Fire history influences reproduction in congeneric food tree species with contrasting post-fire reproductive strategies

Running title: Fire effects on tree reproductive traits

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Author Contributions

FEC: conceptualisation, writing – original draft, writing – review & editing, data curation, formal analysis, investigation, methodology, software, visualisation. **PTM**: conceptualisation, supervision, writing – review & editing. **ALS**: conceptualisation, formal analysis, methodology, visualisation, supervision, writing – review & editing.

Abstract

In fire-prone regions globally, plants have developed reproductive strategies enabling population persistence under historical fire regimes. However, many common plant species are threatened by a mismatch between historical and contemporary fire regimes, which also threatens animal species relying on them for resource provision. We investigated how recent fire history affected reproductive trait variation in two congeneric food tree species (Casuarinaceae) for the threatened Glossy black-cockatoo (*Calyptorhynchus lathami*, Cacatuidae): *Allocasuarina littoralis* (an obligate seeder) and *A. torulosa* (a facultative resprouter). Lab-based germination experiments measured germination responses of seeds exposed to heat shocks of 80° and 95°C, smoke, and combinations of these treatments. Field-based surveys measured demographic structure and reproductive output. Heat and smoke treatments slowed germination in *A. torulosa* but had no effect on germination in *A. littoralis*. Germination rate increased with seed weight but was unaffected by heat and smoke. Heavier seeds were associated with higher fire frequencies and greater temperature variability at seed collection sites. In *A. torulosa*, heavier seeds took longer to germinate, especially when seeds were collected from frequently burnt sites, possibly reflecting a resprouting-seed production trade-off. Fire history did not influence reproductive output or population demographic structure for either species. For restoration, heat and smoke treatments are unlikely to be necessary once seeds are released from cones. However, local fire history and seed weight should be considered when collecting seeds for restoration programs. Differences in species post-fire establishment driven by variation in germination response to fire of *Allocasuarina* could influence a dietary specialist threatened cockatoo.

Keywords: fire ecology, fire management, fire-cued germination, reproductive traits, demography, plant-animal interaction

Highlights

- Fire history shaped germination more than heat and smoke treatments.
- Closely related trees responded differently to recent fire history.
- Accounting for fire history can improve restoration and conservation.

Introduction

Fire is an important driver of plant trait evolution, especially for reproductive traits which are closely associated with plant fitness (Keeley and others, 2011; Villellas and others, 2021; Campbell and others, 2022). 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 and persist through propagules stored in soil or canopy seedbanks (P+) (Pausas and others, 2004; Pausas and Keeley, 2014; Clarke and others, 2015). These strategies result in contrasting life histories: resprouters tend to be long-lived with low population turnover, whereas obligate seeders are short-lived with high population turnover (Pausas and others, 2004; Pausas and Keeley, 2014). Compared with seeders, resprouters generally have lower seed production and seedling densities than seeders, and their higher investment in resprouting tissue production may slow maturation rates (Verdú, 2000; Whelan and others, 2002; Hunter, 2003; Pausas and others, 2004; Pausas and Keeley, 2014; Ojeda and others, 2016; Bendall and others, 2022). Thus, resprouters face a trade-off between investment in seed production and resprouting (Verdú, 2000; Whelan and others, 2002; Hunter, 2003; Pausas and others, 2004; Pausas and Keeley, 2014; Ojeda and others, 2016; Bendall and others, 2022). Conversely, obligate seeders have high seed production and seedling densities, and usually have mass recruitment events post-fire (Keith

and others, 2002; Hunter, 2003; Pausas and Keeley, 2014; Ojeda and others, 2016). Studying closely related species with differing post-fire reproductive modes can be useful because trait variation can be explained by ecology and environmental variation rather than phylogeny (Seglias and others, 2018; Cortés-Flores and others, 2020; Fenollosa and others, 2021; Zhao and others, 2021; Wang and others, 2022).

Since seed regeneration enables successful recolonisation after disturbance, many species from fire prone ecosystems show strong germination responses to fire-related cues of heat and smoke (linked to fire intensity and severity, Bellingham and Sparrow, 2000; Kennard and others, 2002; Hanley and others, 2003; Gómez-González and others, 2008; Pausas and Keeley, 2014; Le Breton and others, 2020). Selection on seed traits over evolutionary timescales is likely stronger in obligate seeders than resprouters due to their reliance on regeneration from seed (Bellingham and Sparrow, 2000; Pausas and Keeley, 2014; Bendall and others, 2022). Obligate seeders can also spread risk and increase reproductive output by producing smaller seeds under certain fire regimes (Verdú, 2000). Heat from fire creates a selection pressure on seed size and how this plays out depends on the type of seedbank (Lamont and others, 2019). Serotinous canopy seedbanks, for example, lack the insulating properties of soil and rely on seed mass to protect the embryo, resulting in selection for larger seeds (Keeley, 1977; Escudero and others, 2000; Hanley and others, 2003; Liyanage and Ooi, 2017; Tangney and others, 2025). Understanding how recent fire history influences post-fire germination could help determine whether enough trait variability exists for species to respond to contemporary and near-future fire regime changes. Integrating fire history information from seed collection sites has been done (e.g., Gómez-González and others, 2011; Vandvik and others, 2014; Gómez-González and others, 2016; Zaki and others, 2021; Kasel and others, 2024; Plumanns-Pouton and others, 2024) but most studies apply

laboratory-based heat and smoke treatments without considering fire history variation at the seed collection site (e.g., Tangney and others, 2020). This is a problem because we might miss recent variation in responses driven by contemporary fire regimes (Gómez-González and others, 2016; Kelly and others, 2025).

Contemporary changes in fire regimes are causing misalignments between plant trait variability and fire regime characteristics (Moritz and others, 2012; Johnstone and others, 2016; Day and others, 2020; Canadell and others, 2021; Harvey and Enright, 2022; Kelly and others, 2025). For example, some fire-adapted sclerophyllous species have failed to regenerate after fires that are too severe or too frequent (Bennett and others, 2016; Etchells and others, 2020; Sano and others, 2025). Declines in regeneration of primary producers could impact plant-animal interactions or food webs (Smith, 2018; Carbone and others, 2019; Ellison, 2019; Kelly and others, 2020; Rainsford and others, 2020; Ballarin and others, 2024). Specialist plant-animal interactions are most vulnerable to changes in fire regimes, yet are drastically understudied in fire ecology (Charles and others, 2025). Whether trees can adapt in situ is unclear, as fire regime changes are often accompanied by climatic changes which can also impact post-fire regeneration success (Stevens-Rumann and others, 2018; Young and others, 2019; Kelly and others, 2025). Understanding how plants respond to fire is especially important when those species form critical habitat for specialised plant-animal interactions (Talluto and Benkman, 2014; Lybbert and St. Clair, 2016; Charles and others, 2025).

