random effect for individual: a null model; six univariate main effect models for fire frequency and environmental attributes; and five multivariate models investigating interactions between fire frequency and environmental attributes.

Age class structure surveys

To analyse fire history effects on age class structure, the proportion of seedlings, saplings, and recruits (i.e., seedlings and saplings) within the total population was calculated by dividing the total number of individuals in an age class by the sum of the number of individuals from that age class and the number of adults. For example, proportion of seedlings within the total population was calculated by $\frac{Number\ of\ seedlings}{Number\ of\ adults+seedlings}$. To analyse the effect of fire and environment on age class structure (**H2a, H3**) I fit twelve models: a null model; six univariate main effect models for the focal fire metric (i.e., fire frequency or time since fire) and environmental attributes; and five multivariate models investigating interactions between the focal fire metric and environmental attributes. To analyse the effect of fire and environment on reproductive output (i.e., cone number, **H2b, H3**), I fit eight models: a null model and seven univariate models for fire frequency, time since fire, and environmental attributes. I did not fit any multivariate models for reproductive output due to a limited number of individuals with cones along our transects. For age class structure and reproductive output analyses, due to the hierarchical structure of data collection (multiple individuals along transects and multiple transects within locations), I included transect nested within location as a random effect in each model.

Results

Germination experiment

Field sample collection resulted in seeds from 115 individual trees across the study region in southeast Queensland, comprising 40 *A. littoralis* and 75 *A. torulosa* individuals. Seven individual trees with less than 60 seeds were excluded resulting in 108 individuals (37 *A. littoralis* and 71 *A. torulosa*) available for the germination experiment. Fire frequencies at seed collection locations ranged from one to three and six fires over 36 years for *A. littoralis* and *A. torulosa*, respectively. Time since fire at collection locations ranged from at least 36 years post-fire to around two-years post-fire for *A. littoralis* and *A. torulosa*, respectively.

Germination rates were not strongly influenced by heat shock or smoke in either species (Fig. S6), with the null model ranked higher than models including seed treatments (Table 2).

Treatments did not reduce seed viability or vary to a strong degree between replicates as no noticeable differences in viability were observed (Fig. S4, S5). Thus, *A. littoralis* and *A. torulosa* are smoke and heat tolerant up to 95 °C with no requirement for fire-cues to germinate once seeds have been released from cones. Seed weight influenced germination rate for *A. littoralis* (ΔAIC_c relative to null model = 3.07; Table 2, Fig. 3), and *A. torulosa* with an interaction between seed weight and fire frequency (ΔAIC_c relative to null model = 10.97; Table 2, Fig. 3). In both species, heavier seeds were associated with greater germination rates (Table 2, Fig. 3). For *A. torulosa* individuals exposed to high fire frequencies, germination rates decreased with increasing seed weight and were highly variable (20-90% proportion of seeds germinated, Fig 3b).

Table 2 Models used to examine the influence of fire frequency and seed treatment on proportion germination in *Allocasuarina littoralis*, and facultative resprouter, *A. torulosa*. For each species, models are ranked from highest to lowest AIC$_c$.

Species	**Model structure**	**Number of parameters**	**AIC$_c$**	**ΔAIC$_c$**	**Log Likelihood**
Allocasuarina littoralis	Seed weight	3	129.07	0.00	-60.46
	Null model	3	132.14	3.07	-63.03
	Seed weight × fire frequency	4	132.81	3.74	-60.25
	Fire frequency	3	133.42	4.34	-62.63
	Treatment	3	136.27	7.20	-59.86
	Treatment × seed weight	4	140.94	11.86	-55.65
	Treatment × fire frequency	4	144.84	15.76	-57.59
Allocasuarina torulosa	Seed weight × fire frequency	4	404.26	0.00	-196.05
	Seed weight	3	408.31	4.05	-200.12
	Null model	3	415.23	10.97	-204.59
	Fire frequency	3	416.75	12.49	-204.34
	Treatment	3	421.81	17.55	-202.77
	Treatment × seed weight	4	422.75	18.49	-196.97
	Treatment × fire frequency	4	430.50	26.24	-200.85

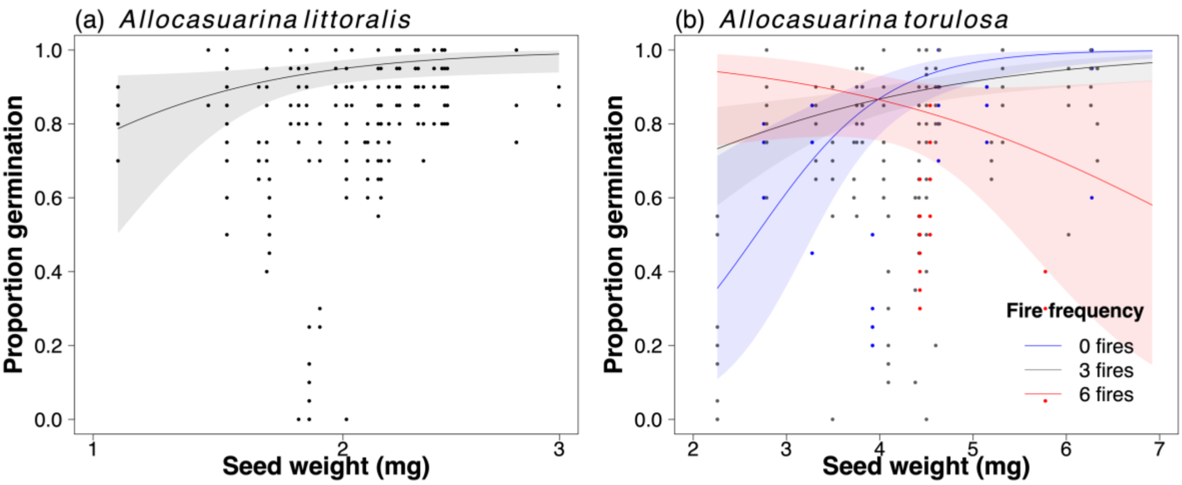

Figure 3 The estimated effect (and 95% confidence intervals) of seed weight on proportion germination in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. The top-ranked model for *A. torulosa* included an interaction between seed weight and fire frequency.

Time to reach 50% germination was influenced by seed treatment in both species (Fig. 4a-b). For *A. littoralis*, there was not strong support for an effect of seed treatment on time to 50% germination as the null model was equivalent to the treatment only model (Table 1). In *A. torulosa*, there was support from the data for three models: treatment only (ΔAIC_c relative to null model = 108.77), treatment and seed weight interactive model (ΔAIC_c relative to the top ranked model = 0.11), and treatment and fire frequency interactive model (ΔAIC_c relative to the top ranked model = 0.67) (Table 3). Time to 50% germination increased for all treatments compared to controls, except for the 80 °C treatment (Fig. 4a). Thus, heat and smoke slowed down germination in *A. torulosa*. In the seed weight interaction model, heavier seeds were typically faster to germinate, an effect which was most pronounced for individuals exposed to the smoke treatment (Fig. 4b). For 95 °C; smoke; and 80 °C + smoke, seeds from historically more frequently burned sampling transects had slower germination (Fig. 4c). However, for individuals exposed to the 95 °C + smoke treatment, this pattern was reversed, with individuals from more frequently burned sampling transects having faster germination than those exposed to less frequent fire (Fig. 4c).

Table 3 Models used to examine the influence of fire frequency, seed weight, and seed treatment on time to reach 50% germination, as a measure of germination speed, in *Allocasuarina littoralis* and *A. torulosa*.

Species	**Model structure**	**Number of parameters**	**AIC$_c$**	**ΔAIC$_c$**	**Log Likelihood**
Allocasuarina littoralis	Treatment	3	1284.18	0.00	-633.81
	Null model	3	1284.99	0.81	-639.45
	Seed weight	3	1286.36	2.18	-639.10
	Fire frequency	3	1286.82	2.64	-639.34
	Seed weight × fire frequency	4	1289.69	5.51	-639.69
	Treatment × seed weight	4	1292.97	8.79	-631.66
	Treatment × fire frequency	4	1295.10	10.92	-632.72
Allocasuarina torulosa	Treatment	3	2579.61	0.00	-1281.67
	Treatment × seed weight	4	2579.72	0.11	-1275.46
	Treatment × fire frequency	4	2580.28	0.67	-1275.74
	Seed weight	3	2680.38	100.77	-1336.15
	Seed weight × fire frequency	4	2682.91	103.30	-1335.38
	Null model	3	2688.38	108.77	-1341.17
	Fire frequency	3	2690.24	110.63	-1341.08

