Fire history influences reproductive traits in congeneric food tree species for a dietary specialist cockatoo

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Abstract

In fire-prone regions globally, plants have developed reproductive traits that enable population persistence under historical fire regimes. However, many common plant species are now threatened by a mismatch between historical and contemporary fire regimes, which also threatens animal species relying on them for food or habitat. We investigated how recent fire history (past 36 years) affected reproductive trait variation in two serotinous congeneric tree species (Casuarinaceae): *Allocasuarina littoralis* (an obligate seeder) and *A. torulosa* (a facultative resprouter). In southeast Queensland, Australia, these species are the primary food trees of the threatened Glossy black-cockatoo (*Calyptorhynchus lathami*, Cacatuidae). Thus, understanding responses to fire through different stages of food tree reproduction could assist conservation of this plant-animal interaction. In both tree species, germination rate (proportion of seeds germinated) increased with seed weight but was unaffected by laboratory treatments of heat and smoke. In both species, 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 trade-off between resprouting and seed production. Heat and smoke treatments slowed germination in *A. torulosa* but had no effect on germination in *A. littoralis*. Fire history did not influence reproductive output or population demographic structure for either species, but reproductive output (number of cones on female plants) was greater in sites with more woody vegetation cover. For restoration, heat and smoke treatments are unlikely to be necessary for successful germination of *A. littoralis* or *A. torulosa* once seeds are released from cones. However, local fire history and seed weight should be considered when collecting seeds for restoration programs, especially for *A. torulosa*. This study suggests that seed germination is influenced not only be laboratory fire treatments, but

also by the recent fire history at the seed collection sites. Variation in germination response to fire of two closely related *Allocasuarina* tree species could influence a dietary specialist threatened cockatoo through differences in species post-fire establishment success and competitiveness.

Introduction

Fire is an important driver of plant trait evolution, especially for reproductive traits which are closely associated with plant fitness (Keeley et al. 2011, Villellas et al. 2021, Campbell et al. 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 et al. 2004, Pausas and Keeley 2014, Clarke et al. 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 et al. 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 et al. 2002, Hunter 2003, Pausas et al. 2004, Pausas and Keeley 2014, Ojeda et al. 2016, Bendall et al. 2022). Thus, resprouters face a trade-off between investment in seed production and resprouting (Verdú 2000, Whelan et al. 2002, Hunter 2003, Pausas et al. 2004, Pausas and Keeley 2014, Ojeda et al. 2016, Bendall et al. 2022). Conversely, obligate seeders have high seed production and seedling densities, and usually have mass recruitment events post-fire (Keith et al. 2002, Hunter 2003, Pausas and Keeley 2014, Ojeda et al. 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 et al. 2018, Cortés-Flores et al. 2020, Fenollosa et al. 2021, Zhao et al. 2021, Wang et al. 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 et al. 2002, Hanley et al. 2003, Gómez-González et al. 2008, Pausas and Keeley 2014, Le Breton et al. 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 et al. 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 et al. 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 et al. 2000, Hanley et al. 2003, Liyanage and Ooi 2017, Tangney et al. 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 et al. 2011, Vandvik et al. 2014, Gómez-González et al. 2016, Zaki et al. 2021, Kasel et al. 2024, Plumanns-Pouton et al. 2024) but most studies apply laboratory-based heat and smoke treatments without considering fire history variation at the seed collection site (e.g., Tangney et al. 2020). This is a problem because we might miss recent variation in responses driven by contemporary fire regimes (Gómez-González et al. 2016, Kelly et al. 2025).

Contemporary changes in fire regimes are causing misalignments between plant trait variability and fire regime characteristics (Moritz et al. 2012, Johnstone et al. 2016, Day et al. 2020, Canadell et al. 2021, Harvey and Enright 2022, Kelly et al. 2025). For example, some fire-adapted sclerophyllous species have failed to regenerate after fires that are too severe or too frequent (Bennett et al. 2016, Etchells et al. 2020, Sano et al. 2025). Declines in regeneration of primary producers could impact plant-animal interactions or food webs (Smith 2018, Carbone et al. 2019, Ellison 2019, Kelly et al. 2020, Rainsford et al. 2020, Ballarin et al. 2024). Specialist plant-animal interactions are most vulnerable to changes in fire regimes, yet are drastically understudied in fire ecology (Charles et al. 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 et al. 2018, Young et al. 2019, Kelly et al. 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 et al. 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 et al. 2011, Smith et al. 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 et al. 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 et al. 1999, Turner et al. 2009, Taylor 2010, Pulsford et al. 2016). This situation reduces the ability of obligate seeders to replenish seedbanks and increases the risk of local extinction (Keith 1996, Agne et al. 2022,

McColl-Gausden et al. 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 et al. 2014, Clarke et al. 2015, Matula et al. 2019). Fire at appropriate intervals, therefore, is critical for both obligate seeders and resprouters to cue regeneration, promote seedling establishment, and stimulate flowering (McCarthy et al. 1999, Taylor 2010, Enright et al. 2011, Zirondi et al. 2021, Agne et al. 2022, Thomsen and Ooi 2022). Research examining population demographic structure in closely related species with contrasting reproductive modes (e.g., Ojeda et al. 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 et al. 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 et al. 2011, Stewart and Moss 2015, Neldner et al. 2019). 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 et al. 2024), making them vulnerable to fire regime changes which impact food resource availability and quality (Cameron et al. 2021, Delzoppo et al. 2021, Mooney et al. 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 et al. 2020, Walsh et al. 2022, Li et al. 2025, Maleki et al. 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 germination rates in response to heat and smoke (Staden et al. 2000, Paula and Pausas 2008).

Second, we aimed to determine how fire frequency, time since fire, and post-fire reproductive mode influenced population demographic structure and reproductive output (i.e., number of cones on female individuals). We expected (**H2**) longer times since fire and low fire frequencies would reduce the ratio of seedlings and saplings to mature individuals but increase reproductive output. Due to immaturity risk, we expected (**H2a**) high fire frequency

and short time since fire would result in a lower ratio of seedlings or saplings to mature individuals in *A. littoralis*, compared with *A. torulosa*. Because high-intensity or frequent fire would reduce the capacity to reach reproductive maturity during inter-fire periods (Enright and Lamont 1989, Pausas and Keeley 2014), we also expected (**H2b**) high fire frequency and short times since fire would be related to lower reproductive output in both species.

Third, we aimed to investigate how environmental attributes relating to site productivity (topographic wetness, water availability (Gallant and Austin 2012); foliage projective cover, woody vegetation cover (Fisher et al. 2018)) and climate (latitude; precipitation seasonality and temperature seasonality (Noce et al. 2020, Wang et al. 2024)) interacted with fire regimes to influence reproductive trait variation. We expected (**H3a**) environments with low productivity and high climate variability to be stressful for *Allocasuarina*, reducing reproductive output, seed weight, and ratios of seedlings and saplings to mature individuals (Enright et al. 2015, McColl-Gausden et al. 2022). Additionally, as lower latitudes are associated with increased temperatures, growth and reproduction, we expected (**H3b**) sampling locations at lower latitudes to have higher reproductive outputs, seed weight and ratios of seedlings and saplings to mature individuals (Moles and Westoby 2003, Chamorro et al. 2018, Käber et al. 2021, Wang et al. 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

176 'sites') included public land (i.e., national parks, state forests, and conservation parks) and
177 private properties (i.e., Hidden Vale Nature Refuge, Gillies Ridge Nature Refuge, Bartopia
178 Nature Refuge, and Bulimbah Nature Refuge) (Fig. 1). The region has a subtropical climate
179 with mean maximum temperatures in summer ranging from 25°C to 32°C, and in winter from
180 17°C to 21°C. Mean annual rainfall in the region ranges from 688 mm to 1584 mm. In our
181 inland study region in southeast Queensland, *A. torulosa* is more common than *A. littoralis*
182 (Atlas of Living Australia 2021a, b). Dominant vegetation at sampling locations included
183 eucalypt woodland to open forest and, for some *A. torulosa* sampling locations, wet eucalypt
184 forest (Neldner et al. 2019). At these sampling locations, the dominant soil orders included
185 tenosols, sodosols and dermosols and soil types included volcanics; red soils; sandstone; and
186 igneous, Cainozoic and sedimentary rocks (Neldner et al. 2019).
187
188 *Allocasuarina littoralis* and *A. torulosa* are dioecious trees growing 5 to 15 m and 5 to 30 m
189 tall, respectively (Australian Biological Resources Study. Advisory Committee 1989, Spencer
190 1995). *Allocasuarina littoralis* has a more coastal distribution on sandy, heavy clay, or stony
191 soils (Australian Biological Resources Study. Advisory Committee 1989, Foreman and Walsh
192 1993) while *Allocasuarina torulosa* is distributed widely from coastal to inland regions in
193 forests on fertile soils (Stanley et al. 1983, Australian Biological Resources Study. Advisory
194 Committee 1989). *Allocasuarina littoralis* lives, on average, 40-70 years (with a potential
195 lifespan up to 100 years), while *A. torulosa* can typically live for 50-100 years as individuals
196 can resprout following fire (Kattge et al. 2020, Falster et al. 2021). Reproductive maturity can
197 be reached in five years for both species, but *A. littoralis* is more likely to take 10 years
198 (Kattge et al. 2020, Falster et al. 2021). Both species gradually release seed from serotinous
199 cones as they dry (Crowley 1986, Kattge et al. 2020, Falster et al. 2021). A number of studies
200 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 et al. 2007, Williams et al. 2012), while others suggest it is a facultative resprouter (R+P+) (Schmidt and Stewart 1997, Knox and Clarke 2005, Clarke et al. 2010, Clarke et al. 2015, Paul et al. 2017, Kattge et al. 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 et al. 2004). *Allocasuarina torulosa* is generally considered to be a resprouter (Kubiak 2009, Williams et al. 2012, Benwell 2024), with some evidence of inter-fire seed regeneration where canopy seedbanks are available (R+P+, facultative resprouter) (Clarke et al. 2015, Kattge et al. 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 et al. 2000). In other Casuarinaceae, seeds have been reported to survive heat shock of up to 120°C (Hanley and Lamont 2000, Callister et al. 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 et al. 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 et al. 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, Fig. 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 et al. 2025) (Appendix S1: Section 1, Fig. 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 et al. 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 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 *A. littoralis* and 20°C for *A. torulosa* (see Appendix S1: Fig. S1). Germination was considered to have occurred upon emergence of the radicle from the testa. After emergence, the germinant was recorded and removed from the petri dish to allow space for other seeds to germinate. Germination trials ran for a minimum of 29 days and stopped when no new seeds had germinated in a 7-day period. This means there was no upper time limit for the germination trial; we continued counting germinates until there was zero germination over a 7-day period.