After germination, individuals must be able to grow and recruit into the adult population, and the environmental conditions driving transitions among growth stages can change rapidly post-fire (Keeley and others, 2011; Smith and others, 2016). Variation in post-fire recruitment rates can result in differing population demographic structure across fire history gradients

(Taylor, 2010; Pausas and Keeley, 2014; Ojeda and others, 2016). In obligate seeders, short inter-fire intervals relative to their age at maturity cause immaturity risk, where two or more fires occur before a species can reach reproductive maturity (McCarthy and others, 1999; Turner and others, 2009; Taylor, 2010; Pulsford and others, 2016). This situation reduces the ability of obligate seeders to replenish seedbanks and increases the risk of local extinction (Keith, 1996; Agne and others, 2022; McColl-Gausden and others, 2022). Conversely, resprouters tend to survive exposure to repeated fire (Taylor, 2010; Pausas and Keeley, 2014), with shifts in demographic structure caused by age- and size-related variation in resprouting capacity or, in facultative resprouters, additional recruitment from seed (Gill and Catling, 2002; Shibata and others, 2014; Clarke and others, 2015; Matula and others, 2019). Fire at appropriate intervals, therefore, is critical for both obligate seeders and resprouters to cue regeneration, promote seedling establishment, and stimulate flowering (McCarthy and others, 1999; Taylor, 2010; Enright and others, 2011; Zirondi and others, 2021; Agne and others, 2022; Thomsen and Ooi, 2022). Research examining population demographic structure in closely related species with contrasting reproductive modes (e.g., Ojeda and others, 2016; Schmidberger and Ladd, 2020) can help untangle the relationship between post-fire reproductive mode and reproductive trait expression.

We investigated the influence of fire history 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 species are common across eastern Australia, where they form mixed stands with *Eucalyptus spp*. in swamps, woodlands, and forests (Neldner and others, 2019; Atlas of Living Australia, 2021a, b). Both species are dioecious and store seeds in serotinous cones in the canopy. Fire management guidelines are often based on the *Eucalyptus* species which co-occur with

Casuarinaceae, but eucalypts require different fire regimes than Casuarinaceae (Kellman, 1986; Moss and others, 2011; Stewart and Moss, 2015; Neldner and others, 2019; Romano and others, 2026). The *Allocasuarina* species we studied are common and widespread, and their seeds are a primary food resource for the threatened dietary specialist Glossy black-cockatoo, *Calyptorhynchus lathami* (Cacatuidae) (listed nationally as Vulnerable, *EPBC* Act 1999). Glossy black-cockatoos have one of the most specialised diets of all Australian birds, feeding on a subset of 12 of 78 Casuarinaceae species (Chapman, 2007; Menkhorst and others, 2024), making them vulnerable to fire regime changes which impact food resource availability and quality (Cameron and others, 2021; Delzoppo and others, 2021; Mooney and others, 2026). 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). Thus, understanding the fire ecology of *Allocasuarina spp*. is fundamental to effective conservation for these cockatoos.

We first aimed to determine how contemporary fire frequency and post-fire reproductive mode affected fire-cued germination responses (heat and smoke, as measures of fire intensity and severity) and seed size. (**H1**) We expected that post-fire reproductive mode would influence germination and seed investment, leading to heavier seeds and higher tolerances to fire cues in *A. littoralis* (obligate seeder) than *A. torulosa* (facultative resprouter). Given the trade-off between post-fire reproductive mode and seed size and number (Leishman, 2001; Pausas and Keeley, 2014; Hodgson and others, 2020; Walsh and others, 2022; Li and others, 2025; Maleki and others, 2025), we expected *A. littoralis* to have (**H1a**) heavier seeds with increasing fire frequency; and (**H1b**) increased germination rates in response to heat and smoke (Paula and Pausas, 2008; Pausas and Keeley, 2014). *Allocasuarina torulosa* was expected to have (**H1c**) lighter seeds with increasing fire frequency; and **(H1d**) lower

151 germination rates in response to heat and smoke (Staden and others, 2000; Paula and Pausas,
152 2008).
153
154 Second, we aimed to determine how fire frequency, time since fire, and post-fire reproductive
155 mode influenced population demographic structure and reproductive output (i.e., number of
156 cones on female individuals). We expected (**H2**) longer times since fire and low fire
157 frequencies would reduce the ratio of seedlings and saplings to mature individuals but
158 increase reproductive output. Due to immaturity risk, we expected (**H2a**) high fire frequency
159 and short time since fire would result in a lower ratio of seedlings or saplings to mature
160 individuals in *A. littoralis*, compared with *A. torulosa*. Because high-intensity or frequent fire
161 would reduce the capacity to reach reproductive maturity during inter-fire periods (Enright
162 and Lamont, 1989; Pausas and Keeley, 2014), we also expected (**H2b**) high fire frequency
163 and short times since fire would be related to lower reproductive output in both species.
164
165 Third, we aimed to investigate how environmental attributes relating to site productivity
166 (topographic wetness, water availability (Gallant and Austin, 2012); foliage projective cover,
167 woody vegetation cover (Fisher and others, 2018)) and climate (latitude; precipitation
168 seasonality and temperature seasonality (Noce and others, 2020; Wang and others, 2024))
169 interacted with fire regimes to influence reproductive trait variation. We expected (**H3a**)
170 environments with low productivity and high climate variability to be stressful for
171 *Allocasuarina*, reducing reproductive output, seed weight, and ratios of seedlings and
172 saplings to mature individuals (Enright and others, 2015; McColl-Gausden and others, 2022).
173 Additionally, as lower latitudes are associated with increased temperatures, growth and
174 reproduction, we expected (**H3b**) sampling locations at lower latitudes to have higher
175 reproductive outputs, seed weight and ratios of seedlings and saplings to mature individuals

(Moles and Westoby, 2003; Chamorro and others, 2018; Käber and others, 2021; Wang and others, 2023).

Methods

Study region

This study took place in southeast Queensland, Australia, within the distributional range of Glossy black-cockatoos, *Allocasuarina littoralis* and *A. torulosa*. Sampling sites (hereafter 'sites') included public land (i.e., national parks, state forests, and conservation parks) and private properties (i.e., Hidden Vale Nature Refuge, Gillies Ridge Nature Refuge, Bartopia Nature Refuge, and Bulimbah Nature Refuge) (Figure 1). The region has a subtropical climate with mean maximum temperatures in summer ranging from 25°C to 32°C, and in winter from 17°C to 21°C. Mean annual rainfall in the region ranges from 688 mm to 1584 mm. In our inland study region in southeast Queensland, *A. torulosa* is more common than *A. littoralis* (Atlas of Living Australia, 2021a, b). Dominant vegetation at sampling locations included eucalypt woodland to open forest and, for some *A. torulosa* sampling locations, wet eucalypt forest (Neldner and others, 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 and others, 2019).

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* is distributed widely from coastal to inland regions in forests on fertile soils (Stanley and others, 1983; Australian Biological Resources Study. Advisory Committee, 1989). *Allocasuarina littoralis* lives, on average, 40-70 years (with a potential lifespan up to 100 years), while *A. torulosa* can typically live for 50-100 years as individuals can resprout following fire (Kattge and others, 2020; Falster and others, 2021). Reproductive maturity can be reached in five years for both species, but *A. littoralis* is more likely to take 10 years (Kattge and others, 2020; Falster and others, 2021). Both species gradually release seed from serotinous cones as they dry (Crowley, 1986; Kattge and others, 2020; Falster and others, 2021). A number of studies have considered post-fire recruitment mode of *A. littoralis* and *A. torulosa*. Some have reported *A. littoralis* to be an obligate seeder (R-P+) which is fire killed and germinates from canopy-stored seed (Burley and others, 2007; Williams and others, 2012), while others suggest it is a facultative resprouter (R+P+) (Schmidt and Stewart, 1997; Knox and Clarke, 2005; Clarke and others, 2010; Clarke and others, 2015; Paul and others, 2017; Kattge and others, 2020). It is unclear from these studies whether *A. littoralis* was classified as a resprouter following the convention of resprouting after 100% scorch or stem death (a condition required for categorisation as R+, Pausas and others, 2004). *Allocasuarina torulosa* is generally considered to be a resprouter (Kubiak, 2009; Williams and others, 2012; Benwell, 2024), with some evidence of inter-fire seed regeneration where canopy seedbanks are available (R+P+, facultative resprouter) (Clarke and others, 2015; Kattge and others, 2020).