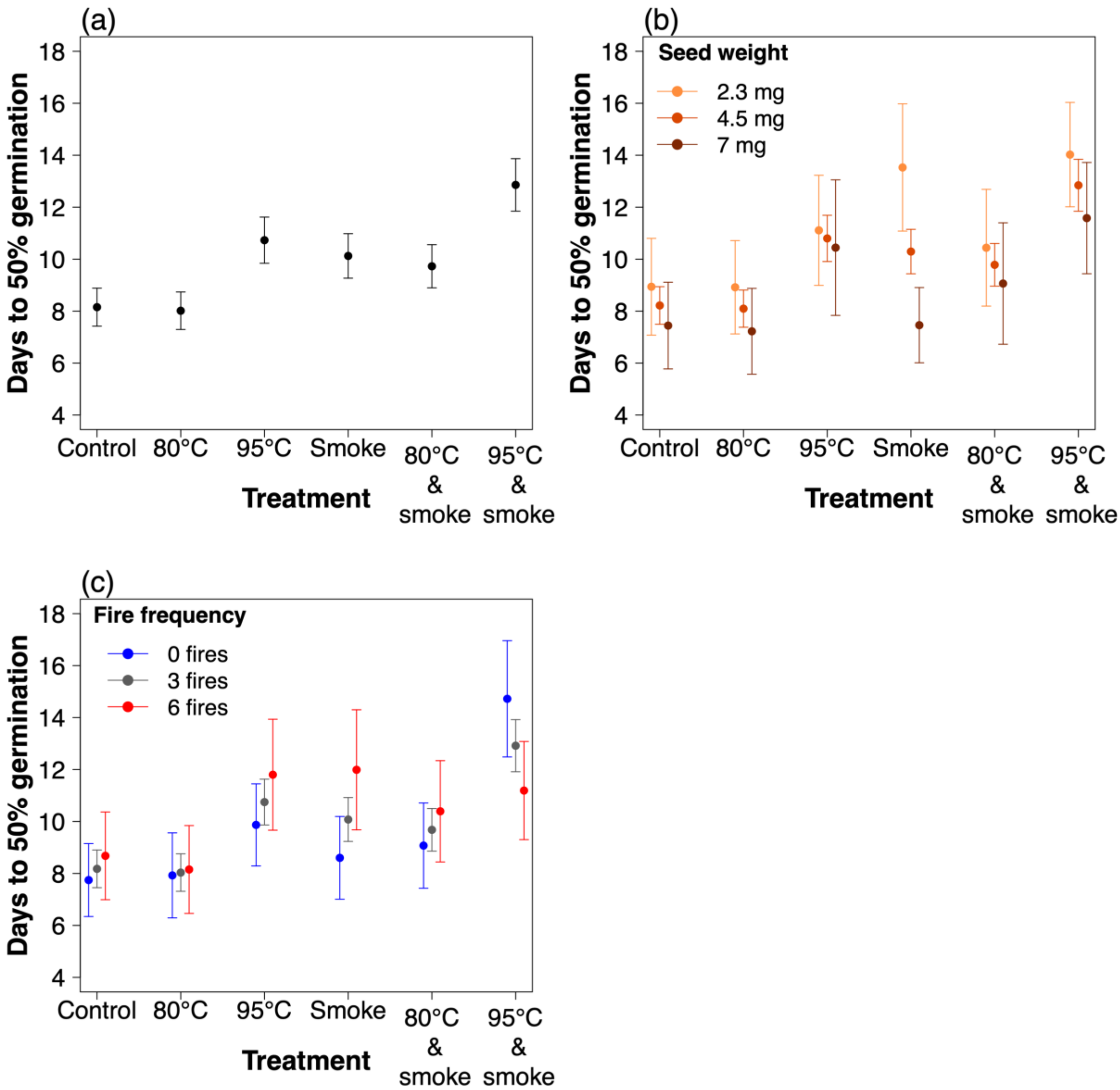

Figure 4 The estimated effect and 95% confidence interval of seed treatment on time to 50% germination (days) for (a) *A. torulosa*. In addition to main effects of treatment, there was evidence for an interaction between treatment and (b) seed weight, and (c) fire frequency on time to 50% germination.

Seed weight was influenced by an interaction between fire frequency and temperature seasonality in *A. littoralis* and between fire frequency and latitude in *A. torulosa* (Table 4, Fig. 5). There was no evidence of any other environmental variables influencing seed weight in either species ($\Delta AIC_c > 5$, Table 4). For *A. littoralis*, seed weight increased with temperature seasonality for seeds collected at frequently burned transects (4 fires over 36 years, Fig. 5a). At low- to intermediate fire frequencies (0-1 fire over 36 years) there was no relationship between seed weight and temperature seasonality (Fig. 5a). For *A. torulosa*, seed weight increased with decreasing latitude for frequently burned transects (6 fires over 36 years) and decreased with decreasing latitude for infrequently burned transects (0 fires over 36 years) (Fig. 5b). There was no relationship between latitude and seed weight for intermediate fire frequencies (3 fires over 36 years, Fig. 5b). In other words, at southern sampling locations seeds were heavier when collected at transects which had experienced frequent fire, compared to relatively unburnt transects. At northern sampling locations, there were no differences in seed weight related to fire history (Fig. 5b).

Table 4 Models used examine the influence of fire frequency and environmental variation on seed weight in *Allocasuarina littoralis* and *A. torulosa*.

Species	**Model structure**	**Number of parameters**	**AIC$_c$**	**ΔAIC$_c$**	**Log Likelihood**
Allocasuarina littoralis	Fire frequency × temperatures seasonality	4	-8418.33	0.00	4215.33
	Null model	3	-8376.10	42.23	4191.10
	Temperature seasonality	3	-8347.75	70.58	4177.95
	Precipitation seasonality	3	-8330.16	88.17	4169.16
	Latitude	3	-8329.41	88.92	4168.78
	Fire frequency	3	-8317.17	101.16	4162.66
	Fire frequency × latitude	4	-8263.94	154.40	4138.13
	Fire frequency × precipitation seasonality	4	-8235.42	182.91	4123.87
	Fire frequency × topographic wetness	4	-8224.59	193.75	4118.45
	Topographic wetness	3	-8215.94	202.40	4112.04
	Foliage projective cover	3	-7533.58	884.75	3770.88
	Fire frequency × foliage projective cover	4	-7521.56	896.77	3766.96
Allocasuarina torulosa	Fire frequency × latitude	4	-16303.73	0.00	8157.95
	Fire frequency × topographic wetness	4	-16297.98	5.75	8155.07
	Topographic wetness	3	-16170.19	133.54	8089.13
	Null model	3	-16126.40	177.33	8066.22
	Precipitation seasonality	3	-16112.83	190.90	8060.45
	Temperature seasonality	3	-16112.83	190.90	8060.45
	Fire frequency	3	-16044.97	258.76	8026.52
	Fire frequency × precipitation seasonality	4	-16034.15	269.59	8023.15
	Fire frequency × temperature seasonality	4	-16034.15	269.59	8023.15
	Latitude	3	-16004.08	299.34	8006.08
	Fire frequency × foliage projective cover	4	-15192.60	1111.13	7602.39
	Foliage projective cover	3	-15158.09	1145.65	7583.08

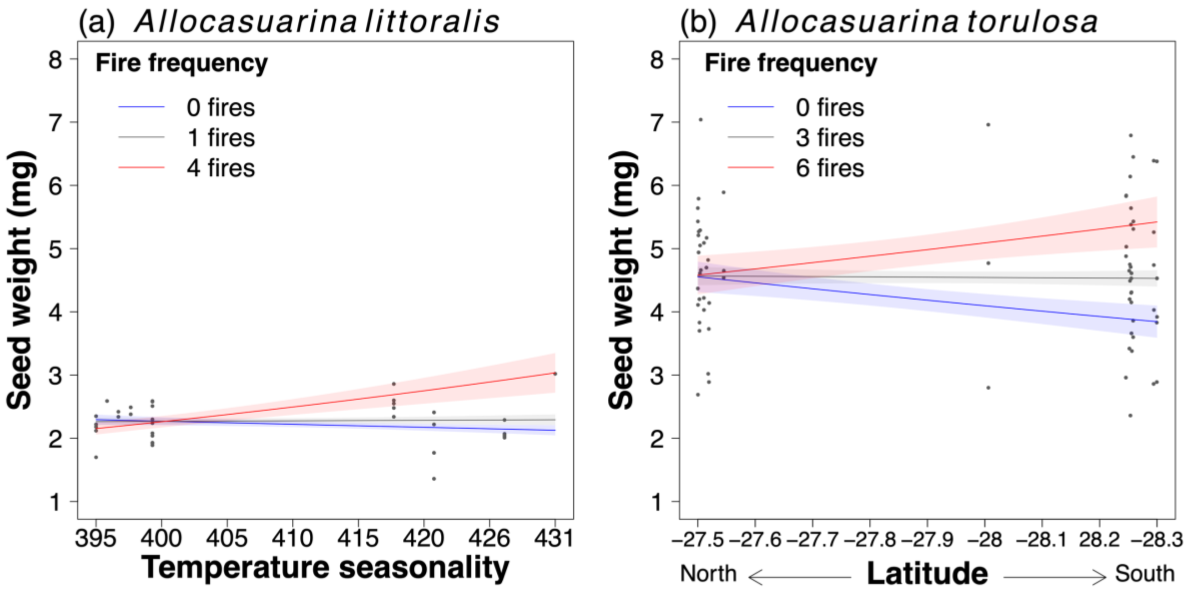

Figure 5 The estimated effect and 95% confidence intervals of fire frequency on seed weight in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. Seed weight was influenced by the interactive effects of fire frequency and (a) temperature seasonality in *A. littoralis*, and (b) latitude in *A. torulosa*.