326

327 Seed viability measurements

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329 Seed viability was measured using two methods: (1) non-destructive x-ray prior to
330 germination experiments to estimate pre-treatment viability without reducing the number of
331 seeds for the experiment; and (2) destructive post-experiment tetrazolium tests to determine
332 whether seeds which remained ungerminated at the end of the trial were viable (Peters 2000).
333 X-rays were taken on a Faxitron MX-20 Imaging system (Lincolnshire, IL, USA), on *ca*. 100
334 seeds from a seed lot with four replicates of 25 seeds at 28 kV for 6.55 seconds. X-ray images
335 were examined to determine seed fill, a metric related to the amount of seed embryo and
336 endosperm which is correlated with viability (Gagliardi and Marcos-Filho 2011, Tausch et al.
337 2024). Unfilled seeds were considered unviable but seeds with partial filling were classed as
338 viable as there was potential for germination. X-ray viability data were summarised as the
339 proportion of viable x-ray imaged seeds for analysis. Tetrazolium tests used a 1% 2,3-5
340 triphenyl tetrazolium chloride (TTC) solution with seeds cut laterally through the distal end
341 of cotyledons and incubated in solution for 18 hours at 30°C in darkness (Peters 2000). After
342 incubation, seeds were observed under a dissection microscope and seeds were classed as
343 viable if the radicle and cotyledons were completely stained pink (Peters 2000). Any TTC
344 staining inconsistencies or lack of staining was considered to indicate unviable seeds (Peters
345 2000).

346

347 Full factorial germination experiment

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349 The full factorial experiment included six treatments: (1) control; (2) 80°C heat shock for 5
350 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, Fig. 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 the collection site (i.e., low fire frequency = 0-3 fires, and high fire frequency = 4-7 fires from 1987-2023). Due to seed limitations, we were unable to assign each individual tree to all six treatments (e.g., an individual with only 120 seeds could only be assigned to 3 treatments). Thus, we used the `arrangements` R package version 1.1.9 (Lai 2019) in R version 4.3.1 (R Core Team 2018) to randomly assign the six treatments to seed lots, with six separate rounds of assignment. We subsequently reduced treatment assignments on a case-by-case basis such that only three treatments were assigned to a seed lot with 120 seeds. During this case-by-case treatment assignment, we ensured 15 individual seed lots were included for all six treatments. Thus, each germination experiment replicate included six treatments with 300 seeds from 15 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.

376

377 *Spatial data compilation*

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379 Fire frequency data from was obtained from Queensland Parks and Wildlife Service (Table 1)
380 and subset temporally (i.e., 1987-2023) to match the temporal resolution of modelled
381 estimates of fire frequency from satellite-derived data (see Charles et al. 2026). Year of last
382 fire was obtained from Queensland Parks and Wildlife fire history data and satellite-derived
383 fire history data. Areas that were unburnt between 1987-2023 were assigned a year of last fire
384 as 1986. Time since fire was calculated by subtracting year of last fire from the sampling
385 year. We obtained data on temperature and precipitation seasonality (Fick and Hijmans 2017),
386 Topographic Wetness Index (TWI) (Gallant and Austin 2012), and Foliage Projective Cover
387 (FPC) (Department of Environment 2020, 2024) (Table 1). Spatial data requiring resolution
388 adjustments were rescaled to 30 m resolution (Table 1) using the `gdalUtilities` R
389 package version 1.2.5 (O'Brien 2023) and nearest neighbour resampling. Foliage Projective
390 Cover (FPC) data was obtained as 0-100% foliage cover, but data from 2014 were on a
391 different scale. Therefore, 2014 FPC data were reclassified to align with other years. Foliage
392 projective cover was then rescaled to 30 m, prior to calculation of the average FPC (Table 1).

393

394 *Analysis*

395

396 Analyses of reproductive trait data were conducted in R version 4.3.1 (R Core Team 2023)
397 using generalised linear mixed models in the `lme4` R package version 1.1-34 (Bates et al.
398 2015). We used the same model structure for each response variable but modified the model
399 family (error structure) as appropriate for each type of response variable. Models were fit
400 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) confidence intervals did not overlap zero (Arnold 2010, Leroux 2019). For top-ranked models which included factorial predictor variables with multiple levels, we calculated least-squares means contrasts to determine differences between levels within the factor. For example, if the top-ranked model included germination treatment, we used least-squares means contrasts to determine if germination rate differed in seed exposed to 95°C and control seeds.

Germination experiment

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 experiment. First and last germination day and time to 50% germination were calculated by adapting functions from the `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 (**H1b**, **H1d**) we 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, we included a random effect for replicate and individual in each model. To analyse the effect of fire frequency and environment on seed weight (**H1a**, **H1c**, **H3a**, **H3b**), we used the calculated average weight of a singular seed (hereafter 'seed weight') as the response variable. We 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.

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 (Fig. 1). Seeds from 115 individuals, comprising 40 *A. littoralis* and 75 *A. torulosa* individuals were sampled at these transects (Fig. 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: Fig. 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: Fig. 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: Fig. S6). Seed weight influenced germination rate for *A. littoralis* (ΔAIC_c relative to null model = 3.07; Table 2, Fig. 2). For germination rate in *A. torulosa*, there was an interaction between seed weight and fire frequency (ΔAIC_c relative to null model = 10.97; Table 2, Fig. 2). In both species, heavier seeds were generally associated with greater germination rates (Table 2, Fig. 2). The *A. torulosa* model with an interaction term showed that, for individuals exposed to high fire frequencies, germination rates decreased with increasing seed weight and were highly variable (20-90% proportion of seeds germinated, Fig 2b).

For *A. littoralis*, there was little support for a seed treatment effect on time to 50% germination as the null model was equivalent to the treatment only model ($\Delta AIC_c = 0.81$; Table 3). The data from *A. torulosa* supported three models: seed treatment only (the top ranked model, ΔAIC_c relative to null model = 108.77); an interaction between seed treatment and seed weight (ΔAIC_c relative to the top ranked model = 0.11); and an interaction between seed treatment and fire frequency (ΔAIC_c relative to the top ranked model = 0.67) (Table 3, Appendix S1: Fig. S7, S8). Time to 50% germination increased for all treatments compared to controls, except for the 80°C treatment (Fig. 3a, Appendix S1: Fig. S7a). Thus, heat and smoke generally slowed 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. 3b, Appendix S1: Fig. S7b, S8a-c). In the fire frequency interaction model, seed from more frequently burned transects had slower

501 germination for 95°C; smoke; and 80°C + smoke treatments (Fig. 3c, Appendix S1: Fig. S7c,
502 S8d-f). However, this pattern was reversed for individuals exposed to the 95°C + smoke
503 treatment, suggesting faster germination for individuals exposed to more frequent fire (Fig.
504 3c, Appendix S1: Fig. S7c, S8d-f).
505
506 Seed weight was influenced by an interaction between fire frequency and temperature
507 seasonality in *A. littoralis*, and an interaction between fire frequency and latitude in *A.*
508 *torulosa* (Table 4, Fig. 4). There was no evidence of any other environmental variables
509 influencing seed weight in either species ($\Delta AIC_c > 5$, Table 4). For *A. littoralis*, seed weight
510 increased with temperature seasonality for seeds collected at frequently burned transects (4
511 fires over 36 years, Fig. 4a). At low to intermediate fire frequencies (0-1 fire over 36 years)
512 there was no relationship between seed weight and temperature seasonality (Fig. 4a). For *A.*
513 *torulosa*, seed weight increased with decreasing latitude for frequently burned transects (6
514 fires over 36 years) and decreased with decreasing latitude for infrequently burned transects
515 (0 fires over 36 years) (Fig. 4b). There was no relationship between latitude and seed weight
516 for intermediate fire frequencies (3 fires over 36 years, Fig. 4b). In other words, at southern
517 sampling locations seeds were heavier when collected at transects which had experienced
518 frequent fire, compared to relatively unburnt transects. At northern sampling locations, there
519 were no differences in seed weight related to fire history (Fig. 4b).
520
521 *Reproductive output and population demographic structure*
522
523 Reproductive output (number of cones per female tree) was not influenced by fire frequency
524 or time since fire (Appendix S1: Table S1). There was a positive effect of foliage projective
525 cover on number of cones in *A. littoralis* (Intercept = -1.793 [standard error (SE) = 1.081],