Both tree species lack seed dormancy, with seed protection and germination timing mediated by storage in serotinous cones (Turnbull and Martensz, 1982; Crowley, 1986). 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, Crowley, 1986; Clarke and others, 2000). In other Casuarinaceae, seeds have been reported to survive heat shock of up to 120°C (Hanley and Lamont, 2000; Callister and others, 2018). Temperature in *Allocasuarina* canopies during wildfire is unknown but flame temperature in eucalypt forests, where *Allocasuarina* commonly occur, can reach 300° to 1100°C (Huss and others, 2019), and *Allocasuarina* leaf litter can burn at high temperatures (e.g., soil temperatures of 60° to 111°C at 1 cm depth, Tangney *et al.* 2020). Storage of *Allocasuarina* seeds in woody cones provides some insulation from fire, reducing extremes of temperature exposure but potentially exposing seeds to temperatures above 100°C during fire (Huss and others, 2019).

Field surveys

We established 40 sampling locations to cover a range of fire histories within the distribution of the Glossy black-cockatoo, *A. littoralis*, and *A. torulosa*. Our primary goal was to sample each tree species across a range of fire histories (**H2**) and environments (**H3**). Thus, we used occurrence records from Atlas of Living Australia to locate areas where *A. littoralis* and *A. torulosa* had been observed within our study region. We then randomly selected occurrence records for each species across a range of fire frequencies. We conducted reconnaissance field surveys at these locations to verify occurrences. Where no *Allocasuarina* were found, we moved to another location with a similar fire frequency until a range of sampling locations was identified. Reconnaissance surveys identified that *A. littoralis* and *A. torulosa* generally occurred in areas with low fire frequency (unburnt or 1-3 fires from 1987-2023) with fewer occurrences (<20 records) in frequently burned areas (4-7 fires from 1987-2023) (Atlas of Living Australia, 2021a, b; The Global Biodiversity Information Facility, 2022a, b). As such, we established more sampling locations in areas with low fire frequency (0-3 fires from

1987-2023; 32 sampling locations) than high fire frequency (4-7 fires from 1987-2023; six sampling locations). Furthermore, high fire frequency sampling locations were in areas where *A. torulosa* was found (26 sampling locations), but not *A. littoralis*, limiting the fire frequency analysis for *A. littoralis*. *Allocasuarina littoralis* might have been excluded from high fire frequency areas due to inappropriate fire regimes, climate, or soil conditions.

Once 40 sampling locations had been identified, a 50 m × 4 m transect was established, beginning at a randomly identified individual tree, and oriented towards other individuals. Within locations where multiple transects were sampled (e.g., 2-7 transects), transects were spaced at least 140 m apart (range = 140 m – 14 km). Multiple individuals were sampled within transects (mean = 27.2 individuals; and range = 7 – 123 individuals). This hierarchical sampling structure was accounted for in the analysis. For each individual tree on a transect, we measured: demographic class (described below); diameter at breast height (DBH, cm), recruitment type (e.g., basal resprout, trunk resprout, seedling, or none); condition (e.g., dead or alive, burnt or unburnt); and height in metres using a Suunto PM5/360 PC Clinometer (Vantaa, Finland) or Nikon Forestry Pro II Laser Rangefinder (Tokyo, Japan). Following another *Allocasuarina* study (Schmidberger and Ladd, 2020), we used demographic class categories to investigate the influence of fire history on population demographic structure (**H2**). These categories were defined as: mature = height >1 m, DBH >3 cm; sapling = height >1 m, DBH <3 cm; and seedling = height <1 m. For female trees, the total number of cones were counted as a measure of reproductive output (**H2b**). Where more than 100 cones were present on a single female tree, we recorded average estimates based on counts from two observers into equal-width intervals of 50 cones (e.g., 100-150, 150-200, 200-250, 250-300, etc.).

Biological material was collected under scientific permits from the Queensland Government (P-PTC-100230959; P-PTUKI-100230962-2; P-PTUKI-100395507-2). 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. Females bearing cones were randomly selected around transects for cone collection, with at least 20 m between individuals (range within sampling locations 20 m – 130 m). On each cone collection tree, we sampled a minimum of two visually mature cones (i.e., brown to grey-brown in colour with closed valves) to maximise the chance that seed was fully developed but not yet released. To increase sample size for the germination experiment, more cones were collected where available, without removing all cones from an individual (up to 73 cones with an average of 12 cones per individual). Cones were stored in paper bags in a warm, dry environment until seeds were shed. Unshed seeds were manually extracted from cones using tweezers. Seeds were then 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

Germination experimental overview

We conducted a full factorial, replicated germination experiment, to test the hypothesis that post-fire reproductive mode and variation in fire frequency influenced fire-cued germination in *Allocasuarina* (**H1**). Three separate rounds of seed germination were conducted, with individuals exposed to the same treatment(s) in each replicate. Before conducting this experiment, we ran a series of optimisation trials on seed from both species to determine optimal incubation temperatures; heat shock temperatures and duration; aerosol smoke

exposure duration; and smoke material (Appendix S1: Section 1). Incubation temperature tests determined optimal germination temperature and baseline germination rate using thermal gradient bars (Appendix S1: Section 1, Figure S1). Heat shock and smoke trials determined (1) upper thresholds for heat tolerance and (2) the level at which seeds showed germination variability. This latter property was considered important to indicate levels of heat and smoke that could drive selection (Kelly and others, 2025) (Appendix S1: Section 1, Figure S2, S3).

After establishing optimal conditions, we began the full factorial experiment. For this experiment, the main response variables were (1) proportion of seeds germinated, as a measure of an individual's resilience to seed treatments (**H1b**, **H1d**); (2) time to 50% germination, as a measure of an individual's competitiveness (**H1b**, **H1d**); and (3) seed weight, as a proxy measure of seed size (**H1a**, **H1c**) (seed weight and size are strongly correlated and relate to investment in sexual reproduction Eriksson, 1999; Verdú, 2000; Gnan and others, 2014). A 'seed lot' was defined as the whole collection of seeds from an individual while a 'seed sample' was defined as 20 seeds from a seed lot used in the germination experiments. Seed weight was measured in two ways: first as the seed lot and, second, as a 10-seed fraction to estimate the total number of seeds in the seed lot. The estimated total number of seeds was used to estimate the average seed weight per seed in a seed lot.