Reproductive output and age class structure

Fire frequency ranged from zero to four and seven fires for *A. littoralis* and *A. torulosa* transects, respectively. Reproductive output (number of cones per tree) was not influenced by fire frequency or time since fire (Table 5). There was a positive effect of foliage projective cover on number of cones in *A. littoralis* (Intercept = -1.793 [se = 1.081], FPC = 0.066 [se = 1.175]) and *A. torulosa* (Intercept = -3.409 [se = 1.1336], FPC = 2.105 [se = 1.303]) (ΔAIC_c relative to the null model = 877.42 for *A. littoralis*, and = 281.39 for *A. torulosa*; Table 5).

Table 5 Models used to examine the influence of fire frequency, time since fire, and environmental variation on reproductive output (i.e., number of cones) in *Allocasuarina littoralis* and *A. torulosa*.

Species	**Model structure**	**Number of parameters**	**AIC$_c$**	**ΔAIC$_c$**	**Log Likelihood**
Allocasuarina littoralis	Foliage projective cover	2	1167.32	0.00	-579.07
	Topographic wetness	2	2017.11	849.79	-1004.05
	Fire frequency	2	2027.42	860.10	-1009.21
	Null model	2	2044.73	877.42	-1019.07
	Latitude	2	2045.50	878.18	-1018.25
	Temperature seasonality	2	2046.23	878.91	-1018.61
	Precipitation seasonality	2	2046.27	878.95	-1018.63
	Time since fire	2	2046.27	879.25	-1018.78
Allocasuarina torulosa	Foliage projective cover	2	1221.68	0.00	-606.15
	Fire frequency	2	1380.78	159.10	-685.72
	Precipitation seasonality	2	1496.76	275.08	-743.71
	Null model	2	1503.06	281.39	-748.15
	Time since fire	2	1504.76	283.08	-747.71
	Topographic wetness	2	1504.89	283.21	-747.78
	Latitude	2	1504.25	283.57	-747.96
	Temperature seasonality	2	1505.52	283.84	-748.09

Population age structure in *A. littoralis* was not influenced by fire frequency, time since fire, or environmental variability, with the null model being top ranked for all analyses (Table S1). In *A. torulosa*, foliage projective cover influenced the proportion of seedings within the total population (Intercept = -3.409 [se = 1.336]; FPC = 2.105 [se = 1.303], Table 6). Greater temperature seasonality reduced the proportion of saplings within the total population (Intercept = -1.040 [se = 0.482], temperature seasonality = -1.136 [se = 0.481]) and recruits within the total population (Intercept = -0.919 [se = -1.833]), temperature seasonality = -1.642 [se = 0.535], Table 6). The interaction between temperature seasonality and time since fire on the proportion of *A. torulosa* recruits within the total population was ranked within ΔAIC$_c$ < 2, but confidence intervals of the interaction term overlapped zero (Fig. S9). Thus, fire history did not strongly influence *A. littoralis* or *A. torulosa* reproductive output or population age structure, with environmental variability more important in constraining recruitment processes (Table 5, 6, S1).

Table 6 Models used to examine the influence of fire frequency, time since fire, and environmental variation on population age structure in *Allocasuarina torulosa*.

Fire metric	**Age class**	**Model structure**	**Number of parameters**	**AIC$_c$**	**ΔAIC$_c$**	**Log likelihood**
Fire frequency	Seedlings	Foliage projective cover	2	24.62	0.00	-7.54
		Null model	2	26.77	2.15	-9.96
		Precipitation seasonality	2	28.56	3.94	-9.54
		Fire frequency	2	28.72	4.10	-9.62
		Fire frequency × foliage projective cover	3	28.85	4.23	-6.67
		Temperature seasonality	2	29.14	4.52	-9.83
		Latitude	2	29.25	4.63	-9.88
		Topographic wetness	2	29.37	4.75	-9.94
		Fire frequency × precipitation seasonality	3	32.55	7.93	-8.59
		Fire frequency × topographic wetness	3	33.03	8.41	-8.84
		Fire frequency × temperature	3	34.17	9.55	-9.40
		Fire frequency × latitude	3	34.39	9.78	-9.52
	Saplings	Temperature seasonality	2	39.69	0.00	-15.01
		Latitude	2	43.14	3.45	-16.83
		Fire frequency × temperature seasonality	3	45.33	5.64	-14.99
		Precipitation seasonality	2	45.69	6.00	-18.11
		Null model	2	46.23	6.55	-19.69
		Foliage projective cover	2	46.55	6.86	-18.50
		Topographic wetness	2	48.85	9.16	-19.68
		Fire frequency	2	48.85	9.16	-19.68
		Fire frequency × latitude	3	48.99	9.30	-16.82
		Fire frequency × precipitation seasonality	3	49.27	9.58	-16.95
		Fire frequency × foliage projective cover	3	51.85	12.16	-18.18
		Fire frequency × topographic wetness	3	52.35	12.67	-18.50
	Recruits	Temperature seasonality	2	37.02	0.00	-13.77
		Latitude	2	42.24	5.22	-16.38

		Fire frequency × temperature seasonality	3	42.77	5.74	-13.70
		Foliage projective cover	2	47.29	10.27	-18.88
		Null model	2	47.51	10.48	-20.32
		Precipitation seasonality	2	47.83	10.80	-19.17
		Fire frequency × latitude	3	47.94	10.91	-16.29
		Topographic wetness	2	50.13	13.11	-20.32
		Fire frequency	2	50.13	13.11	-20.32
		Fire frequency × precipitation	3	51.56	14.54	-18.10
		Fire frequency × foliage projective cover	3	52.61	15.59	-18.56
		Fire frequency × topographic wetness	3	53.56	16.54	-19.10
Time since fire	Seedlings	Foliage projective cover	2	24.62	0.00	-7.54
		Null model	2	26.77	2.15	-9.96
		Precipitation seasonality	2	28.56	3.94	-9.54
		Temperature seasonality	2	29.14	4.52	-9.83
		Latitude	2	29.25	4.63	-9.88
		Topographic wetness	2	29.37	4.75	-9.94
		Time since fire	2	29.37	4.76	-9.95
		Time since fire × foliage projective cover	3	30.26	5.64	-7.38
		Time since fire × topographic wetness	3	32.01	7.40	-8.33
		Time since fire × precipitation seasonality	3	34.29	9.68	-9.47
		Time since fire × temperature seasonality	3	34.92	10.31	-9.78
		Time since fire × latitude	3	35.12	10.51	-9.88
	Saplings	Temperature seasonality	2	39.39	0.00	-15.10
		Time since fire × precipitation seasonality	3	42.30	2.61	-13.47
		Time since fire × temperature seasonality	3	42.52	2.83	-13.58
		Latitude	2	43.14	3.45	-16.83
		Time since fire	2	45.35	5.66	-17.93
		Time since fire × topographic wetness	3	45.62	5.93	-15.13

	Time since fire × latitude	3	45.62	5.93	-15.13
	Precipitation seasonality	2	45.69	6.00	-18.11
	Null model	2	46.23	6.55	-19.69
	Foliage projective cover	2	46.55	6.86	-18.50
	Time since fire × foliage projective cover	3	48.23	8.54	-16.37
	Topographic wetness	2	48.85	9.16	-19.68
Recruits	Temperature seasonality	2	37.02	0.00	-13.77
	Time since fire × temperature seasonality	3	37.88	0.85	-11.26
	Latitude	2	42.24	5.22	-16.38
	Time since fire × latitude	3	43l35	6.33	-14.00
	Time since fire × precipitation seasonality	3	44.25	7.22	-14.44
	Time since fire × topographic wetness	3	45.65	8.63	-15.15
	Time since fire	2	45.69	8.67	-18.10
	Foliage projective cover	2	47.29	10.27	-18.88
	Null model	2	47.51	10.48	-20.32
	Precipitation seasonality	2	47.83	10.80	-19.17
	Time since fire × foliage projective cover	3	48.63	11.61	-16.57
	Topographic wetness	2	50.13	13.11	-20.32

Discussion

Determining optimal fire regimes for ecosystem restoration is hindered by a lack of knowledge of plant responses to fire regimes at critical life stages of germination and through transitions to adulthood. Furthermore, a lack of integration of fire history in germination studies, and how these influence age class structures limits our understanding of the influence of fire history on population level changes. My results showed that fire history, specifically frequency, influenced variation in germination; but foliage projective cover and temperature seasonality had more influence than fire history on reproductive output and age class structure. These results point to environments with greater climate stability and photosynthetic potential leading to greater reproductive output. Post-fire reproductive mode influenced traits relevant to germination success as individual trees of the facultative resprouter, *A. torulosa*, exposed to higher fire frequencies had lower proportion germination with increasing seed weight. This decreased germination success with increasing fire frequency may have reflected stronger resprouting responses, with higher investment in resprouting bud banks than seed production (Bendall *et al.* 2022; Pausas and Keeley 2014; Verdú 2000). These results can inform restoration and conservation actions of these *Allocasuarina* species, important food trees of the vulnerable dietary specialist Glossy black-cockatoos.