526 FPC = 0.066 [SE = 1.175], Appendix S1: Table S1) and *A. torulosa* (Intercept = -3.409 [SE =
527 1.1336], FPC = 2.105 [SE = 1.303], Appendix S1: Table S1).
528
529 Population demographic structure in *A. littoralis* was not influenced by fire frequency, time
530 since fire, or environmental variability, with the null model being top ranked for all analyses
531 (Appendix S1: Table S2). In *A. torulosa*, foliage projective cover influenced the proportion of
532 seedings within the total population (Intercept = -3.409 [SE = 1.336]; FPC = 2.105 [SE =
533 1.303], Appendix S1: Table S3). Increasing temperature seasonality reduced the proportion of
534 saplings within the total population (Intercept = -1.040 [SE = 0.482], temperature seasonality
535 = -1.136 [SE = 0.481], Appendix S1: Table S3) and recruits within the total population
536 (Intercept = -0.919 [SE = -1.833]), temperature seasonality = -1.642 [SE = 0.535], Appendix
537 S1: Table S3). The interaction between temperature seasonality and time since fire on the
538 proportion of *A. torulosa* recruits within the total population was ranked within $\Delta AIC_c < 2$ of
539 the top-ranked model, but confidence intervals of the interaction term overlapped zero
540 (Appendix S1: Fig. S9). Thus, fire history did not strongly influence reproductive output or
541 population demographic structure in *A. littoralis* or *A. torulosa*, with environmental
542 variability being more important in constraining recruitment processes (Appendix S1: Table
543 S1, S2, S3).
544
545 **Discussion**
546
547 This study showed that seed responses to fire history and fire-related germination cues varied
548 in two closely related tree species with differing post-fire reproductive modes. Fire frequency
549 from seed collection locations was found to influence variation in laboratory-based
550 germination experiments. This is important because it indicates that reproduction in plant

551 species from fire-prone ecosystems is influenced not only by fire-related germination cues,
552 but also the recent fire history to which they have been exposed. Variation in germination
553 response to fire of these two closely related tree species could influence a dietary specialist
554 threatened cockatoo through differences in species post-fire establishment success and
555 competitiveness. Thus, investigating how fire drives selection on reproductive traits and
556 controls population demographic structure is vital for conservation and restoration actions to
557 mitigate the effects of future fire regime changes.
558
559 Fast germination provides individuals with a competitive advantage (Hodges et al. 2021);
560 therefore, overall germination and germination speed can be promoted by fire-related cues,
561 especially in obligate seeders adapted for post-fire germination (Ramos et al. 2019, Tangney
562 et al. 2020, Hodges et al. 2021, Pausas and Lamont 2022). Results from this study ran
563 contrary to this general prediction: exposure of seeds to heat and smoke did not enhance
564 germination rate and speed of the obligate seeder *A. littoralis* (**H1b**) while it slowed
565 germination rate in the facultative resprouter *A. torulosa* (**H1d**). Reduced germination speed
566 with temperature increase may be related to lethal temperature thresholds which lower seed
567 viability. This was supported by the reduction in germination speed being stronger in *A.*
568 *torulosa* (lethal temperature threshold *ca.* 100°C) than *A. littoralis* (lethal temperature
569 threshold *ca.* 110°C) (Hanley et al. 2003, Emery et al. 2011). Nevertheless, *Allocasuarina*
570 seeds were generally resilient to heat shocks up to 95°C with little loss in seed viability. This
571 was not unexpected as temperatures inside cone follicles of other serotinous species during
572 fire can reach 100°C (Huss et al. 2019) and fire triggers seed release in serotinous species
573 such as *Allocasuarina* to coincide with favourable post-fire conditions (Lamont et al. 2019,
574 Lamont et al. 2020). However, obligate seeders are more likely to have increased post-fire
575 germination speed due to their greater investment in seeds than congeneric resprouters

(Zammit and Westoby 1987, Pausas and Keeley 2014, Tangney et al. 2020), and our study supported this prediction (**H1b**). For the facultative resprouter, fire-cues inhibited germination, to some extent, with inhibition especially extreme in individuals not pre-adapted to fire or exposed to high fire frequencies.

A trade-off between reproductive output and resprouting capacity is often seen in plants from fire-prone ecosystems, whereby greater seed production is usually associated with lower resprouting capacity (Bellingham and Sparrow 2000). This trade-off might have influenced fire frequency effects on overall germination and germination speed in this study. As expected, (**H1d**) the facultative resprouting tree, *A. torulosa* had greater reductions in germination speed when seed were collected from frequently burnt environments compared with those from lower fire frequencies. This might reflect a higher investment in resprouting from bud banks than in seed production, trading off seed germination performance in individuals exposed to frequent fire (Bellingham and Sparrow 2000, Verdú 2000, Pausas and Keeley 2014, Bendall et al. 2022). However, the facultative resprouter produced heavier seeds with increasing fire frequency, contrary to expectations (**H1c**). Nevertheless, heavier *A. torulosa* seeds from collection sites exposed to frequent fire had slower germination speed, indicating lower competitiveness compared to the obligate seeder (**H1**). Thus, production of heavier seeds in *A. torulosa* could have reflected lower investment in seeds (i.e., fewer seeds produced as seed weight increased) in frequently burnt environments (Hodgson et al. 2020, Li et al. 2025, Maleki et al. 2025). An alternative explanation is that delayed germination occurred as a response to heat induced stress and seed tissue repair prior to germination (Visscher et al. 2021) and further research on this is warranted.

Selection on seed traits may also be driven by environmental variation, with strongly seasonal environments generally favouring heavier seeds that have greater energy reserves (Leishman et al. 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 et al. 2020, Hamann et al. 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 et al. 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 et al. 1981, Gill and Catling 2002, Clarke et al. 2015, McColl-Gausden et al. 2022). Thus, further experimental research is needed to better understand fire history effects on reproduction and population demographic structure in *Allocasuarina*.

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. 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 decades), as more moderate fire regimes showed stronger fire-cued germination responses in *A. torulosa*.

Current fire histories appear to be suitable for persistence of *A. littoralis* and *A. torulosa* in our study region (i.e., up to four and seven fires in 36 years, respectively). However, climate change projections in many regions are associated with fire regime changes, including increasing frequency, intensity, severity and extent of fire (Di Virgilio et al. 2019, Hantson et al. 2024, Oliveira and Gil Martins 2026). Such changes could threaten the persistence of *Allocasuarina* populations under future fire regimes, especially obligate seeders. For restoration of food trees, we recommend targeting areas with higher annual temperature variability and low woody vegetation cover as *Allocasuarina* might otherwise decline under high environmental stress with low population turnover. Trends toward warmer annual temperatures are also occurring, increasing evapotranspiration (Hughes 2003), which could further limit growth and reproduction processes in these species (Gallagher et al. 2019, Zhang et al. 2020, Hamann et al. 2021). In our study region, restoration is likely to be most successful for *A. torulosa* due to their widespread distribution and higher likelihood of persistence under projected higher fire activity (Hantson et al. 2016, Di Virgilio et al. 2019, Dowdy et al. 2019). Nevertheless, restoring other food tree species would 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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693
694 **Conflict of interest statement**
695
696 The authors declare no conflicts of interest.
697
698 **References**

Aaravind, J., S. Vimala Devi, J. Radhamani, S. R. Jacob, and K. Srinivasan (2022) germinationmetrics: seed germination indices and curve fitting. R package version 0.1.7. viewed 6th October 2022, <https://github.com/aravind-j/germinationmetricshttps://cran.r-project.org/package=germinationmetrics.>.

Agne, M. C., J. B. Fontaine, N. J. Enright, S. M. Bisbing, and B. J. Harvey. 2022. Demographic processes underpinning post-fire resilience in California closed-cone pine forests: the importance of fire interval, stand structure, and climate. Plant ecology **223**:751-767 https://doi.org/10.1007/s11258-022-01228-7.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of wildlife management **74**:1175-1178 https://doi.org/10.1111/j.1937-2817.2010.tb01236.x.

Atlas of Living Australia (2021a) *Allocasuarina littoralis* **(Salisb.) L.A.S.Johnson**. (Atlas of Living AustraliaAustralia). viewed 29th October 2021, <https://bie.ala.org.au/species/https://id.biodiversity.org.au/node/apni/2907962#overview>.

Atlas of Living Australia (2021b) *Allocasuarina torulosa* **(Aiton) L.A.S.Johnson**. (Atlas of Living AustraliaAustralia). viewed 29th October 2021, <https://bie.ala.org.au/species/https://id.biodiversity.org.au/node/apni/2898576#overview>.

Australian Biological Resources Study. Advisory Committee. 1989. Flora of Australia. Australian Government Publishing Service, Canberra, ACT, Australia.

Ballarin, C. S., G. J. Mores, G. Alcarás de Goés, A. Fidelis, and T. Cornelissen. 2024. Trends and gaps in the study of fire effects on plant–animal interactions in Brazilian ecosystems. Austral Ecology **49**:e13420 https://doi.org/10.1111/aec.13420.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effect models using lme4. Journal of Statistical Software **67**:1-48 https://dio.org/10.18637/jss.v067.i01.

Bellingham, P. J., and A. D. Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. Oikos **89**:409-416 https://doi.org/10.1034/j.1600-0706.2000.890224.x.

Bendall, E. R., M. Bedward, M. Boer, H. Clarke, L. Collins, A. Leigh, and R. A. Bradstock. 2022. Mortality and resprouting responses in forest trees driven more by tree and

ecosystem characteristics than drought severity and fire frequency. Forest ecology and management **509**:120070 https://doi.org/10.1016/j.foreco.2022.120070.

Bennett, L. T., M. J. Bruce, J. MacHunter, M. Kohout, M. A. Tanase, and C. Aponte. 2016. Mortality and recruitment of fire-tolerant eucalypts as influenced by wildfire severity and recent prescribed fire. Forest ecology and management **380**:107-117 https://doi.org/10.1016/j.foreco.2016.08.047.

Benwell, A. 2024. Fire responses of flora in a sclerophyll–rainforest vegetation complex in the Nightcap Range, north coast, New South Wales. Australian journal of botany **72**:BT23049 https://doi.org/10.1071/BT23049.

Burley, A. L., S. Phillips, and M. K. J. Ooi. 2007. Can age be predicted from diameter for the obligate seeder *Allocasuarina littoralis* (Casuarinaceae) by using dendrochronological techniques? Australian journal of botany **55**:433-438 https://doi.org/10.1071/BT06160.

Callister, K. E., S. K. Florentine, and M. E. Westbrooke. 2018. An investigation of the soil seedbank and seed germination of perennial species in belah (*Casuarina pauper*) woodlands in north-west Victoria. Australian journal of botany **66**:202-212 https://doi.org/10.1071/BT17160.