For all germination experiments, seed samples 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 new sterile petri dishes prior to germination to reduce exposure to accumulated smoke residues. Seeds exposed to a

326 combination of heat shock and smoke treatments were heat shocked prior to aerosol smoke
327 exposure. Seeds in all experiments (excluding incubation temperature optimisation) were
328 germinated in illuminated refrigerated incubators (TRIL495-1-SD, Thermoline Scientific,
329 Wetherhill Park, New South Wales, Australia) with a 12-hour photoperiod provided by
330 Grolux fluorescent lighting (36W) and temperatures set to 17°C for *A. littoralis* and 20°C for
331 *A. torulosa* (see Appendix S1: Figure S1). Germination was considered to have occurred
332 upon emergence of the radicle from the testa. After emergence, the germinant was recorded
333 and removed from the petri dish to allow space for other seeds to germinate. Germination
334 trials ran for a minimum of 29 days and stopped when no new seeds had germinated in a 7-
335 day period. This means there was no upper time limit for the germination trial; we continued
336 counting germinates until there was zero germination over a 7-day period.
337
338 Seed viability measurements
339
340 Seed viability was measured using two methods: (1) non-destructive x-ray prior to
341 germination experiments to estimate pre-treatment viability without reducing the number of
342 seeds for the experiment; and (2) destructive post-experiment tetrazolium tests to determine
343 whether seeds which remained ungerminated at the end of the trial were viable (Peters, 2000).
344 X-rays were taken on a Faxitron MX-20 Imaging system (Lincolnshire, IL, USA), on *ca*. 100
345 seeds from a seed lot with four replicates of 25 seeds at 28 kV for 6.55 seconds. X-ray images
346 were examined to determine seed fill, a metric related to the amount of seed embryo and
347 endosperm which is correlated with viability (Gagliardi and Marcos-Filho, 2011; Tausch and
348 others, 2024). Unfilled seeds were considered unviable but seeds with partial filling were
349 classed as viable as there was potential for germination. X-ray viability data were
350 summarised as the proportion of viable x-ray imaged seeds 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, seeds were observed under a dissection microscope and seeds were classed as viable if the radicle and cotyledons were completely stained pink (Peters, 2000). Any TTC staining inconsistencies or lack of staining was considered to indicate unviable seeds (Peters, 2000).

Full factorial germination experiment

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 (see Appendix S1: Section 1, Figure S2, S3 for optimisation). Three replicates for each treatment combination were conducted, with each replicate staggered by 14 days to account for potential starting condition biases. Seed germination was recorded on the first day after plating then every second to third day until germination ceased. For calculation of germination metrics, the germination period length (in days) had to be standardised across all replicates. Germination period lengths varied across replicates; thus, the germination period length was assigned a value of 46 days which was the longest germination period in the dataset. For replicates with germination periods shorter than this, a value of zero was assigned to each day beyond the germination period end date.

To test the hypothesis that variation in post-fire reproductive mode influenced fire-cued germination (**H1b**, **H1d**) and seed size (**H1a**, **H1c**), species were considered separately for analysis. Seed lots for *A. torulosa* were assigned to a fire frequency category based on that at

376 the collection site (i.e., low fire frequency = 0-3 fires, and high fire frequency = 4-7 fires
377 from 1987-2023). Due to seed limitations, we were unable to assign each individual tree to all
378 six treatments (e.g., an individual with only 120 seeds could only be assigned to 3
379 treatments). Thus, we used the `arrangements` R package version 1.1.9 (Lai, 2019) in R
380 version 4.3.1 (R Core Team, 2018) to randomly assign the six treatments to seed lots, with six
381 separate rounds of assignment. We subsequently reduced treatment assignments on a case-by-
382 case basis such that only three treatments were assigned to a seed lot with 120 seeds. During
383 this case-by-case treatment assignment, we ensured 15 individual seed lots were included for
384 all six treatments. Thus, each germination experiment replicate included six treatments with
385 300 seeds from 15 seeds lots, totalling 1800 seeds for *A. littoralis*, 1800 seeds for *A. torulosa*
386 low fire frequency, and 1800 seeds for *A. torulosa* high fire frequency.
387
388 *Spatial data compilation*
389
390 Fire frequency data from was obtained from Queensland Parks and Wildlife Service (Table 1)
391 and subset temporally (i.e., 1987-2023) to match the temporal resolution of modelled
392 estimates of fire frequency from satellite-derived data (see Charles and others, 2026). Year of
393 last fire was obtained from Queensland Parks and Wildlife fire history data and satellite-
394 derived fire history data. Areas that were unburnt between 1987-2023 were assigned a year of
395 last fire as 1986. Time since fire was calculated by subtracting year of last fire from the
396 sampling year. We obtained data on temperature and precipitation seasonality (Fick and
397 Hijmans, 2017), Topographic Wetness Index (TWI) (Gallant and Austin, 2012), and Foliage
398 Projective Cover (FPC) (Department of Environment, 2020, 2024) (Table 1). Spatial data
399 requiring resolution adjustments were rescaled to 30 m resolution (Table 1) using the
400 `gdalUtilities` R package version 1.2.5 (O'Brien, 2023) and nearest neighbour

resampling. Foliage Projective Cover (FPC) data was obtained 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).

Analysis

Analyses of reproductive trait data were conducted in R version 4.3.1 (R Core Team, 2023) using generalised linear mixed models in the `lme4` R package version 1.1-34 (Bates and others, 2015). We 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. To investigate the influence of fire and (**H1**, **H2**) environmental variation (**H3**) on reproductive trait variation, we fit models with and without a main effect for fire frequency, time since fire, or another environmental variable. 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 the `AICcmodavg` R package version 2.3-3 (Mazerolle, 2020). The best model in the candidate set was chosen as the model which (1) had the lowest AIC_c and (2) improved model fit over the null model by $\Delta AIC_c > |2|$ (Arnold, 2010; Leroux, 2019). Where two or more models were ranked within 2 AIC_c units of the top model and included one additional parameter, we 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)

426 confidence intervals did not overlap zero (Arnold, 2010; Leroux, 2019). For top-ranked
427 models which included factorial predictor variables with multiple levels, we calculated least-
428 squares means contrasts to determine differences between levels within the factor. For
429 example, if the top-ranked model included germination treatment, we used least-squares
430 means contrasts to determine if germination rate differed in seed exposed to 95°C and control
431 seeds.
432
433 Germination experiment
434
435 Cumulative proportion germination for each individual was calculated by dividing the
436 cumulative sum of germination by the total number of seeds germinated at the end of the
437 experiment. First and last germination day and time to 50% germination were calculated by
438 adapting functions from the `germinationmetrics` R package version 0.1.8 (Aaravind
439 and others, 2022). To analyse the effect of seed treatment and fire frequency on fire-cued
440 germination (**H1b**, **H1d**) we fit seven models each for proportion of seeds germinated and
441 time to 50% germination: a null model; three univariate models with main effects for
442 treatment, fire frequency, and seed weight; and three multivariate models investigating
443 interactions between treatment, fire frequency and seed weight. To account for individual-
444 level similarities in responses and potential effects of replicates, we included a random effect
445 for replicate and individual in each model. To analyse the effect of fire frequency and
446 environment on seed weight (**H1a**, **H1c**, **H3a**, **H3b**), we used the calculated average weight
447 of a singular seed (hereafter 'seed weight') as the response variable. We fit twelve models
448 with a random effect for individual: a null model; six univariate main effect models for fire
449 frequency and environmental attributes; and five multivariate models investigating
450 interactions between fire frequency and environmental attributes.