In this study, the obligate seeder, *A. littoralis* was less sensitive to extreme heat shocks and variable smoke exposure than the facultative resprouter, *A. torulosa*. Despite occurring in fire-prone environments, germination of *A. littoralis* and *A. torulosa* was not enhanced by application of fire-related germination cues as seeds exposed to heat shocks up to 95 °C showed comparative germination to controls. However, obligate seeders are more likely to express traits increasing post-fire germination due to their greater investment in seeds than congeneric resprouters (Pausas and Keeley 2014; Tangney *et al.* 2020; Zammit and Westoby 1987). Strongly seasonal environments also generally favour heavier seeds, which provide greater reserves for seeds to withstand seasonal variation in water availability (Leishman *et al.* 2000; Muller-Landau 2010). This was reflected in my experiment as in variable climatic conditions, with high fire frequency (i.e., 4 fires over 36 years), seed weight was greater in the obligate seeder than the facultative resprouter. In the facultative resprouter, *A. torulosa*, seed investment was more likely driven by exposure to recurrent fire as seed weight decreased in the absence of fire even under more seasonal climates. However, *A. torulosa* had high germination variability when seeds were larger, possibly because seed reproductive effort was traded-off with resource allocation to resprouting (Bellingham and Sparrow 2000). Where species show plasticity in regeneration modes, high fire frequency could result in more resources being allocated to resprouting capabilities than production of viable seeds (Bellingham and Sparrow 2000; Verdú 2000).

Fast germination provides individuals with a competitive advantage (Hodges *et al.* 2021); therefore, germination speed can be promoted by fire-related germination cues, especially in obligate seeders which are adapted for post-fire germination (Hodges *et al.* 2021; Pausas and Lamont 2022; Ramos *et al.* 2019; Tangney *et al.* 2020). Results from this study ran contrary to this general prediction (**H1**): heat and smoke did not strongly affect germination in the obligate seeder *A. littoralis* but slowed germination in the facultative resprouter *A. torulosa*. The stronger reduction in germination speed as temperature increased for *A. torulosa* was likely linked to temperatures being closer to the lethal temperature threshold of *A. torulosa* than *A. littoralis* (i.e., *A. torulosa* = *ca.* 100 °C; *A. littoralis* = *ca.* 110 °C), so reductions may be related to lower seed viability (Emery *et al.* 2011; Hanley *et al.* 2003). In the natural environment, these higher temperatures could be linked to higher fire intensities (Rossi *et al.* 2018), indicating that *A. littoralis* to some extent may be faster to establish than *A. torulosa* after higher intensity fire. However, in *A. torulosa* germination speed was also influenced by seed size and fire history. Heavier seeds have higher energy reserves which support faster germination rates (Kołodziejek 2017) and provide greater heat insulation (Escudero *et al.* 2000; Gómez-González *et al.* 2011; Lamont *et al.* 2019), reducing potential decreases in viability and germination speed due to fire-cues.

It seems likely that fire frequency effects on germination speed in this study were influenced by the reproductive output and resprouting capacity trade-off (Bellingham and Sparrow 2000). Individuals of the facultative resprouter *A. torulosa* from environments that experienced frequent fire had greater reductions in germination speed than those from lower fire frequencies. Individuals exposed to intermediate fire frequencies where this trade-off may be reduced had lower variability in germination speeds. Therefore, fire could potentially inhibit germination for species if they have not been previously exposed to a flammable environment. My results support this prediction as post-fire reproductive mode and the post-fire environment in which the species occurs influenced germination rates.

Through later life stages in *A. torulosa*, woody foliage cover and climate variability were stronger drivers of reproductive output and population age structure than fire history, respectively. Higher woody foliage cover resulted in an increased number of cones for *A. torulosa* likely due to higher photosynthetic potential in these environments associated with greater resource availability for reproduction (Wheelwright and Logan 2004). Lower annual climate variability may have been a stronger driver of *A. torulosa* age class structure as stressful environments impose limitations on growth, with more variable climates likely to increase the trade-off between survival and reproduction (Hamann *et al.* 2021; Zhang *et al.* 2020). Conversely, I found no effect of climate or environmental attributes on *A. littoralis* reproduction or age class structure, but establishment of *A. littoralis* was likely limited by these attributes as sampling occurred outside of the preferred coastal habitat (Australian Biological Resources Study. Advisory Committee 1989; Foreman and Walsh 1993). For both species, I found no effect of time since fire on the number of cones, as while recent fire activity could be associated with lower cone number, most sampling in this study occurred in areas two or more years post-fire which is sufficient time for cone production (Plumanns-Pouton *et al.* 2024). Thus, my results indicate that reproductive effort and age class structure appear to be independent of fire history, even with up to seven fires over 36 years. However, more extreme fire frequencies are likely to filter populations as such frequent fire could compromise resprouting or reproduction and seedling establishment abilities (Christensen *et al.* 1981; Clarke *et al.* 2015; Gill and Catling 2002; McColl-Gausden *et al.* 2022). Therefore, further experimental research in this system remains vital to understanding fire history effects on *A. littoralis* and *A. torulosa* reproductive output and age class structure.

My results have important implications for Glossy black-cockatoo conservation and food tree restoration actions. Restoration programs producing seed collections should consider seed weight, because heavier seeds were more likely to have a competitive advantage (i.e., reduced time to reach 50% germination). However, restoration programs should also consider fire history in locations where the seed are collected. For *A. littoralis*, I recommend collecting seeds from individuals exposed to higher fire frequencies, such as four fires over past 36 years, and high annual temperature variability in my study region. Conversely, it may not be optimal to collect *A. torulosa* seeds from individuals exposed to high fire frequencies, such as six fires over past the 36 years, as while seeds were likely to be heavier, overall germination was much more variable. For *A. torulosa*, I would recommend collecting seeds from individuals exposed to intermediate fire frequencies such as three fires over the past 36 years. I also recommend restoration efforts focus on areas with higher annual temperature variability due to the higher likelihood of aging populations with low population turnover (i.e., low proportions of seedlings and saplings to adults). In my inland study region within southeast Queensland, restoration effort is best invested in *A. torulosa* food trees as this species is found more commonly throughout the region and, as a facultative resprouter, is likely to have higher resilience under projected fire regime changes. Nevertheless, coastal regions where *A. littoralis* is abundant may benefit from restoring patches of both *A. littoralis* and *A. torulosa* as a buffer against high fire frequencies and immaturity risk in *A. littoralis*.

Conclusion

Plant responses to fire vary throughout their life cycle, especially at critical life stages such as germination and transitions from seedlings through to adults. Thus, investigating how fire drives selection on reproductive traits and controls age class structure is vital for conservation and restoration actions to mitigate the effects of future fire regime changes. In this study I investigated the influence of fire history and environmental attributes on fire-cued germination responses, reproductive output, and age class structure in congeneric obligate seeding and facultative resprouting *Allocasuarina spp.*. Exposure to fire-cues were not essential for germination of either species but for the facultative resprouter fire-cues, to some extent, inhibited germination. This inhibition was especially extreme in individuals not pre-adapted to fire or exposed to high fire frequencies. Thus, selection for reproductive traits conferring higher resilience to fire-cues was more likely to be exerted on the obligate seeder *A. littoralis*. However, reproductive trait selection in the facultative resprouter *A. torulosa* was dependent on fire history likely due to a reproduction – resprouting trade-off. *Allocasuarina torulosa* seeds from environments experiencing higher fire frequencies were less resilient to fire-cues compared to seeds from more moderate fire frequencies. Nevertheless, fire history effects were not a strong driver during later life stages with climate and environmental attributes being stronger drivers of reproductive output and age class structure. However, fire frequency is likely to impact age class structure due to age-related effects, but areas at higher fire frequencies with *Allocasuarina spp.* in my study region were limited. Thus, further research in this system is recommended to better understand the impacts of fire history on reproduction and age class structure, with a particular focus on sampling higher fire frequencies.