Cameron, M., G. Castley, D. Teixeira, P. W. Menkhorst, and S. T. Garnett. 2021. South-eastern glossy black-cockatoo *Calyptorhynchus lathami lathami*. Pages 395-398 *in* S. T. G. a. G. B. Baker, editor. The Action Plan for Australian Birds 2020. CSIRO Publishing, Melbourne.

Campbell, D. R., R. A. Raguso, M. Midzik, M. Bischoff, and G. T. Broadhead. 2022. Genetic and spatial variation in vegetative and floral traits across a hybrid zone. American Journal of Botany **109**:1780-1793 https://doi.org/10.1002/ajb2.16067.

Canadell, J. G., C. P. Meyer, G. D. Cook, A. Dowdy, P. R. Briggs, J. Knauer, A. Pepler, and V. Haverd. 2021. Multi-decadal increase of forest burned area in Australia is linked to climate change. Nature Communications **12**:6921 https://doi.org/10.1038/s41467-021-27225-4.

Carbone, L. M., J. Tavella, J. G. Pausas, and R. Aguilar. 2019. A global synthesis of fire effects on pollinators. Global ecology and biogeography **28**:1487-1498 https://doi.org/10.1111/geb.12939.

Chamorro, D., B. Luna, and J. M. Moreno. 2018. Local climate controls among-population variation in germination patterns in two *Erica* species across western Iberia. Seed science research **28**:112-122 https://doi.org/10.1017/S0960258518000041.

766 Chapman, T. F. 2007. Foods of the glossy black-cockatoo: *Calyptorhynchus lathami*.
767 Australian Field Ornithology **24**:30-36
768 Charles, F. E., A. E. Reside, P. T. Moss, and A. L. Smith. 2026. Integrating public land fire
769 data and satellite imagery improves fire frequency estimates across the landscape.
770 International Journal of Wildland Fire https://doi.org/10.1071/WF25076.
771 Charles, F. E., A. E. Reside, and A. L. Smith. 2025. The influence of changing fire regimes on
772 specialised plant-animal interactions. Philosophical Transactions of the Royal Society
773 of London. Series B: Biological Sciences **380**:20230448
774 https://doi.org/10.1098/rstb.2023.0448.
775 Charles, F. E., and A. L. Smith (2025) Data and code: Influence of fire history on
776 reproductive traits in a congeneric obligate seeder and facultative resprouter tree
777 species (Dataset). (F. E. Charles GitHub: Brisbane, Queensland, Australia). Available
778 at https://doi.org/10.5281/zenodo.20602455 [Verified 20/02/2026]
779 Christensen, P., H. Recher, and J. Hoare. 1981. Responses of open forests (dry sclerophyll
780 forests) to fire regimes Pages 367-393 *in* A. M. Gill, R. H. Groves, and I. R. Noble,
781 editors. Fire and the Australian biota. Australian Academy of Science, Canberra, ACT,
782 Australia.
783 Clarke, P. J., E. A. Davison, and L. Fulloon. 2000. Germination and dormancy of grassy
784 woodland and forest species: effects of smoke, heat, darkness and cold. Australian
785 journal of botany **48**:687-699 https://doi.org/10.1071/BT99077.
786 Clarke, P. J., K. J. E. Knox, M. L. Campbell, and L. M. Copeland. 2010. Post-fire recovery of
787 woody plants in the New England Tableland Bioregion.
788 Clarke, P. J., M. J. Lawes, B. P. Murphy, J. Russell-Smith, C. E. M. Nano, R. Bradstock, N. J.
789 Enright, J. B. Fontaine, C. R. Gosper, I. Radford*, et al.* 2015. A synthesis of postfire
790 recovery traits of woody plants in Australian ecosystems. Science of The Total
791 Environment **534**:31-42 https://doi.org/10.1016/j.scitotenv.2015.04.002.
792 Collett, L. (2021) Annual Fire Scars - Landsat, QLD DES algorithm, QLD coverage
793 (Dataset). (Terrestrial Ecosystem Research Network (TERN) TERN: Brisbane,
794 Queensland, Australia). Available at
795 http://geonetwork.tern.org.au/geonetwork/srv/eng/catalog.search#/metadata/461074b3
796 -5272-4e4e-886f-df26bd2426ad, https://portal.tern.org.au/annual-scars-landsat-qld-
797 coverage [Verified 2021-12-01]
798 Cortés-Flores, J., G. Cornejo-Tenorio, M. E. Sánchez-Coronado, A. Orozco-Segovia, and G.
799 Ibarra-Manríquez. 2020. Disentangling the influence of ecological and historical

factors on seed germination and seedling types in a neotropical dry forest. PLoS One **15**:e0231526 https://doi.org/10.1371/journal.pone.0231526.

Crowley, G. M. 1986. Ecology of *Allocasuarina littoralis (Salisb.) L. Johnson and A. torulosa (Ait.) L. Johnson* in north Queensland. James Cook University, Townsville, QLD, Australia.

Day, N. J., A. L. White, J. F. Johnstone, G. E. Degré-Timmons, S. G. Cumming, M. C. Mack, M. R. Turetsky, X. J. Walker, and J. L. Baltzer. 2020. Fire characteristics and environmental conditions shape plant communities via regeneration strategy. Ecography **43**:1464-1474 https://doi.org/10.1111/ecog.05211.

Delzoppo, N. A., K. K. Berris, D. Teixeira, and B. van Rensburg. 2021. The impact of fire on the quality of drooping sheoak (*Allocasuarina verticillata*) cones for the endangered Kangaroo Island glossy black-cockatoo (*Calyptorhynchus lathami halmaturinus*). Global Ecology and Conservation **28**:e01645 https://doi.org/10.1016/j.gecco.2021.e01645.

Department of Environment, Tourism, Science and Innovation (2020) Landsat foliage projective cover - Queensland 2014 (Dataset). (Queensland Department of Environment, Tourism, Science and Innovation Queensland Spatial Catalogue: Brisbane, Queensland, Australia). Available at https://www.data.qld.gov.au/dataset/landsat-foliage-projective-cover-queensland-2014 [Verified 6 April 2023]

Department of Environment, Tourism, Science and Innovation (2024) Statewide Landcover and Trees Study (SLATS) Sentinel - 2 Foliage Projective Cover (FPC) Queensland (Dataset). (Queensland Department of Environment, Tourism, Science and Innovation Queensland Spatial Catalogue: Brisbane, Queensland, Australia). Available at https://www.data.qld.gov.au/dataset/statewide-landcover-and-trees-study-queensland-sentinel-2-series [Verified 16 April 2024]

Di Virgilio, G., J. P. Evans, S. A. P. Blake, M. Armstrong, A. J. Dowdy, J. Sharples, and R. McRae. 2019. Climate change increases the potential for extreme wildfires. Geophysical Research Letters **46**:8517-8526 https://doi.org/10.1029/2019GL083699.

Dowdy, A. J., H. Ye, A. Pepler, M. Thatcher, S. L. Osbrough, J. P. Evans, G. Di Virgilio, and N. McCarthy. 2019. Future changes in extreme weather and pyroconvection risk factors for Australian wildfires. Scientific reports **9**:10073-10011 https://doi.org/10.1038/s41598-019-46362-x.

833 Ellison, A. M. 2019. Foundation species, non-trophic interactions, and the value of being
834 common. iScience **13**:254-268 https://doi.org/10.1016/j.isci.2019.02.020.
835 Emery, S. M., J. Uwimbabazi, and S. L. Flory. 2011. Fire intensity effects on seed
836 germination of native and invasive eastern deciduous forest understory plants. Forest
837 ecology and management **261**:1401-1408
838 https://doi.org/10.1016/j.foreco.2011.01.024.
839 Enright, N. J., J. B. Fontaine, D. M. J. S. Bowman, R. A. Bradstock, and R. J. Williams. 2015.
840 Interval squeeze: altered fire regimes and demographic responses interact to threaten
841 woody species persistence as climate changes. Frontiers in ecology and the
842 environment **13**:265-272 https://doi.org/10.1890/140231.
843 Enright, N. J., J. B. Fontaine, V. C. Westcott, J. C. Lade, and B. P. Miller. 2011. Fire interval
844 effects on persistence of resprouter species in Mediterranean-type shrublands. Plant
845 ecology **212**:2071-2083 https://doi.org/10.1007/s11258-011-9970-7.
846 Enright, N. J., and B. B. Lamont. 1989. Seed banks, fire season, safe sites and seedling
847 recruitment in five co-occurring banksia species. Journal of Ecology **77**:1111-1122
848 https://doi.org/10.2307/2260826.
849 Eriksson, O. 1999. Seed size variation and its effect on germination and seedling performance
850 in the clonal herb *Convallaria majalis*. Acta Oecologica **20**:61-66
851 https://doi.org/10.1016/S1146-609X(99)80016-2.
852 Escudero, A., Y. Núñez, and F. Pérez-García. 2000. Is fire a selective force of seed size in
853 pine species? Acta Oecologica **21**:245-256 https://doi.org/10.1016/S1146-
854 609X(00)01083-3.
855 Etchells, H., A. J. O'Donnell, W. Lachlan McCaw, and P. F. Grierson. 2020. Fire severity
856 impacts on tree mortality and post-fire recruitment in tall eucalypt forests of
857 southwest Australia. Forest ecology and management **459**:117850
858 https://doi.org/10.1016/j.foreco.2019.117850.
859 Falster, D., R. Gallagher, E. H. Wenk, I. J. Wright, D. Indiarto, S. C. Andrew, C. Baxter, J.
860 Lawson, S. Allen, A. Fuchs, *et al.* 2021. AusTraits, a curated plant trait database for
861 the Australian flora. Scientific Data **8**:254 https://doi.org/10.1038/s41597-021-01006-
862 6.
863 Fenollosa, E., L. Jené, and S. Munné-Bosch. 2021. Geographic patterns of seed trait variation
864 in an invasive species: how much can close populations differ? Oecologia **196**:747-
865 761 https://doi.org/10.1007/s00442-021-04971-2.