Population demographic structure surveys

To analyse the effect of fire history on population demographic structure, we first calculated the ratio of seedlings, saplings, and recruits (i.e., grouped seedlings and saplings) to mature individuals plus individuals from that demographic class. For example, proportion of seedlings was calculated as $\frac{Number\ seedlings}{Number\ mature+seedlings}$. To analyse the effect of fire (**H2**) and environment (**H3a**, **H3b**) on population demographic structure, we 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. We did not fit multivariate models including interactions for *A. littoralis* as there were too few transects which would lead to overfitting. To analyse the effect of fire (**H2b**) and environment (**H3a**, **H3b**) on reproductive output (i.e., cone number), we fit eight models: a null model and seven univariate models for fire frequency, time since fire, and environmental attributes. We did not fit multivariate models for reproductive output as there were too few individuals with cones which led to overfitting. For population demographic structure and reproductive output, we included 'transect' nested within 'site' as a random effect in each model, to account for the hierarchical structure of data.

Results

Overview

We sampled eight *A. littoralis* and 32 *A. torulosa* transects across the study region (Figure 1). Seeds from 115 individuals, comprising 40 *A. littoralis* and 75 *A. torulosa* individuals were sampled at these transects (Figure 1). Seven individuals with less than 60 seeds were excluded from the germination experiment, resulting in 108 individuals (37 *A. littoralis* and 71 *A. torulosa*). Estimated fire frequency ranged from zero to four (*A. littoralis*) and zero to seven (*A torulosa*) fires at sampling locations over a 36-year time period. Time since fire at sampling locations for both species ranged from at least 36 years (i.e., those sites where the time since last fire was unknown) to two-years post-fire.

Germination experiment

Seed viability was high across all experimental replicates and seed treatments for *A. littoralis* (mean = 0.813-0.854) and *A. torulosa* (mean = 0.767-0.880) (Appendix S1: Figure S4, S5). Viability assessed by the x-ray and tetrazolium methods were correlated for both species (*A. litoralis* $r > 0.71$, $p < 0.001$; *A. torulosa* $r > 0.74$, $p < 0.001$) and there were no noticeable differences in viability among experimental replicates or seed treatments (Appendix S1: Figure S4, S5). Germination rates were not strongly influenced by heat shock or smoke in either species, with null models ranked higher than models including seed treatments (Table 2, Appendix S1: Figure S6). Seed weight influenced germination rate for *A. littoralis* (ΔAIC_c relative to null model = 3.07; Table 2, Figure 2). For germination rate in *A. torulosa*, there was an interaction between seed weight and fire frequency (ΔAIC_c relative to null model =

496 10.97; Table 2, Figure 2). In both species, heavier seeds were generally associated with
497 greater germination rates (Table 2, Figure 2). The *A. torulosa* model with an interaction term
498 showed that, for individuals exposed to high fire frequencies, germination rates decreased
499 with increasing seed weight and were highly variable (20-90% proportion of seeds
500 germinated, Fig 2b).
501
502 For *A. littoralis*, there was little support for a seed treatment effect on time to 50%
503 germination as the null model was equivalent to the treatment only model ($\Delta AIC_c = 0.81$;
504 Table 3). The data from *A. torulosa* supported three models: seed treatment only (the top
505 ranked model, ΔAIC_c relative to null model = 108.77); an interaction between seed treatment
506 and seed weight (ΔAIC_c relative to the top ranked model = 0.11); and an interaction between
507 seed treatment and fire frequency (ΔAIC_c relative to the top ranked model = 0.67) (Table 3,
508 Appendix S1: Figure S7, S8). Time to 50% germination increased for all treatments
509 compared to controls, except for the 80°C treatment (Figure 3a, Appendix S1: Figure S7a).
510 Thus, heat and smoke generally slowed germination in *A. torulosa*. In the seed weight
511 interaction model, heavier seeds were typically faster to germinate, an effect which was most
512 pronounced for individuals exposed to the smoke treatment (Figure 3b, Appendix S1: Figure
513 S7b, S8a-c). In the fire frequency interaction model, seed from more frequently burned
514 transects had slower germination for 95°C; smoke; and 80°C + smoke treatments (Figure 3c,
515 Appendix S1: Figure S7c, S8d-f). However, this pattern was reversed for individuals exposed
516 to the 95°C + smoke treatment, suggesting faster germination for individuals exposed to more
517 frequent fire (Figure 3c, Appendix S1: Figure S7c, S8d-f).
518
519 Seed weight was influenced by an interaction between fire frequency and temperature
520 seasonality in *A. littoralis*, and an interaction between fire frequency and latitude in *A.*

torulosa (Table 4, Figure 4). 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, Figure 4a). At low to intermediate fire frequencies (0-1 fire over 36 years) there was no relationship between seed weight and temperature seasonality (Figure 4a). 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) (Figure 4b). There was no relationship between latitude and seed weight for intermediate fire frequencies (3 fires over 36 years, Figure 4b). 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 (Figure 4b).

Reproductive output and population demographic structure

Reproductive output (number of cones per female tree) was not influenced by fire frequency or time since fire (Appendix S1: Table S1). There was a positive effect of foliage projective cover on number of cones in *A. littoralis* (Intercept = -1.793 [standard error (SE) = 1.081], FPC = 0.066 [SE = 1.175], Appendix S1: Table S1) and *A. torulosa* (Intercept = -3.409 [SE = 1.1336], FPC = 2.105 [SE = 1.303], Appendix S1: Table S1).

Population demographic 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 (Appendix S1: Table S2). 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 =

546 1.303], Appendix S1: Table S3). Increasing temperature seasonality reduced the proportion of
547 saplings within the total population (Intercept = -1.040 [SE = 0.482], temperature seasonality
548 = -1.136 [SE = 0.481], Appendix S1: Table S3) and recruits within the total population
549 (Intercept = -0.919 [SE = -1.833]), temperature seasonality = -1.642 [SE = 0.535], Appendix
550 S1: Table S3). The interaction between temperature seasonality and time since fire on the
551 proportion of *A. torulosa* recruits within the total population was ranked within $\Delta AIC_c < 2$ of
552 the top-ranked model, but confidence intervals of the interaction term overlapped zero
553 (Appendix S1: Figure S9). Thus, fire history did not strongly influence reproductive output or
554 population demographic structure in *A. littoralis* or *A. torulosa*, with environmental
555 variability being more important in constraining recruitment processes (Appendix S1: Table
556 S1, S2, S3).
557

558 **Discussion**

559

560 This study showed that seed responses to fire history and fire-related germination cues varied
561 in two closely related tree species with differing post-fire reproductive modes. Fire frequency
562 from seed collection locations was found to influence variation in laboratory-based
563 germination experiments. This is important because it indicates that reproduction in plant
564 species from fire-prone ecosystems is influenced not only by fire-related germination cues,
565 but also the recent fire history to which they have been exposed. Variation in germination
566 response to fire of these two closely related tree species could influence a dietary specialist
567 threatened cockatoo through differences in species post-fire establishment success and
568 competitiveness, driving food resource availability (Delzoppo and others, 2021; Menkhorst
569 and others, 2024). Although we did not study the cockatoo distribution directly, the cockatoos
570 are such specialist feeders and so cryptic and difficult to study that the results from our study