Data and code availability

Data and code are currently stored as a public repository on GitHub (Charles and Smith 2025): https://github.com/felicityeloise/Allocasuarina_germfire.

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APPENDIX

Incubation temperature optimisation

Incubation temperature optimisation tests show that low temperatures of 6 °C and 10 °C slowed germination rates or stopped germination over the 28-day sampling period, and these temperatures were not considered further (Fig. S1). *Allocasuarina littoralis* germination was most consistent in chamber temperatures from 14 °C to 32 °C (70-90%, Fig. S1). For *Allocasuarina littoralis*, 17 °C was determined optimal as this chamber had the highest overall germination for two of the three individuals tested (85-95%, Fig. S1). Germination in *Allocasuarina torulosa* was similar at 17 °C and 20 °C (85-90%, Fig. S1). *Allocasuarina torulosa* germination was most consistent across the range of temperatures from 14 °C to 36 °C. I selected 20 °C for the experimental tests as it fell within the range of temperatures suggested by Turnbull and Martensz (1982).

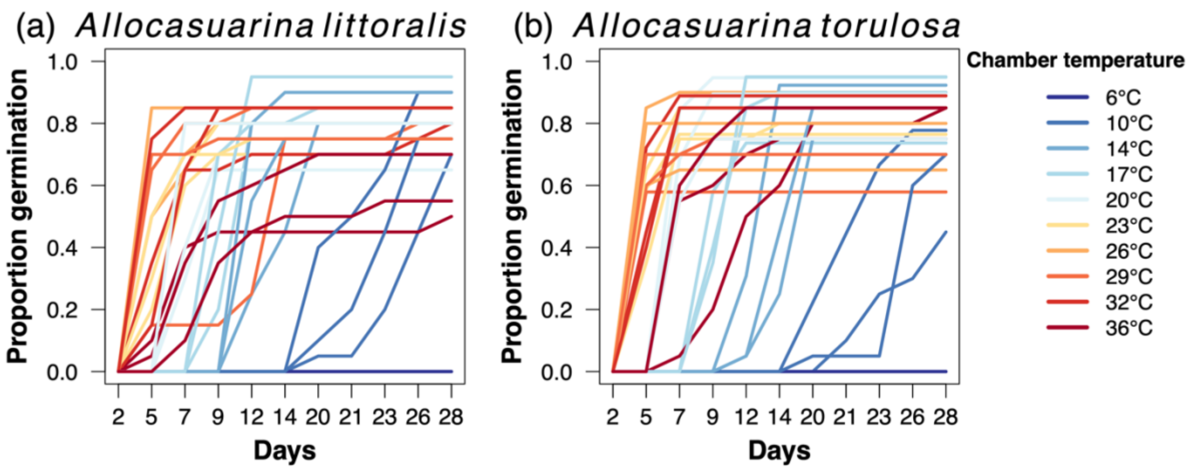

Figure S6 Cumulative proportion of seeds germinated along a thermal gradient bar ranging from 6 °C to 36 °C for (a) *Allocasuarina littoralis* and (b) *A. torulosa*. No germination occurred in either species in chambers at 6 °C.

Heat shock and smoke exposure tests

Heat shock optimisation tests showed consistently high germination in both species at 80 °C, but variable germination responses between the species as temperature and duration increased (Fig. S2). In *Allocasuarina littoralis*, the lethal temperature threshold was between 110 °C to

120 °C as no germination occurred in seeds exposed to 125 °C (data not plotted). At 110 °C, *A. littoralis* germination varied widely and began to decline: some individuals had high germination at exposures of 10 minutes, while others had poor germination at this temperature, even with exposure times as low as 1 minute (Fig. S2a). In *A. littoralis*, exposures of 5 minutes at 80 °C and 95 °C produced relatively consistently high germination rates, with germination being the same or greater than the control, respectively (Fig. S2a). In *A. torulosa*, the lethal temperature threshold was between 95 °C to 105 °C, as only seeds exposed to short durations at 110 °C germinated (Fig. S2b). Exposure times of 5 minutes at 85 °C and 95 °C produced consistently high germination, which was similar or greater than that of the controls. Therefore, for both species a 5-minute exposure time at 85 °C and 95 °C was selected for heat shock in the main experiment.

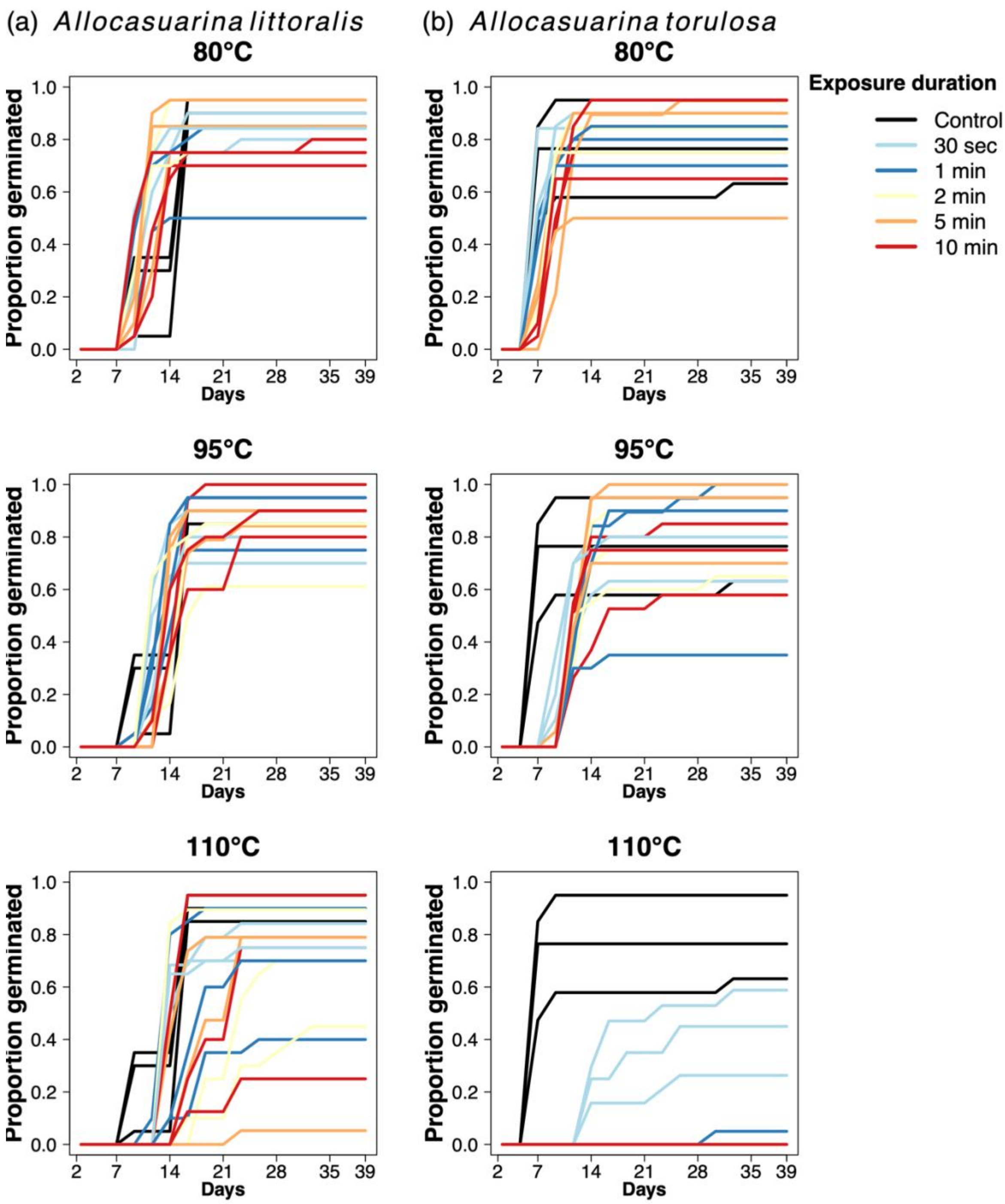

Figure S7 Cumulative proportion of seeds germinated in heat shock optimisation tests at 80 °C, 95 °C, and 110 °C compared to a control (black) in (a) *Allocasuarina littoralis* and (b) *A. torulosa*.

Smoke exposure optimisation tests showed similar germination rates between *Allocasuarina* leaf litter and pine sawdust (Fig. S3). However, short exposures to *Allocasuarina* leaf litter resulted in more variable germination rates than other treatments (Fig. S3), for unknown reasons. Seeds that remained ungerminated after smoke treatments were all deemed unviable by TTC testing (see seed viability and trait measurements section). A 20-minute exposure to aerosol smoke was selected as optimal as it produced high germination rates for both species and smoke types which was comparable to the controls (Fig. S3). At this 20-minute smoke exposure time, *Allocasuarina* leaf litter smoke produced higher germination rates than pine sawdust (Fig. S3). Thus, *Allocasuarina* leaf litter derived smoke was selected for the main experiment.