866 Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate
867 surfaces for global land areas. International Journal of Climatology **37**:4302-4315
868 https://doi.org/10.1002/joc.5086.
869 Fisher, A., P. Scarth, J. Armston, and T. Danaher. 2018. Relating foliage and crown projective
870 cover in Australian tree stands. Agricultural and Forest Meteorology **259**:39-47
871 https://doi.org/10.1016/j.agrformet.2018.04.016.
872 Foreman, D. B., and N. G. Walsh. 1993. Flora of Victoria. Inkata Press, Melbourne, VIC,
873 Australia.
874 Gagliardi, B., and J. Marcos-Filho. 2011. Relationship between germination and bell pepper
875 seed structure assessed by the x-ray test. Scientia Agricola **68**:411-416
876 https://doi.org/10.1590/S0103-90162011000400004.
877 Gallagher, R. V., S. Allen, and I. J. Wright. 2019. Safety margins and adaptive capacity of
878 vegetation to climate change. Scientific reports **9**:8241
879 https://doi.org/10.1038/s41598-019-44483-x.
880 Gallant, J., and J. Austin (2012) Topographic Wetness Index derived from 1" SRTM DEM-H.
881 v2 (Dataset). (CSIRO CSIRO: Australia). Available at
882 https://doi.org/10.4225/08/57590B59A4A08 [Verified 18 August 2023]
883 Gill, A. M., and P. C. Catling. 2002. Fire regimes and biodiversity of forested landscapes of
884 southern. Page 351 *in* R. A. Bradstock, J. E. Williams, and A. M. Gill, editors.
885 Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge
886 University Press, Cambridge, United Kingdom; New York, United States of America.
887 Gnan, S., A. Priest, and P. X. Kover. 2014. The genetic basis of natural variation in seed size
888 and seed number and their trade-off using *Arabidopsis thaliana* MAGIC lines.
889 Genetics **198**:1751-1758 https://doi.org/10.1534/genetics.114.170746.
890 Gómez-González, S., F. Ojeda, P. Torres-Morales, and J. E. Palma. 2016. Seed pubescence
891 and shape modulate adaptive responses to fire cues. PLoS One **11**:e0159655
892 https://doi.org/10.1371/journal.pone.0159655.
893 Gómez-González, S., A. Sierra-Almeida, and L. A. Cavieres. 2008. Does plant-derived smoke
894 affect seed germination in dominant woody species of the Mediterranean matorral of
895 central Chile? Forest ecology and management **255**:1510-1515
896 https://doi.org/10.1016/j.foreco.2007.11.006.
897 Gómez-González, S., C. Torres-Díaz, C. Bustos-Schindler, and E. Gianoli. 2011.
898 Anthropogenic fire drives the evolution of seed traits. PNAS Nexus **108**:18743-18747
899 https://doi.org/10.1073/pnas.1108863108.

900 Hamann, E., S. M. Wadgymar, and J. T. Anderson. 2021. Costs of reproduction under
901 experimental climate change across elevations in the perennial forb *Boechera stricta*.
902 Proceedings of the Royal Society B: Biological Sciences **288**:20203134
903 https://doi.org/10.1098/rspb.2020.3134.
904 Hanley, M., J. Unna, and B. Darvill. 2003. Seed size and germination response: a relationship
905 for fire-following plant species exposed to thermal shock. Oecologia **134**:18-22
906 10.1007/s00442-002-1094-2.
907 Hanley, M. E., and B. B. Lamont. 2000. Heat pre-treatment and the germination of soil- and
908 canopy-stored seeds of south-western Australian species. Acta Oecologica **21**:315-321
909 https://doi.org/10.1016/S1146-609X(00)01087-0.
910 Hantson, S., A. Arneth, S. P. Harrison, D. I. Kelley, I. C. Prentice, S. S. Rabin, S. Archibald,
911 F. Mouillot, S. R. Arnold, P. Artaxo*, et al.* 2016. The status and challenge of global
912 fire modelling. Biogeosciences **13**:3359-3375 10.5194/bg-13-3359-2016.
913 Hantson, S., D. S. Hamilton, and C. Burton. 2024. Changing fire regimes: ecosystem impacts
914 in a shifting climate. One Earth **7**:942-945
915 https://doi.org/10.1016/j.oneear.2024.05.021.
916 Harvey, B. J., and N. J. Enright. 2022. Climate change and altered fire regimes: impacts on
917 plant populations, species, and ecosystems in both hemispheres. Plant ecology
918 **223**:699-709 https://doi.org/10.1007/s11258-022-01248-3.
919 Hodges, J. A., J. N. Price, A. B. Nicotra, T. Neeman, and L. K. Guja. 2021. Smoke and heat
920 accelerate and increase germination in fire-prone temperate grassy ecosystems.
921 Ecosphere **12**:n/a https://doi.org/10.1002/ecs2.3851.
922 Hodgson, J. G., G. Montserrat Marti, B. Šerá, G. Jones, A. Bogaard, M. Charles, X. Font, M.
923 Ater, A. Taleb, B. A. Santini*, et al.* 2020. Seed size, number and strategies in annual
924 plants: a comparative functional analysis and synthesis. Annals of Botany **126**:1109-
925 1128 https://doi.org/10.1093/aob/mcaa151.
926 Hughes, L. 2003. Climate change and Australia: trends, projections and impacts. Austral
927 Ecology **28**:423-443 https://doi.org/10.1046/j.1442-9993.2003.01300.x.
928 Hunter, J. T. 2003. Persistence on inselbergs: the role of obligate seeders and resprouters.
929 Journal of Biogeography **30**:497-510 https://doi.org/10.1046/j.1365-
930 2699.2003.00876.x.
931 Huss, J. C., P. Fratzl, J. W. C. Dunlop, D. J. Merritt, B. P. Miller, and M. Eder. 2019.
932 Protecting offspring against fire: lessons from banksia seed pods. Frontiers in Plant
933 Science **10**:12 https://doi.org/10.3389/fpls.2019.00283.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, *et al.* 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in ecology and the environment **14**:369-378 https://doi.org/10.1002/fee.1311.

Käber, Y., P. Meyer, J. Stillhard, E. De Lombaerde, J. Zell, G. Stadelmann, H. Bugmann, and C. Bigler. 2021. Tree recruitment is determined by stand structure and shade tolerance with uncertain role of climate and water relations. Ecology and Evolution **11**:12182-12203 https://doi.org/10.1002/ece3.7984.

Kasel, S., T. A. Fairman, and C. R. Nitschke. 2024. Short-interval, high-severity wildfire depletes diversity of both extant vegetation and soil seed banks in fire-tolerant eucalypt forests. Fire **7**:148 https://doi.org/10.3390/fire7040148.

Kattge, J., G. Bönisch, S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. A. Werner, T. Aakala, M. Abedi, *et al.* 2020. TRY plant trait database - enhanced coverage and open access. Global Change Biology **26**:119-188 https://doi.org/10.1111/gcb.14904.

Keeley, J. E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparal shrubs. Ecology **58**:820-829 https://doi.org/10.2307/1936217.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science **16**:406-411 https://doi.org/10.1016/j.tplants.2011.04.002.

Keith, D. A. 1996. Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. Proceedings of the Linnean Society of New South Wales **116**:37-78

Keith, D. A., W. L. McCaw, and R. J. Whelan. 2002. Fire regimes in Australian heathlands and their effects on plants and animals. Pages 199-237 *in* R. A. Bradstock, J. E. Williams, and A. M. Gill, editors. Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, United Kingdom; New York, United States of America.

Kellman, M. 1986. Fire sensitivity of *Casuarina torulosa* in north Queensland, Australia. Biotropica **18**:107-110 https://doi.org/10.2307/2388752.

Kelly, L. T., K. M. Giljohann, A. Duane, N. Aquilue, S. Archibald, E. Batllori, A. F. Bennett, S. T. Buckland, Q. Canelles, M. F. Clarke, *et al.* 2020. Fire and biodiversity in the Anthropocene. Science **370**:929 https://doi.org/10.1126/science.abb0355.

968 Kelly, L. T., A. A. Hoffmann, C. R. Nitschke, and J. G. Pausas. 2025. Can plants keep up with
969 fire regime changes through evolution? Trends in Ecology & Evolution
970 https://doi.org/10.1016/j.tree.2025.04.009.
971 Kennard, D. K., K. Gould, F. E. Putz, T. S. Fredericksen, and F. Morales. 2002. Effect of
972 disturbance intensity on regeneration mechanisms in a tropical dry forest. Forest
973 ecology and management **162**:197-208 https://doi.org/10.1016/S0378-1127(01)00506-
974 0.
975 Knox, K. J. E., and P. J. Clarke. 2005. Nutrient availability induces contrasting allocation and
976 starch formation in resprouting and obligate seeding shrubs. Functional Ecology
977 **19**:690-698 https://doi.org/10.1111/j.1365-2435.2005.01006.x.
978 Kubiak, P. J. 2009. Fire responses of bushland plants after the January 1994 wildfires in
979 northern Sydney. Cunninghamia **11**:131-165
980 Lai, R. (2019) Arrangements: fast generators and iterators for permutations, combinations,
981 integer partitions and compositions. (GitHubVienna, Austria). viewed 4 April 2024,
982 <https://github.com/randy3k/arrangements>.
983 Lamont, B. B., T. He, and Z. Yan. 2019. Evolutionary history of fire-stimulated resprouting,
984 flowering, seed release and germination. Biological Reviews **94**:903-928
985 https://doi.org/10.1111/brv.12483.
986 Lamont, B. B., J. G. Pausas, T. He, E. T. F. Witkowski, and M. E. Hanley. 2020. Fire as a
987 selective agent for both serotiny and nonserotiny over space and time. Critical
988 Reviews in Plant Sciences **39**:140-172
989 https://doi.org/10.1080/07352689.2020.1768465.
990 Le Breton, T. D., S. Natale, K. French, B. Gooden, and M. K. J. Ooi. 2020. Fire-adapted traits
991 of threatened shrub species in riparian refugia: implications for fire regime
992 management. Plant ecology **221**:69-81 https://doi.org/10.1007/s11258-019-00993-2.
993 Leishman, M. R. 2001. Does the seed size/number trade-off model determine plant
994 community structure? An assessment of the model mechanisms and their generality.
995 Oikos **93**:294-302 https://doi.org/10.1034/j.1600-0706.2001.930212.x.
996 Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology
997 of seed size. Pages 31-57 Seeds: the ecology of regeneration in plant communities.
998 CABI Publishing, Wallingford, United Kingdom.
999 Leroux, S. J. 2019. On the prevalence of uninformative parameters in statistical models
1000 applying model selection in applied ecology. PLoS One **14**:e0206711
1001 https://doi.org/10.1371/journal.pone.0206711.