571 can inform food tree conservation and restoration actions (Chapman, 2007). Thus,
572 investigating how fire drives selection on reproductive traits and controls population
573 demographic structure is vital for conservation and restoration actions to mitigate the effects
574 of future fire regime changes.
575
576 Fast germination provides individuals with a competitive advantage (Hodges and others,
577 2021); therefore, overall germination and germination speed can be promoted by fire-related
578 cues, especially in obligate seeders adapted for post-fire germination (Ramos and others,
579 2019; Tangney and others, 2020; Hodges and others, 2021; Pausas and Lamont, 2022).
580 Results from this study ran contrary to this general prediction: exposure of seeds to heat and
581 smoke did not enhance germination rate and speed of the obligate seeder *A. littoralis* (**H1b**)
582 while it slowed germination rate in the facultative resprouter *A. torulosa* (**H1d**). Reduced
583 germination speed with temperature increase may be related to lethal temperature thresholds
584 which lower seed viability. This was supported by the reduction in germination speed being
585 stronger in *A. torulosa* (lethal temperature threshold *ca.* 100°C) than *A. littoralis* (lethal
586 temperature threshold *ca.* 110°C) (Hanley and others, 2003; Emery and others, 2011).
587 Nevertheless, *Allocasuarina* seeds were generally resilient to heat shocks up to 95°C with
588 little loss in seed viability. This was not unexpected as temperatures inside cone follicles of
589 other serotinous species during fire can reach 100°C (Huss and others, 2019) and fire triggers
590 seed release in serotinous species such as *Allocasuarina* to coincide with favourable post-fire
591 conditions (Lamont and others, 2019; Lamont and others, 2020). However, obligate seeders
592 are more likely to have increased post-fire germination speed due to their greater investment
593 in seeds than congeneric resprouters (Zammit and Westoby, 1987; Pausas and Keeley, 2014;
594 Tangney and others, 2020), and our study supported this prediction (**H1b**). For the facultative

595 resprouter, fire-cues inhibited germination, to some extent, with inhibition especially extreme
596 in individuals not pre-adapted to fire or exposed to high fire frequencies.
597
598 A trade-off between reproductive output and resprouting capacity is often seen in plants from
599 fire-prone ecosystems, whereby greater seed production is usually associated with lower
600 resprouting capacity (Bellingham and Sparrow, 2000). This trade-off might have influenced
601 fire frequency effects on overall germination and germination speed in this study. As
602 expected, (**H1d**) the facultative resprouting tree, *A. torulosa* had greater reductions in
603 germination speed when seed were collected from frequently burnt environments compared
604 with those from lower fire frequencies. This might reflect a higher investment in resprouting
605 from bud banks than in seed production, trading off seed germination performance in
606 individuals exposed to frequent fire (Bellingham and Sparrow, 2000; Verdú, 2000; Pausas and
607 Keeley, 2014; Bendall and others, 2022). However, the facultative resprouter produced
608 heavier seeds with increasing fire frequency, contrary to expectations (**H1c**). Nevertheless,
609 heavier *A. torulosa* seeds from collection sites exposed to frequent fire had slower
610 germination speed, indicating lower competitiveness compared to the obligate seeder (**H1**).
611 Thus, production of heavier seeds in *A. torulosa* could have reflected lower investment in
612 seeds (i.e., fewer seeds produced as seed weight increased) in frequently burnt environments
613 (Hodgson and others, 2020; Li and others, 2025; Maleki and others, 2025). An alternative
614 explanation is that delayed germination occurred as a response to heat induced stress and seed
615 tissue repair prior to germination (Visscher and others, 2021) and further research on this is
616 warranted.
617
618 Selection on seed traits may also be driven by environmental variation, with strongly seasonal
619 environments generally favouring heavier seeds that have greater energy reserves (Leishman

and others, 2000; Muller-Landau, 2010). This was reflected in our experiment where seeds collected from areas with variable climate conditions and high fire frequency (i.e., 4 fires over 36 years) had greater seed weight for the obligate seeder, *A. littoralis*, than the facultative resprouter, *A. torulosa* (**H3a**, **H3b**). 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 heavier, 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). Thus, exposure to fire was likely important for maintaining fire-cued germination in *A. torulosa*.

Our results indicate that reproductive effort and population demographic structure appear to be independent of fire history for both *Allocasuarina* species at later life stages (**H2**). In *A. torulosa*, higher woody foliage cover increased reproduction, which might be related to higher photosynthetic potential in these environments (**H3a**) (Wheelwright and Logan, 2004). Population demographic structure in *A. torulosa* might have been more strongly driven by annual climate variability as stressful environments impose limitations on growth (**H3a**), with more variable climates likely to increase the trade-off between survival, growth, and reproduction (Zhang and others, 2020; Hamann and others, 2021). Conversely, for *A. littoralis* the lack of effect of fire, climate, or environmental attributes on reproduction or population demographic structure may be linked to these attributes already limiting establishment of *A. littoralis* in our inland study region (**H3a**, **H3b**) (Australian Biological Resources Study. Advisory Committee, 1989; Foreman and Walsh, 1993). For both species,

the lack of effect of recent fire activity on reproductive output was likely due to most sampling occurring in areas two or more years post-fire, sufficient time for cone production (**H2b**) (Plumanns-Pouton and others, 2024). However, more extreme fire frequencies than sampled here (i.e., up to seven fires over 36 years) are likely to filter populations meaning that frequent fire could compromise seedling establishment and resprouting or reproduction abilities (Christensen and others, 1981; Gill and Catling, 2002; Clarke and others, 2015; McColl-Gausden and others, 2022). Thus, further experimental research is needed to better understand fire history effects on reproduction and population demographic structure in *Allocasuarina*.

Conservation implications

Our results have important implications for Glossy black-cockatoo conservation and food tree restoration actions. For restoration of food trees, seed collections should contain a range of seed weights. Heavier seeds which provide a greater competitive advantage (i.e., reduced time to reach 50% germination) are likely to aid restoration success and secure future food resources for Glossy black-cockatoos. Restoration programs might also consider fire history at seed collection sites. For *A. littoralis*, we recommend collecting seeds from individuals exposed to high fire frequencies (e.g., four or more fires in recent decades) and from areas with high annual temperature variability, as these had the greatest germination outcomes. Conversely *A. torulosa* seeds from individuals exposed to high fire frequencies (e.g., six or more fires in recent decades) might result in heavier seeds for restoration, but our data show that overall germination could be more variable. For *A. torulosa*, we recommend collecting seeds from individuals exposed to intermediate fire frequencies (e.g., three fires in recent

669 decades), as more moderate fire regimes showed stronger fire-cued germination responses in
670 *A. torulosa*.
671
672 Current fire histories appear to be suitable for persistence of *A. littoralis* and *A. torulosa* in
673 our study region (i.e., up to four and seven fires in 36 years, respectively). However, climate
674 change projections in many regions are associated with fire regime changes, including
675 increasing frequency, intensity, severity and extent of fire (Di Virgilio and others, 2019;
676 Hantson and others, 2024; Oliveira and Gil Martins, 2026). Such changes could threaten the
677 persistence of *Allocasuarina* populations under future fire regimes, especially obligate
678 seeders, and, thus, food resource availability for Glossy black-cockatoos. For restoration of
679 food trees, we recommend targeting areas with higher annual temperature variability and low
680 woody vegetation cover as *Allocasuarina* might otherwise decline under high environmental
681 stress with low population turnover (Romano and others, 2026). These areas are also likely to
682 be lower quality foraging for Glossy black-cockatoos which generally show preferences for
683 *Allocasuarina* stands burnt in the last 10-60 years (Delzoppo and others, 2021; Menkhorst
684 and others, 2024), further supporting requirement for food tree restoration. Trends toward
685 warmer annual temperatures are also occurring, increasing evapotranspiration (Hughes,
686 2003), which could further limit growth and reproduction processes in these species
687 (Gallagher and others, 2019; Zhang and others, 2020; Hamann and others, 2021), and alter
688 Glossy black-cockatoo food resource availability. In our study region, restoration is likely to
689 be most successful for *A. torulosa* due to their widespread distribution and higher likelihood
690 of persistence under projected higher fire activity (Hantson and others, 2016; Di Virgilio and
691 others, 2019; Dowdy and others, 2019). Nevertheless, restoring other food tree species would
692 provide a range of food resources for Glossy black-cockatoos, with *A. torulosa* buffering

against high fire frequencies and immaturity risk in *A. littoralis* or other obligate seeding food trees.