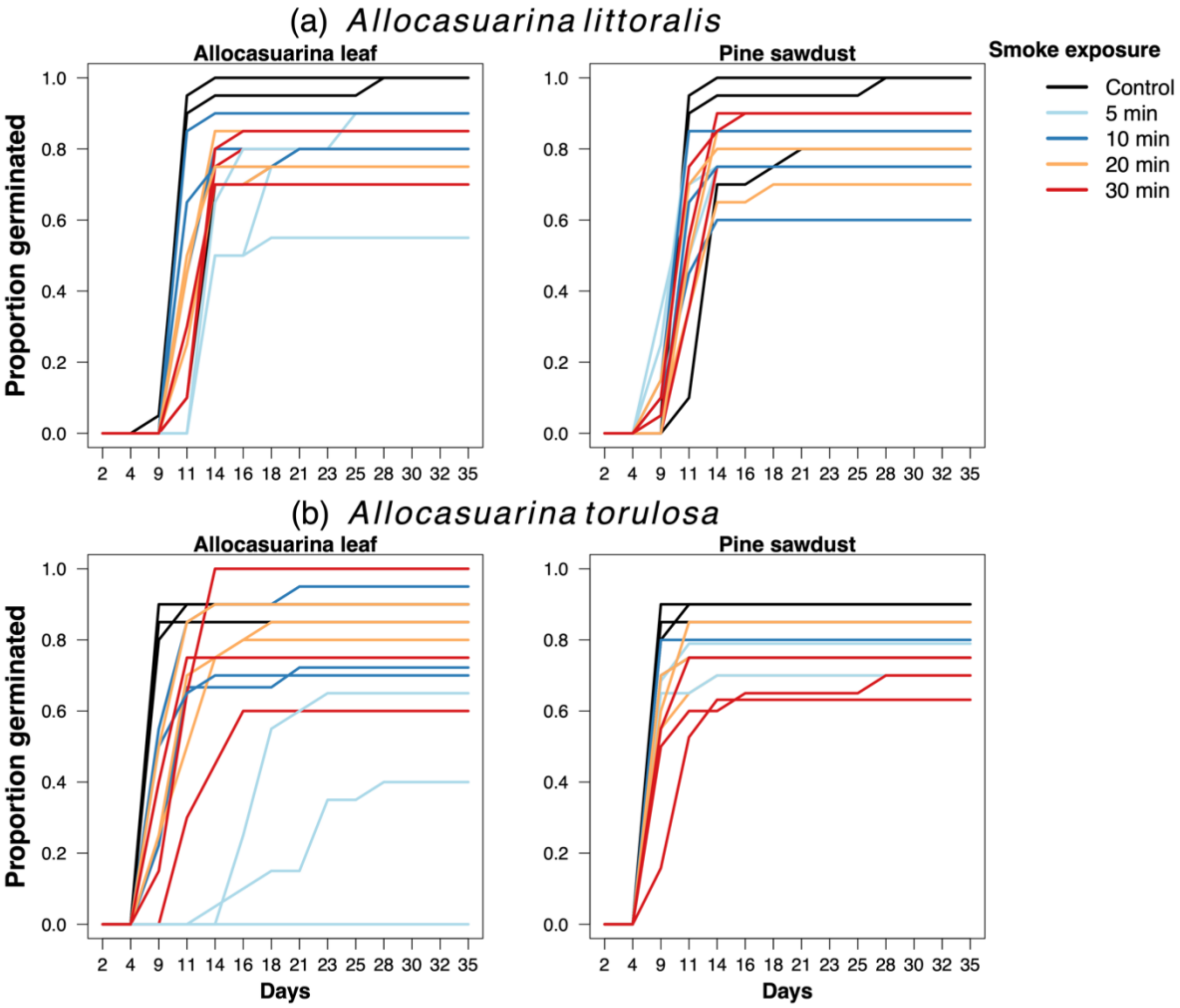

Figure S8 Cumulative proportion of seeds germinated after exposure to aerosol *Allocasuarina* leaf litter or pine sawdust derived smoke in (a) *Allocasuarina littoralis* and (b) *A. torulosa*.

Full factorial experiment seed viability

Viability rates assessed by the x-ray and tetrazolium methods were correlated for both *A. littoralis* and *A. torulosa* across experimental replicates (71% and 74%, respectively, Fig. S4), indicating no effect of treatment on seed viability. Despite the expectation that higher heat treatments (e.g., 95 °C) would result in variable post-germination viability, tetrazolium tests (TTC) showed that seed viability across all treatments was high for *A. littoralis* and *A. torulosa* (Fig. S5). Furthermore, there was also high correlation between the viability test methods post-treatment and germination (85% and 79% respectively, Fig. S5).

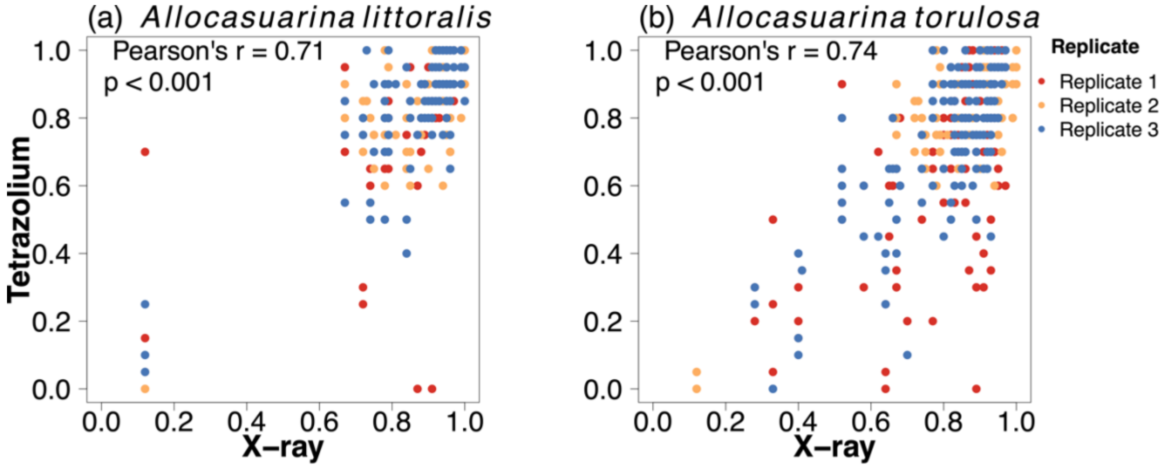

Figure S9 Average pre-germination x-ray and post-germination TTC viability rate correlations for (a) *Allocasuarina littoralis*, and (b) *A. torulosa* individuals across experimental replicates.

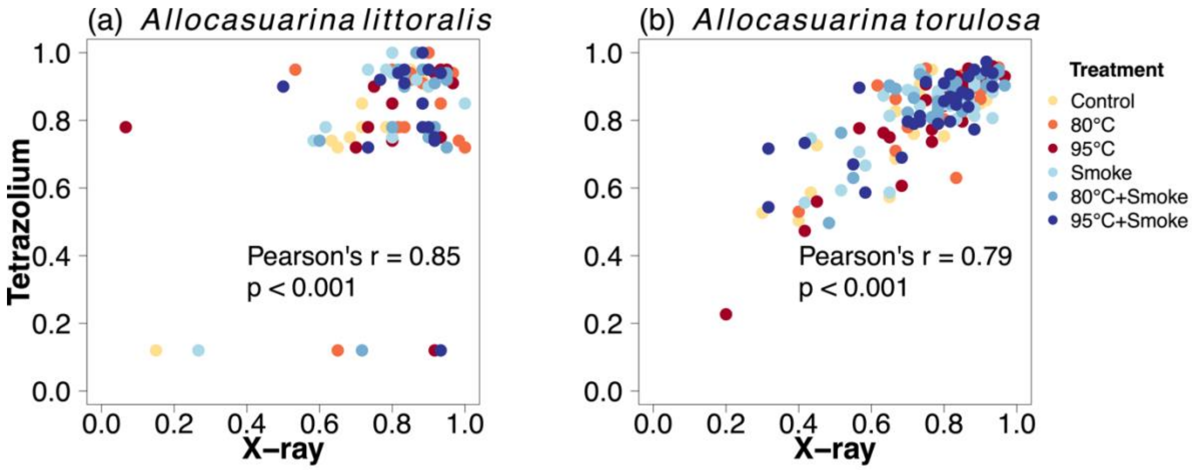

Figure S10 Average pre-germination x-ray and post-germination TTC viability rate correlation for (a) *Allocasuarina littoralis*, and (b) *A. torulosa* individuals across seed treatments.