Li, X. Q., H. Y. Zhu, A. C. Ochola, L. Qiong, Z. M. Ye, and C. F. Yang. 2025. To produce many small or a few large seeds: size-dependent germination strategies of herbs in a species-rich natural alpine grassland. Plant Biology **27**:1441-1449 https://doi.org/10.1111/plb.70081.

Liyanage, G. S., and M. K. J. Ooi. 2017. Seed size-mediated dormancy thresholds: a case for the selective pressure of fire on physically dormant species. Biological Journal of the Linnean Society **123**:135-143 10.1093/biolinnean/blx117.

Lybbert, A. H., and S. B. St. Clair. 2016. Wildfire and floral herbivory alter reproduction and pollinator mutualisms of yuccas and yucca moths. Journal of Plant Ecology **10**:851-858 https://doi.org/10.1093/jpe/rtw077.

Maleki, K., F. Vandelook, A. Saatkamp, K. Maleki, S. Heshmati, and E. Soltani. 2025. Global patterns in the evolutionary relations between seed mass and germination traits. Ecology and Evolution **15**:e71543 https://doi.org/10.1002/ece3.71543.

Matula, R., M. Šrámek, J. Kvasnica, B. Uherková, J. Slepička, M. Matoušková, E. Kutchartt, and M. Svátek. 2019. Pre-disturbance tree size, sprouting vigour and competition drive the survival and growth of resprouting trees. Forest ecology and management **446**:71-79 https://doi.org/10.1016/j.foreco.2019.05.012.

Mazerolle, M. J. (2020) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. (The Comprehensive R Research NetworkVienna, Austria). viewed 10th March 2021, <https://cran.r-project.org/package=AICcmodavg>.

McCarthy, M. A., A. Malcolm Gill, and D. B. Lindenmayer. 1999. Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. Forest ecology and management **124**:193-203 https://doi.org/10.1016/S0378-1127(99)00066-3.

McColl-Gausden, S. C., L. T. Bennett, D. A. Ababei, H. G. Clarke, and T. D. Penman. 2022. Future fire regimes increase risks to obligate-seeder forests. Diversity and Distributions **28**:542-558 https://doi.org/10.1111/ddi.13417.

Menkhorst, P., M. Schulz, and K. Stamation. 2024. Impacts of bushfire on the glossy black-cockatoo *Calyptorhynchus lathami* and its single food source in eastern Victoria. Australian Field Ornithology **41**:48-55 https://doi.org/10.20938/afo41048055.

Moles, A. T., and M. Westoby. 2003. Latitude, seed predation and seed mass. Journal of Biogeography **30**:105-128 https://doi.org/10.1046/j.1365-2699.2003.00781.x.

Mooney, P., K. K. Berris, M. Kaestli, and S. T. Garnett. 2026. Threatened cockatoo adapts foraging strategy to survive habitat loss from fire. Ibis **n/a** https://doi.org/10.1111/ibi.70052.

Moritz, M. A., M.-A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere **3**:49 https://doi.org/10.1890/ES11-00345.1.

Moss, P. T., L. Petherick, and D. Neil. 2011. Environmental change at Myora Springs, North Stradbroke island over the last millennium. Proceedings of the Royal Society of Queensland **117**:113-140 https://doi.org/10.5962/p.357751.

Muller-Landau, H. C. 2010. The tolerance–fecundity trade-off and the maintenance of diversity in seed size. PNAS Nexus **107**:4242-4247 https://doi.org/10.1073/pnas.0911637107.

Neldner, V., D. Butler, and G. Guymer. 2019. Queensland's regional ecosystems: building and maintaining a biodiversity inventory, planning framework and information system for Queensland version 2. Queensland Herbarium, Department of Science, Informatoin Technology and Innovation, Brisbane, QLD, Australia.

Noce, S., L. Caporaso, and M. Santini. 2020. A new global dataset of bioclimatic indicators. Scientific Data **7**:398 https://doi.org/10.1038/s41597-020-00726-5.

O'Brien, J. (2023) gdalUtilities: wrappers for 'GDAL' utilities executables. (The Comprehensive R Archive NetworkVienna, Austria). viewed 5 October 2023, <https://github.com/JoshOBrien/gdalUtilities/, https://joshobrien.github.io/gdalUtilities/>.

Ojeda, F., T. van der Niet, M. C. Malan, J. J. Midgley, and J. G. Segarra-Moragues. 2016. Strong signature of selection in seeder populations but not in resprouters of the fynbos heath *Erica coccinea* (Ericaceae). Botanical Journal of the Linnean Society **181**:115-126 https://doi.org/10.1111/boj.12395.

Oliveira, A. P., and P. Gil Martins. 2026. Global shifts in fire regimes under climate change: patterns, drivers, and ecological implications across biomes. Forests **17**:104 https://doi.org/10.3390/f17010104.

Paul, R. W., C. Patrick, and P. Mark. 2017. The fire ecology of '*Allocasuarina littoralis*' and '*Banksia plagiocarpa*' in montane heath of the southern Wet Tropics. North Queensland Naturalist **47**:43-48 https://doi.org/10.3316/informit.461115844543262.

1067 Paula, S., and J. G. Pausas. 2008. Burning seeds: germinative response to heat treatments in
1068 relation to resprouting ability. Journal of Ecology **96**:543-552
1069 https://doi.org/10.1111/j.1365-2745.2008.01359.x.
1070 Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in
1071 relation to fire in crown-fire ecosystems. Ecology **85**:1085-1100
1072 https://doi.org/10.1890/02-4094.
1073 Pausas, J. G., and J. E. Keeley. 2014. Evolutionary ecology of resprouting and seeding in fire-
1074 prone ecosystems. New Phytologist **204**:55-65 https://doi.org/10.1111/nph.12921.
1075 Pausas, J. G., and B. B. Lamont. 2022. Fire-released seed dormancy - a global synthesis.
1076 Biological Reviews **97**:1612-1639 https://doi.org/10.1111/brv.12855.
1077 Peters, J. 2000. Tetrazolium testing handbook : contribution no. 29 to the handbook on seed
1078 testing. The Association of Official Seed Analysts, Lincoln, Nebraska, United States
1079 of America.
1080 Plumanns-Pouton, E. S., M. Swan, T. Penman, and L. T. Kelly. 2024. How do intervals
1081 between fires influence canopy seed production and viability? Functional Ecology
1082 **38**:1915-1930 https://doi.org/10.1111/1365-2435.14619.
1083 Pulsford, S. A., D. B. Lindenmayer, and D. A. Driscoll. 2016. A succession of theories:
1084 purging redundancy from disturbance theory. Biological Reviews **91**:148-167
1085 https://doi.org/10.1111/brv.12163.
1086 Queensland Parks and Wildlife Service (2023) Fire history - Queensland Parks and Wildlife
1087 Service (Dataset). (Queensland Parks and Wildlife Service Queensland Spatial:
1088 Brisbane, Queensland, Australia). Available at
1089 https://www.data.qld.gov.au/dataset/fire-history-queensland-parks-and-wildlife-
1090 service [Verified 18 August 2023]
1091 R Core Team (2018) The R Project for statistical computing. (R Foundation for Statistical
1092 ComputingVienna, Austria). viewed 12th September 2020, <https://www.r-
1093 project.org>.
1094 R Core Team (2023) R: a language and environment for statistical computing. (R Foundation
1095 for Statistical ComputingVienna, Austria). viewed 1 August 2023, <https://www.R-
1096 project.org/>.
1097 Rainsford, F. W., L. T. Kelly, S. W. J. Leonard, and A. F. Bennett. 2020. Post-fire
1098 development of faunal habitat depends on plant regeneration traits. Austral Ecology
1099 **45**:800-812 https://doi.org/10.1111/aec.12896.

Ramos, D. M., J. F. M. Valls, F. Borghetti, and M. K. J. Ooi. 2019. Fire cues trigger germination and stimulate seedling growth of grass species from Brazilian savannas. American Journal of Botany **106**:1190-1201 https://doi.org/10.1002/ajb2.1345.

Sano, M., R. Tangney, A. Thomsen, and M. K. J. Ooi. 2025. Extreme fire severity interacts with seed traits to moderate post-fire species assemblages. American Journal of Botany:e70012 https://doi.org/10.1002/ajb2.70012.

Schmidberger, J. W., and P. G. Ladd. 2020. Geographic distribution and the reproductive and demographic ecology of two congeneric seeder and resprouter tree species. Forest ecology and management **475**:118428 https://doi.org/10.1016/j.foreco.2020.118428.

Schmidt, S., and G. R. Stewart. 1997. Waterlogging and fire impacts on nitrogen availability and utilization in a subtropical wet heathland (wallum). Plant, Cell & Environment **20**:1231-1241 https://doi.org/10.1046/j.1365-3040.1997.d01-20.x.

Seglias, A. E., E. Williams, A. Bilge, and A. T. Kramer. 2018. Phylogeny and source climate impact seed dormancy and germination of restoration-relevant forb species. PLoS One **13**:e0191931 https://doi.org/10.1371/journal.pone.0191931.