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Data accessibility statement: Data and code are available as an archived repository on Zenodo at https://doi.org/10.5281/zenodo.20602455. Data has also been supplied for peer review as additional supplementary information files not for publication.

Tables

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	30 m	Unchanged	1998-2014	Department of Environment 2020
- Landsat 2014				
- Statewide Landcover and Trees Study Sentinel-2	10 m, 30 m	30 m, Unchanged	2018, 2019, 2020, 2021	Department of Environment 2024

QLD = Queensland, DES = Department of Environment and Science.;

Table 2 Models Used to Examine the Influence of Fire Frequency and Seed Treatment on Proportion Germination in *Allocasuarina littoralis* and *A. torulosa* from Southeast Queensland, Australia. Models for Each Species Are Ranked from Lowest to Highest AICc, and the Top-Ranked Models Are Indicated in Bold.

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

AIC_c = Akaike's Information Criterion corrected for small sample sizes; Δ = change in.

Table 3 Models Used to Examine the Influence of Fire Frequency, Seed Weight, and Seed Treatment on Time to Reach 50% Germination in *Allocasuarina littoralis* and *A. torulosa* from Southeast Queensland, Australia. Models for Each Species Are Ranked from Lowest to Highest AICc, and the Top-Ranked Models Are Indicated in Bold.

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

AIC_c = Akaike's Information Criterion corrected for small sample sizes; Δ = change in.

Table 4 Models Used Examine the Influence of Fire Frequency and Environmental Variation on Seed Weight in *Allocasuarina littoralis* and *A. torulosa* from Southeast Queensland, Australia. Models for Each Species Are Ranked from Lowest to Highest AICc, and the Top-Ranked Models Are Indicated in Bold.

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

AIC_c = Akaike's Information Criterion corrected for small sample sizes; Δ = change in.

Figure legends

Figure 1 Sampling locations of *Allocasuarina littoralis* (n = 385 individuals from 8 transects) and *A. torulosa* (n = 703 individual from 32 transects) in southeast Queensland, Australia. Protected areas are displayed with black outlines including public land (conservation parks, state forests and national parks) and privately managed nature refuges. Fire frequency between 1987-2023 is show in red shading and was derived from integrating fire history records from Queensland Parks and Wildlife service and satellite imagery (Charles and others, 2026). Fire frequency 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 among transects, fire frequency was rescaled, so areas burnt 7 or more times are represented by the darkest shade of red.

Figure 2 The estimated effect (and 95% confidence intervals) of seed weight on proportion germination in (a) *Allocasuarina littoralis* and (b) *A. torulosa* from the top-ranked models for each species. The model for *A. torulosa* included an interaction between seed weight and fire frequency.

Figure 3 The estimated effect (and 95% confidence intervals) of seed treatment on time to 50% germination (days) from the three top-ranked models for *A. torulosa* ($\Delta AIC_c < 2$), (a) top-ranked model with a treatment effect; (b) second ranked model with an interaction between treatment and seed weight; and (c) third-ranked model with an interaction between treatment and fire frequency. For A. littoralis, there was little evidence of treatment effects on time to 50% germination (see Table 3).

Figure 4 The estimated effect (and 95% confidence intervals) of fire frequency on seed weight in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. (a) In *Allocasuarina littoralis*, seed weight was influenced by an interaction between fire frequency and temperature seasonality. (b) In *Allocasuarina torulosa*, seed weight was influenced by an interaction between fire frequency and latitude.

Figures

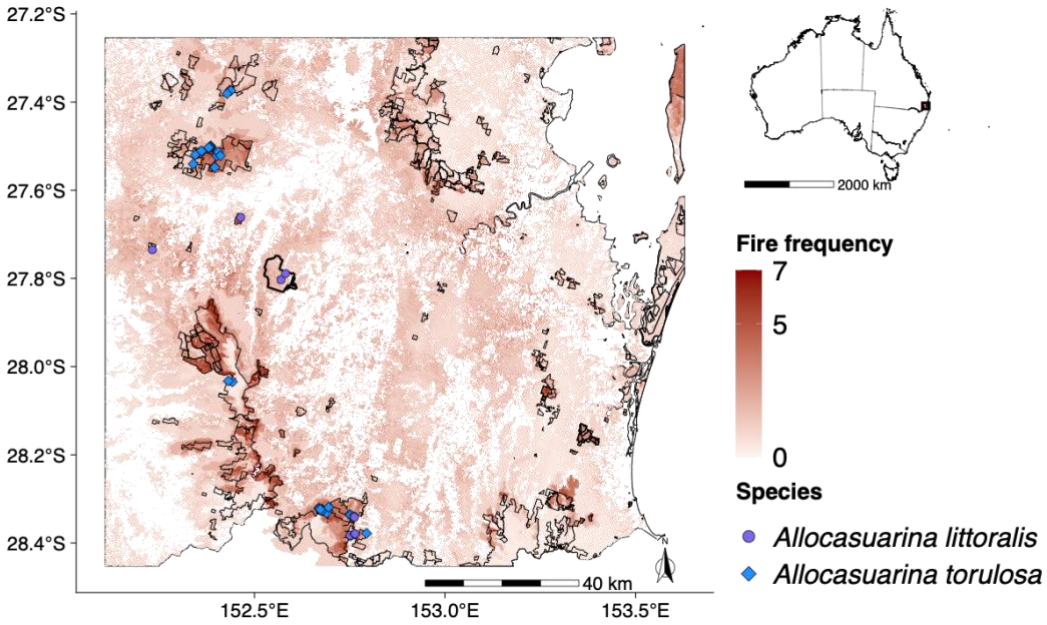


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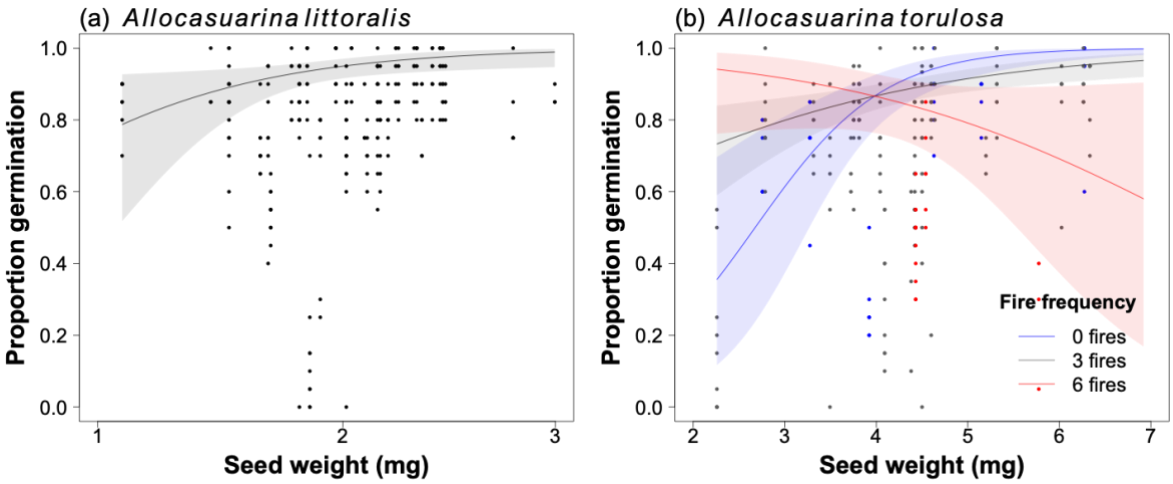