Full factorial germination experiment

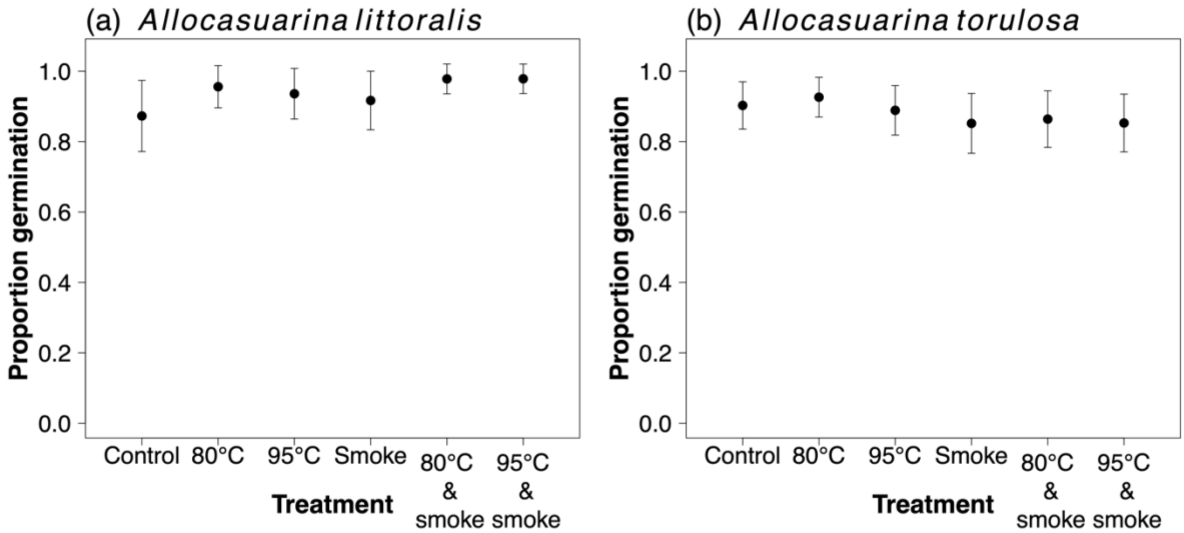

Figure S6 The estimated effect and 95% confidence intervals of seed treatments on proportion germination of (a) *Allocasuarina littoralis* and (b) *A. torulosa*.

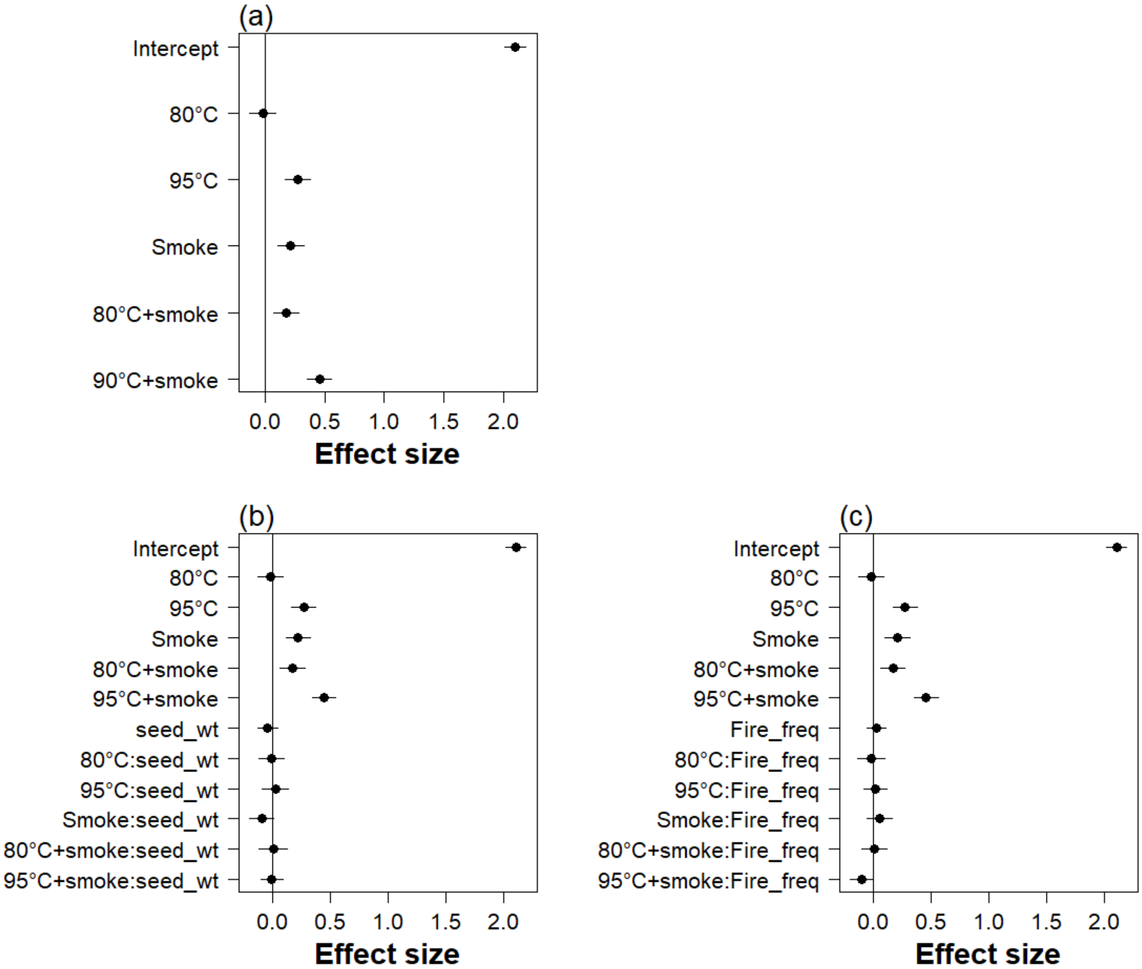

Figure S7Effect sizes of coefficients and 95% confidence intervals for models examining time to 50% germination in *Allocasuarina torulosa*. Effect sizes were examined to determine the strength of effects for models including (a) treatment, (b) treatment × seed weight, and (c) treatment ×fire frequency.