Shibata, R., M. Shibata, H. Tanaka, S. Iida, T. Masaki, F. Hatta, H. Kurokawa, and T. Nakashizuka. 2014. Interspecific variation in the size-dependent resprouting ability of temperate woody species and its adaptive significance. Journal of Ecology **102**:209-220 https://doi.org/10.1111/1365-2745.12174.

Smith, A. L. 2018. Successional changes in trophic interactions support a mechanistic model of post-fire population dynamics. Oecologia **186**:129-139 https://doi.org/10.1007/s00442-017-4016-z.

Smith, A. L., W. Blanchard, D. P. Blair, L. McBurney, S. C. Banks, D. A. Driscoll, and D. B. Lindenmayer. 2016. The dynamic regeneration niche of a forest following a rare disturbance event. Diversity and Distributions **22**:457-467 https://doi.org/10.1111/ddi.12414.

Spencer, R. 1995. Horticultural flora of South-eastern Australia: the identification of garden and cultivated plants. University of New South Wales Press, Sydney, NSW, Australia.

Staden, J. V., N. A. C. Brown, A. K. Jäger, and T. A. Johnson. 2000. Smoke as a germination cue. Plant Species Biology **15**:167-178 https://doi.org/10.1046/j.1442-1984.2000.00037.x.

Stanley, T. D., E. M. Ross, and L. W. Jessup. 1983. Flora of south-eastern Queensland. Queensland Department of Primary Industries, Brisbane, QLD, Australia.

1133 Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato,
1134 P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to
1135 wildfires under climate change. Ecology Letters **21**:243-252
1136 https://doi.org/10.1111/ele.12889.
1137 Stewart, P. L. C. F., and P. T. Moss. 2015. Fire patterns of south eastern Queensland in a
1138 global context: a review. Pages 227-236 *in* Proceedings of the Large Wildland Fires
1139 Conference. U.S. Department of Agriculture, Forest Service, Rocky Mountains
1140 Research Station, Missoula, Montana, United States of America.
1141 Talluto, M. V., and C. W. Benkman. 2014. Conflicting selection from fire and seed predation
1142 drives fine-scaled phenotypic variation in a widespread North American conifer.
1143 PNAS Nexus **111**:9543-9548 https://doi.org/10.1073/pnas.1400944111.
1144 Tangney, R., S. J. McInnes, E. L. Dalziell, W. K. Cornwell, B. P. Miller, T. D. Auld, and M.
1145 K. J. Ooi. 2025. Defining the pyro-thermal niche: do seed traits, ecosystem type and
1146 phylogeny influence thermal thresholds in seeds with physical dormancy? New
1147 Phytologist **246**:1567-1582 https://doi.org/10.1111/nph.70061.
1148 Tangney, R., D. J. Merritt, J. N. Callow, J. B. Fontaine, and B. P. Miller. 2020. Seed traits
1149 determine species' responses to fire under varying soil heating scenarios. Functional
1150 Ecology **34**:1967-1978 https://doi.org/10.1111/1365-2435.13623.
1151 Tausch, S., M. Leipold, C. Reisch, and P. Poschlod. 2024. How precisely can x-ray predict
1152 the viability of wild flower plant seeds? Seed Science and Technology **52**:109-123
1153 https://doi.org/10.15258/sst.2024.52.1.10.
1154 Taylor, A. H. 2010. Fire disturbance and forest structure in an old-growth *Pinus ponderosa*
1155 forest, southern Cascades, USA. Journal of vegetation science **21**:561-572
1156 https://doi.org/10.1111/j.1654-1103.2009.01164.x.
1157 The Global Biodiversity Information Facility (2022a) *Allocasuarina littoralis*. (The Global
1158 Biodiversity Information Facility). viewed 10 March 2022,
1159 <https://www.gbif.org/occurrence/download/0178150-210914110416597>.
1160 The Global Biodiversity Information Facility (2022b) *Allocasuarina torulosa*. (The Global
1161 Biodiversity Information Facility). viewed 10 March 2022,
1162 <https://www.gbif.org/occurrence/download/0178104-210914110416597>.
1163 Thomsen, A. M., and M. K. J. Ooi. 2022. Shifting season of fire and its interaction with fire
1164 severity: impacts on reproductive effort in resprouting plants. Ecology and Evolution
1165 **12**:e8717-n/a https://doi.org/10.1002/ece3.8717.

1166 Turnbull, J. W., and P. N. Martensz. 1982. Aspects of seed collection, storage and germination
1167 in Casuarinaceae. Australian Forest Research **12**:2810249
1168 Turner, P. A. M., J. Balmer, and J. B. Kirkpatrick. 2009. Stand-replacing wildfires?: The
1169 incidence of multi-cohort and single-cohort *Eucalyptus regnans* and *E. obliqua* forests
1170 in southern Tasmania. Forest ecology and management **258**:366-375
1171 https://doi.org/10.1016/j.foreco.2009.04.021.
1172 van den Berg, D. (2021) Sentinel-2 fire scars - QLD DES algorithm, QLD coverage.
1173 (Terrestrial Ecosystem Research NetworkAustralia). viewed 7th November 2024,
1174 <https://portal.tern.org.au/metadata/TERN/7b6d2b84-cbf3-46e8-aa8c-c49352f9ffd5>.
1175 Vandvik, V., J. P. Töpper, Z. Cook, M. I. Daws, E. Heegaard, I. E. Måren, and L. G. Velle.
1176 2014. Management-driven evolution in a domesticated ecosystem. Biology letters
1177 **10**:20131082 https://doi.org/10.1098/rsbl.2013.1082.
1178 Verdú, M. 2000. Ecological and evolutionary differences between Mediterranean seeders and
1179 resprouters. Journal of vegetation science **11**:265-268
1180 https://doi.org/10.2307/3236806.
1181 Villellas, J., J. Ehrlén, E. E. Crone, A. M. Csergő, M. B. Garcia, A.-L. Laine, D. A. Roach, R.
1182 Salguero-Gómez, G. M. Wardle, D. Z. Childs*, et al.* 2021. Phenotypic plasticity masks
1183 range-wide genetic differentiation for vegetative but not reproductive traits in a short-
1184 lived plant. Ecology Letters **24**:2378-2393 https://doi.org/10.1111/ele.13858.
1185 Visscher, A. M., A. Latorre Frances, M. Yeo, J. Yan, L. Colville, P. Gomez Barreiro, and H.
1186 W. Pritchard. 2021. Comparative analyses of extreme dry seed thermotolerance in five
1187 Cactaceae species. Environmental and experimental botany **188**:104514
1188 https://doi.org/10.1016/j.envexpbot.2021.104514.
1189 Walsh, S. F., R. Trouvé, P. A. Vesk, B. von Takach, and C. R. Nitschke. 2022. The cost of fruit
1190 and the penalty of youth: Predicting mean annual seed production in single-species
1191 forest stands. Forest ecology and management **508**:119978
1192 https://doi.org/10.1016/j.foreco.2021.119978.
1193 Wang, H., P. J. Eyk, P. R. Medwell, C. H. Birzer, Z. F. Tian, M. Possell, and X. Huang. 2022.
1194 Smouldering fire and emission characteristics of Eucalyptus litter fuel. Fire and
1195 materials **46**:576-586 10.1002/fam.3004.
1196 Wang, X., M. Luo, F. Song, S. Wu, Y. D. Chen, and W. Zhang. 2024. Precipitation seasonality
1197 amplifies as Earth warms. Geophysical Research Letters **51**:e2024GL109132
1198 https://doi.org/10.1029/2024GL109132.

1199 Wang, X., X. Morin, J. Zhang, G. Chen, L. Mao, Y. Chen, Z. Song, Y. Du, and K. Ma. 2023.
1200 Geographical patterns and determinants in plant reproductive phenology duration.
1201 Frontiers in Plant Science **14** https://doi.org/10.3389/fpls.2023.1199316.
1202 Webb, M. H., S. Wotherspoon, D. Stojanovic, R. Heinsohn, R. B. Cunningham, P. Bell, and
1203 A. Terauds. 2014. Location matters: using spatially explicit occupancy models to
1204 predict the distribution of the highly mobile, endangered swift parrot. Biological
1205 Conservation **176**:99-108 https://doi.org/10.1016/j.biocon.2014.05.017.
1206 Wheelwright, N. T., and B. A. Logan. 2004. Previous-year reproduction reduces
1207 photosynthetic capacity and slows lifetime growth in females of a neotropical tree.
1208 PNAS Nexus **101**:8051-8055 https://doi.org/10.1073/pnas.0402735101.
1209 Whelan, R., L. Rogerson, C. Dickman, and E. Sutherland. 2002. Critical life cycles of plants
1210 and animals: developing a process-based understanding of population changes in fire-
1211 prone landscapes. Pages 94-124 *in* R. A. Bradstock, J. E. Williams, and A. M. Gill,
1212 editors. Flammable Australia: the fire regimes and biodiversity of a continent.
1213 Cambridge University Press, Cambridge, United Kingdom.
1214 Williams, P. R., M. Parsons, R. Jensen, and C. Tran. 2012. Mechanisms of rainforest
1215 persistence and recruitment in frequently burnt wet tropical eucalypt forests. Austral
1216 Ecology **37**:268-275 https://doi.org/10.1111/j.1442-9993.2011.02271.x.
1217 Young, D. J. N., C. M. Werner, K. R. Welch, T. P. Young, H. D. Safford, and A. M. Latimer.
1218 2019. Post-fire forest regeneration shows limited climate tracking and potential for
1219 drought-induced type conversion. Ecology **100**:13 https://doi.org/10.1002/ecy.2571.
1220 Zaki, E., M. Abedi, and A. Naqinezhad. 2021. How fire history affects germination cues of
1221 three perennial grasses from the mountain steppes of Golestan National Park. Flora
1222 **280**:151835 https://doi.org/10.1016/j.flora.2021.151835.
1223 Zammit, C., and M. Westoby. 1987. Seedling recruitment strategies in obligate-seeding and
1224 resprouting banksia shrubs. Ecology **68**:1984-1992 https://doi.org/10.2307/1939889.
1225 Zhang, H., Y. Zhao, and J.-K. Zhu. 2020. Thriving under stress: how plants balance growth
1226 and the stress response. Developmental Cell **55**:529-543
1227 https://doi.org/10.1016/j.devcel.2020.10.012.
1228 Zhao, M., Z. Liu, H. Zhang, Y. Wang, and H. Yan. 2021. Germination characteristics is more
1229 associated with phylogeny-related traits of species in a salinized grassland of
1230 Northeastern China. Frontiers in Ecology and Evolution **9**
1231 https://doi.org/10.3389/fevo.2021.748038.