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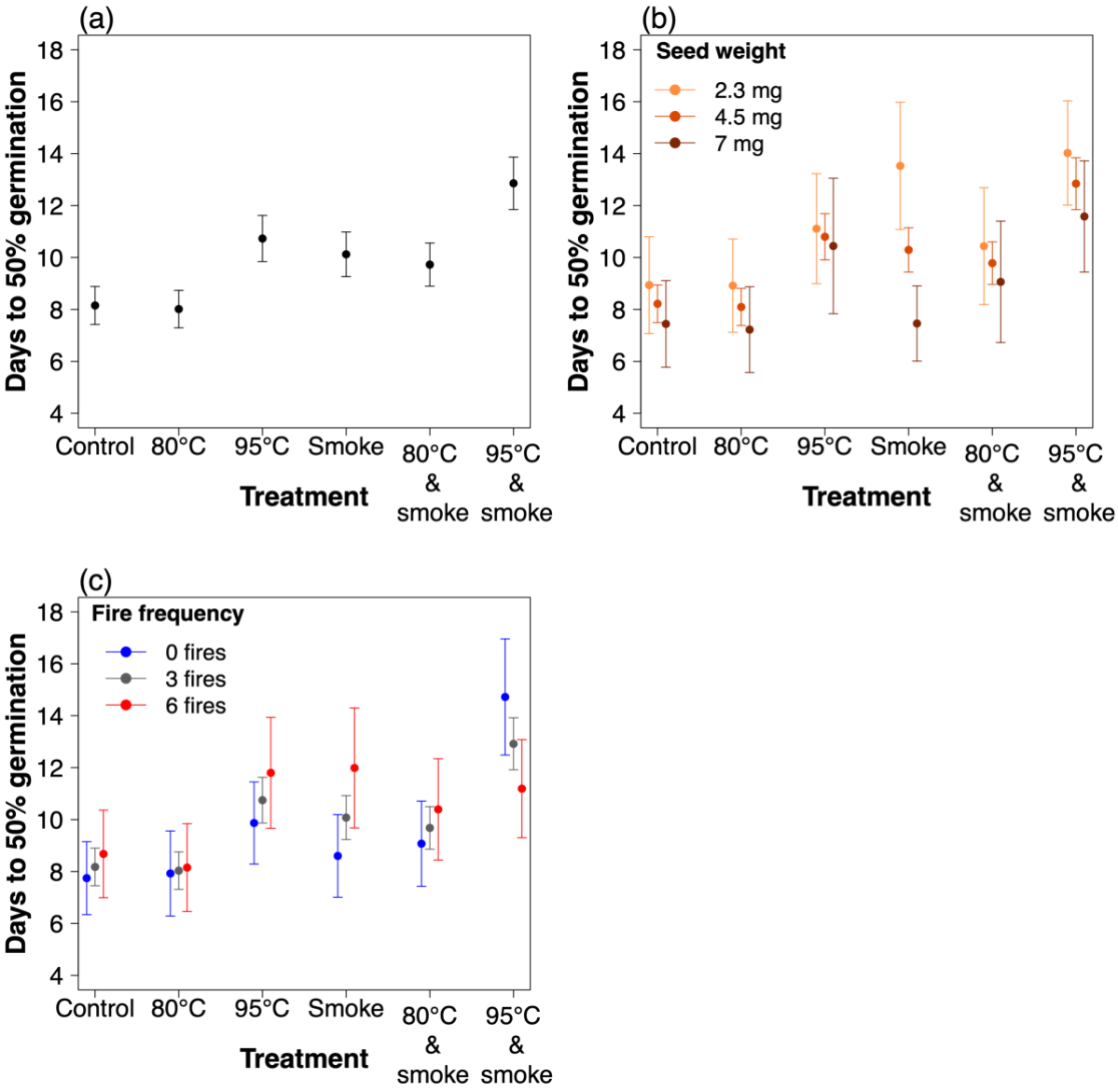


Figure 3 The estimated effect (and 95% confidence intervals) of seed treatment on time to 50% germination (days) from the three top-ranked models for *A. torulosa* (ΔAIC_c <2), (a) top-ranked model with a treatment effect; (b) second ranked model with an interaction between treatment and seed weight; and (c) third-ranked model with an interaction between treatment and fire frequency. For A. littoralis, there was little evidence of treatment effects on time to 50% germination (see Table 3).

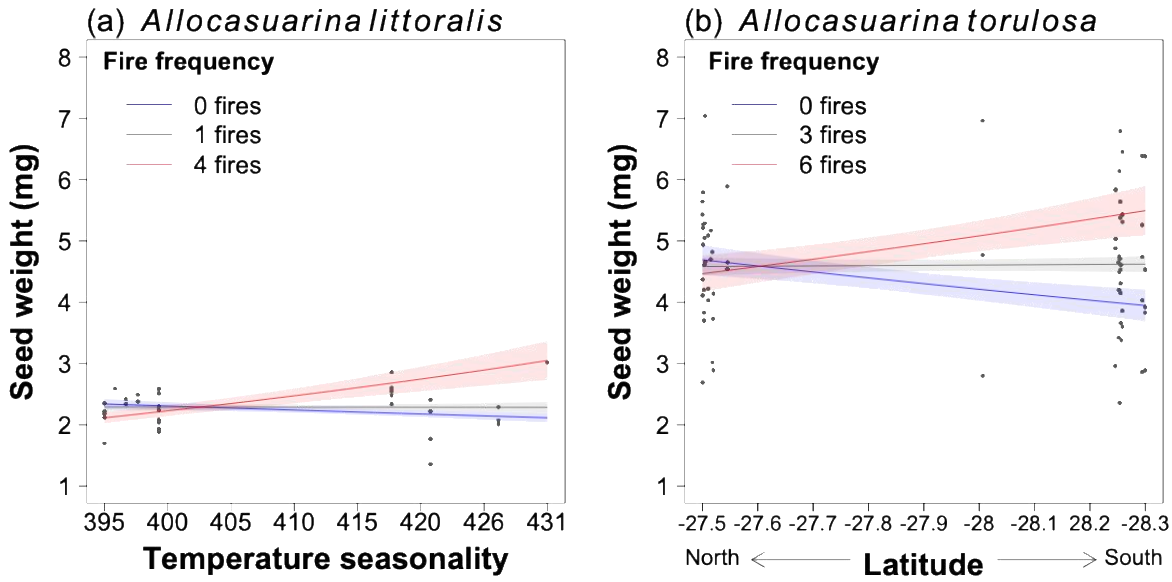


Figure 4 The estimated effect (and 95% confidence intervals) of fire frequency on seed weight in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. (a) In *Allocasuarina littoralis*, seed weight was influenced by an interaction between fire frequency and temperature seasonality. (b) In *Allocasuarina torulosa*, seed weight was influenced by an interaction between fire frequency and latitude.