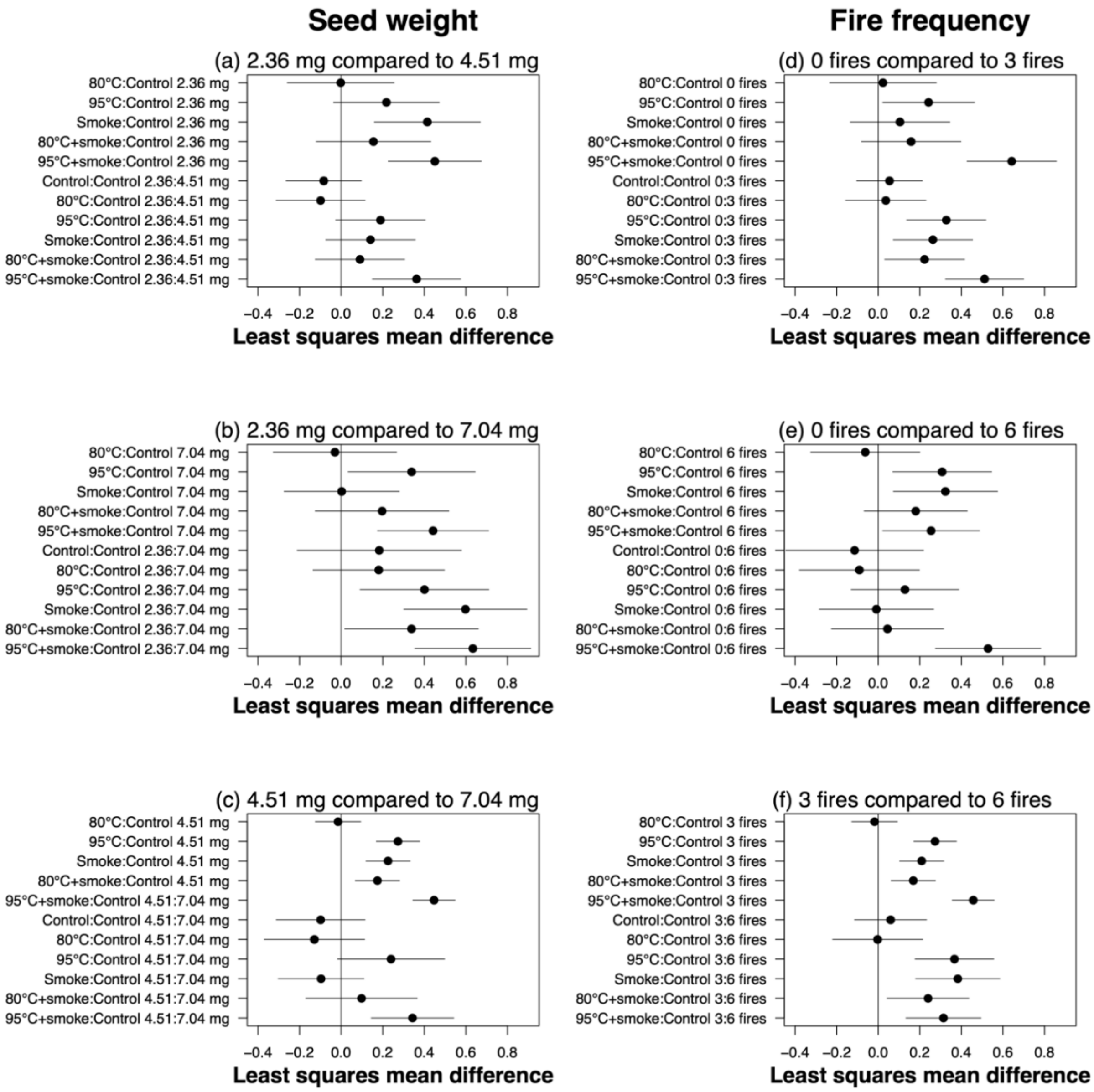

Figure S8 Least squares mean differences and 95% confidence intervals for models examining the effect of seed treatments compared to controls on time to 50% germination in *Allocasuarina torulosa*. Models included an interaction between treatment and (a-c) seed weight, or (d-f) fire frequency. To aid comparisons between different seed weights or fire frequencies, differences were examined for (a, d) minimum seed weight = 2.36 mg or fire frequency = 0; (b, e) average seed weight = 4.51 mg or fire frequency = 3; and (d, f) maximum seed weight =7.04 or fire frequency = 6.

Population age structure

Table S7 Models used to examine the influence of fire frequency, time since fire, and environmental variation on age class structure in *Allocasuarina littoralis*.

Fire metric	Age class	Model structure	Number of parameters	AIC_c	ΔAIC_c	Log likelihood
Fire frequency	Seedlings	Null model	2	18.03	0.00	-3.01
		Temperature seasonality	2	21.33	3.31	0.00
		Topographic wetness	2	21.33	3.31	0.00
		Latitude	2	21.56	3.53	-0.11
		Fire frequency	2	25.52	7.49	-2.09
		Precipitation seasonality	2	27.10	9.07	-2.88
		Foliage projective cover	2	33.74	15.71	-2.87
		Fire frequency × precipitation seasonality	3	96.00	77.97	0.00
		Fire frequency × temperature seasonality	3	96.00	77.97	0.00
		Fire frequency × topographic wetness	3	96.00	77.97	0.00
		Fire frequency × latitude	3	96.02	78.00	-0.01
		Fire frequency × foliage projective cover	3	Inf	Inf	0.00
	Saplings	Null model	2	18.03	0.00	-3.01
		Fire frequency	2	21.89	3.87	-0.28
		Temperature seasonality	2	22.46	4.44	-0.57
		Latitude	2	23.23	5.20	-0.95
		Precipitation seasonality	2	27.23	9.20	-2.95
		Topographic wetness	2	27.35	9.32	-3.01
		Foliage projective cover	2	28.53	10.51	-0.27
		Fire frequency × precipitation seasonality	3	96.00	77.97	0.00
		Fire frequency × temperature seasonality	3	96.00	77.97	0.00
		Fire frequency × latitude	3	96.00	77.97	0.00
		Fire frequency × topographic wetness	3	96.05	78.02	-0.03

		Fire frequency × foliage projective cover	3	Inf	Inf	0.00
	Recruits	Null model	2	18.03	0.00	-3.01
		Fire frequency	2	21.89	3.86	-0.28
		Temperature seasonality	2	22.91	4.88	-0.79
		Latitude	2	23.18	5.15	-0.92
		Precipitation seasonality	2	27.23	9.20	-2.95
		Topographic wetness	2	27.35	9.32	-3.01
		Foliage projective cover	2	29.96	11.93	-0.98
		Fire frequency × temperature seasonality	3	96.00	77.97	0.00
		Fire frequency × precipitation seasonality	3	96.00	77.98	0.00
		Fire frequency × topographic wetness	3	96.02	77.99	-0.01
		Fire frequency × latitude	3	96.026	78.23	-0.13
		Fire frequency × foliage projective cover	3	Inf	Inf	0.00
Time since fire	Seedlings	Null model	2	18.03	0.00	-3.01
		Temperature seasonality	2	21.33	3.31	0.00
		Topographic wetness	2	21.33	3.31	0.00
		Latitude	2	21.56	3.53	-0.11
		Time since fire	2	24.39	6.36	-1.53
		Precipitation seasonality	2	27.10	9.07	-2.88
		Foliage projective cover	2	33.74	15.71	-2.87
		Time since fire × latitude	3	96.00	77.97	0.00
		Time since fire × precipitation seasonality	3	96.00	77.97	0.00
		Time since fire × topographic wetness	3	96.00	77.97	0.00
		Time since fire × temperature seasonality	3	96.17	78.14	-0.09
		Time since fire × foliage projective cover	3	Inf	Inf	0.00
	Saplings	Null model	2	18.03	0.00	-3.01
		Temperature seasonality	2	22.46	4.44	-0.57
		Latitude	2	23.23	5.20	-0.95
		Time since fire	2	23.86	5.83	-2.26
		Precipitation seasonality	2	27.23	9.20	-2.95

	Topographic wetness index	2	27.53	9.32	-3.01
	Foliage projective cover	2	28,53	10.51	-0.27
	Time since fire × temperature seasonality	3	96.00	77.97	0.00
	Time since fire × precipitation seasonality	3	96.01	77.98	0.00
	Time since fire × topographic wetness	3	96.03	78.00	-0.02
	Time since fire × latitude	3	96.11	78.08	-0.06
	Time since fire × foliage projective cover	3	Inf	Inf	0.00
Recruits	Null model	2	18.03	0.00	-3.01
	Temperature seasonality	2	22.91	4.88	-0.79
	Latitude	2	23.18	5.15	-0.92
	Time since fire	2	23.81	5.78	-1.24
	Precipitation seasonality	2	27.23	9.20	-2.95
	Topographic wetness	2	27.35	9.32	-3.01
	Foliage projective cover	2	29.96	11.93	-0.98
	Time since fire × temperature seasonality	3	96.00	77.97	0.00
	Time since fire × topographic wetness	3	96.00	77.97	0.00
	Time since fire × precipitation seasonality	3	96.01	77.98	-0.01
	Time since fire × latitude	3	96.10	78.07	-0.05
	Time since fire × foliage projective cover	3	Inf	Inf	-0.12

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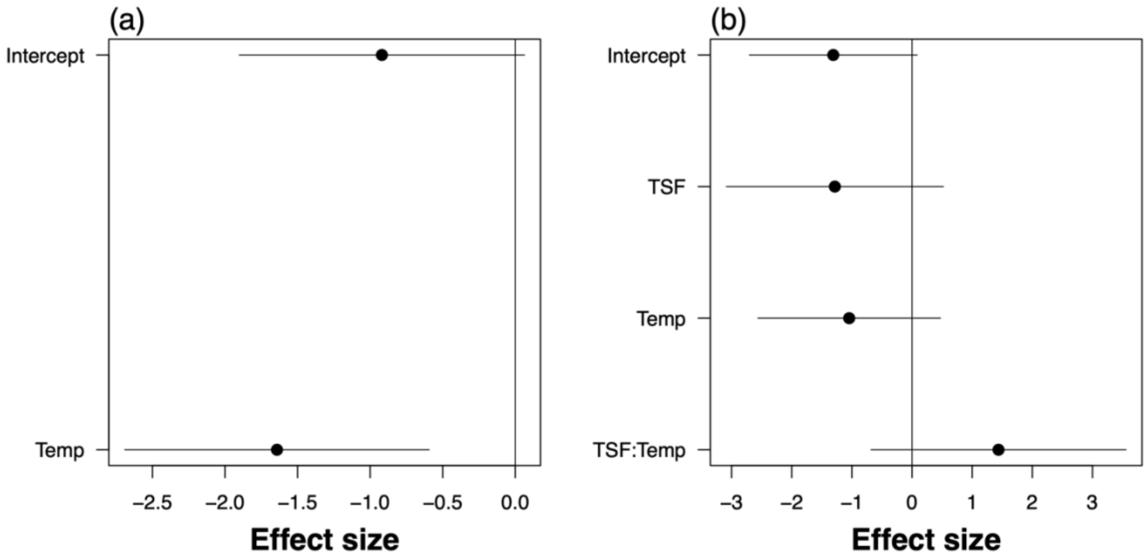

Figure S11 Effect sizes of coefficients and 95% confidence intervals for the influence of (a) temperature seasonality, and (b) temperature seasonality and time since fire (TSF) interaction on the proportion of recruits to adults in *Allocasuarina torulosa*.

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