1232 Zirondi, H. L., M. K. J. Ooi, and A. Fidelis. 2021. Fire-triggered flowering is the dominant
1233 post-fire strategy in a tropical savanna. Journal of vegetation science **32**:e12995
1234 https://doi.org/10.1111/jvs.12995.
1235

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

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 AIC_c 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

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 AIC_c 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

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 AIC_c 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

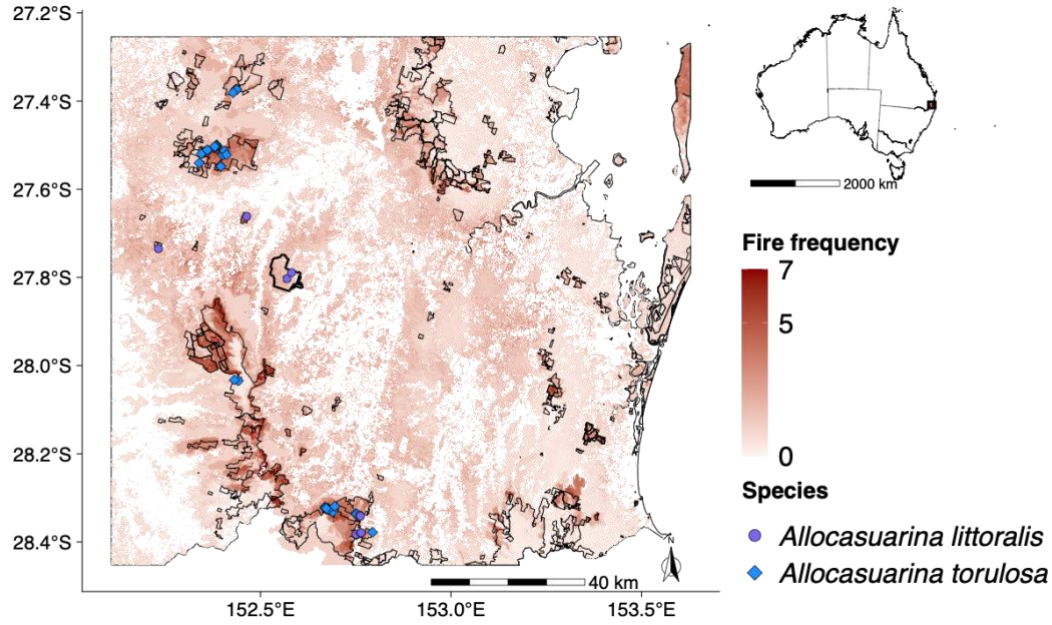

Figure 1 Sampling locations of Allocasuarina littoralis (n = 385 individuals from 8 transects) and A. torulosa (n = 703 individual from 32 transects) in southeast Queensland, Australia. Protected areas are displayed with black outlines including public land (*conservation parks,* state forests *and* 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 et al. 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.

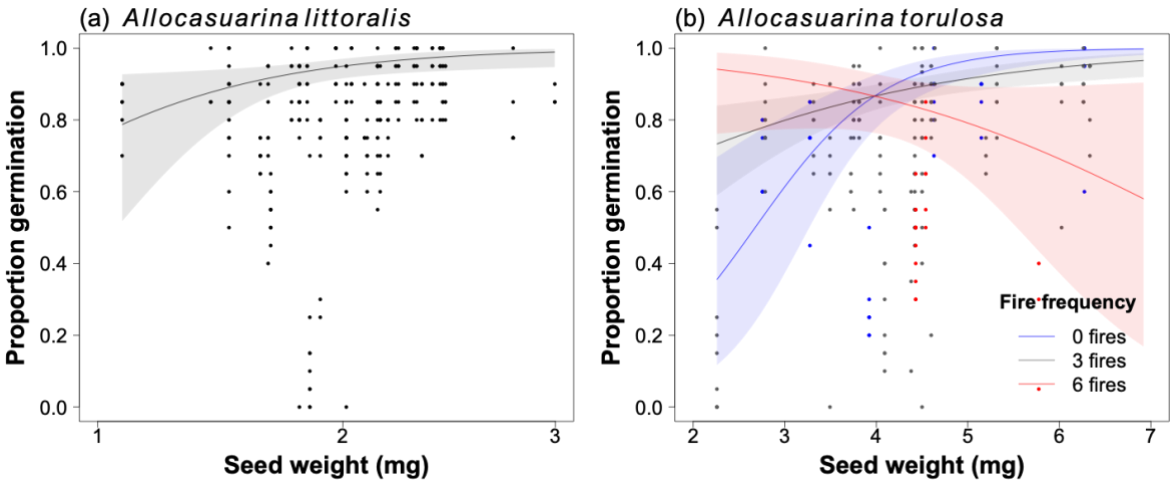

Figure 2 The estimated effect (and 95% confidence intervals) of seed weight on proportion germination in (a) *Allocasuarina littoralis* and (b) *A. torulosa* from the top-ranked models for each species. The model for *A. torulosa* included an interaction between seed weight and fire frequency.

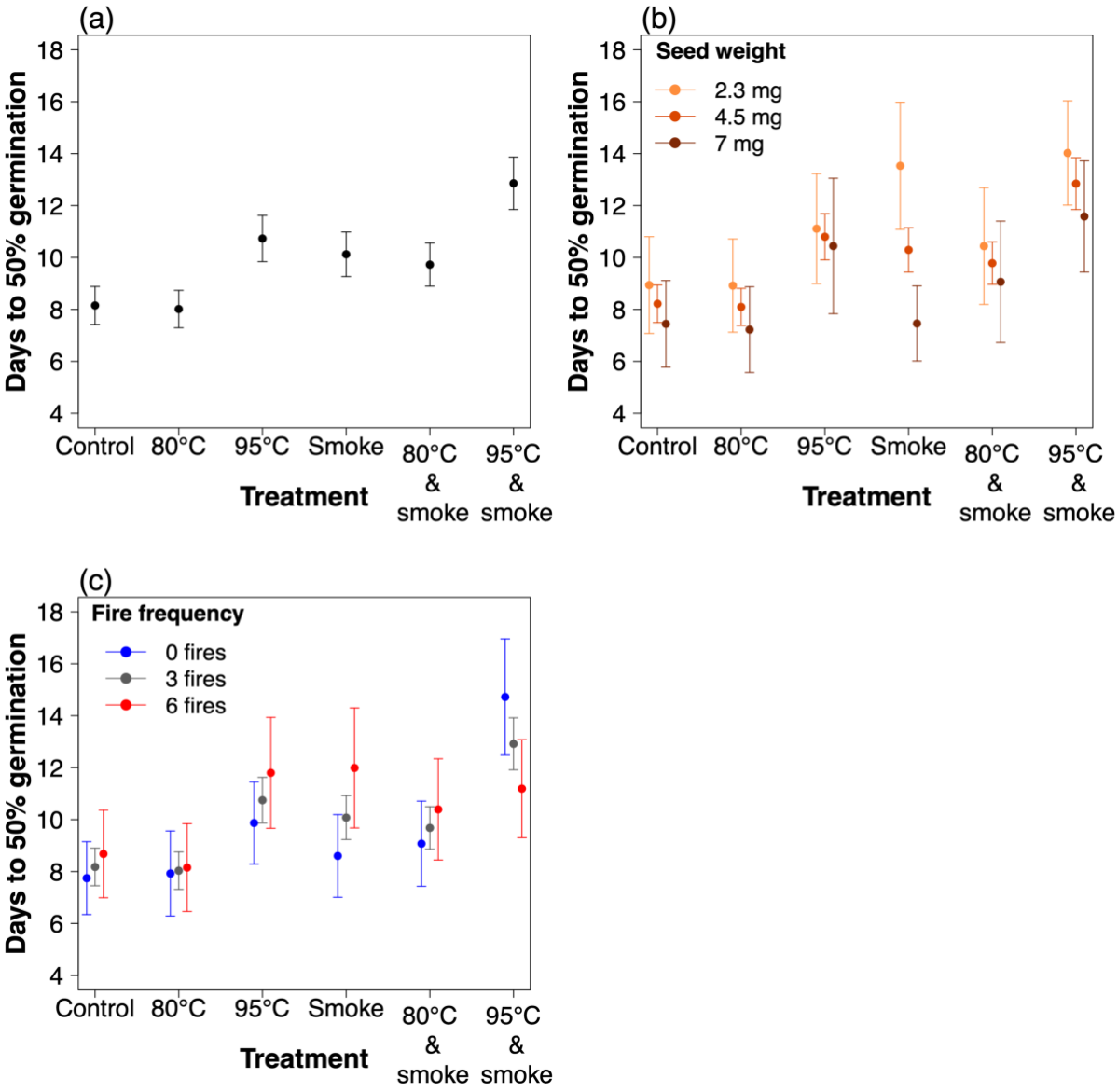

Figure 3 The estimated effect (and 95% confidence intervals) of seed treatment on time to 50% germination (days) from the three top-ranked models for A. torulosa (ΔAIC_c <2), (a) top-ranked model with a treatment effect; (b) second ranked model with an interaction between treatment and seed weight; and (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).

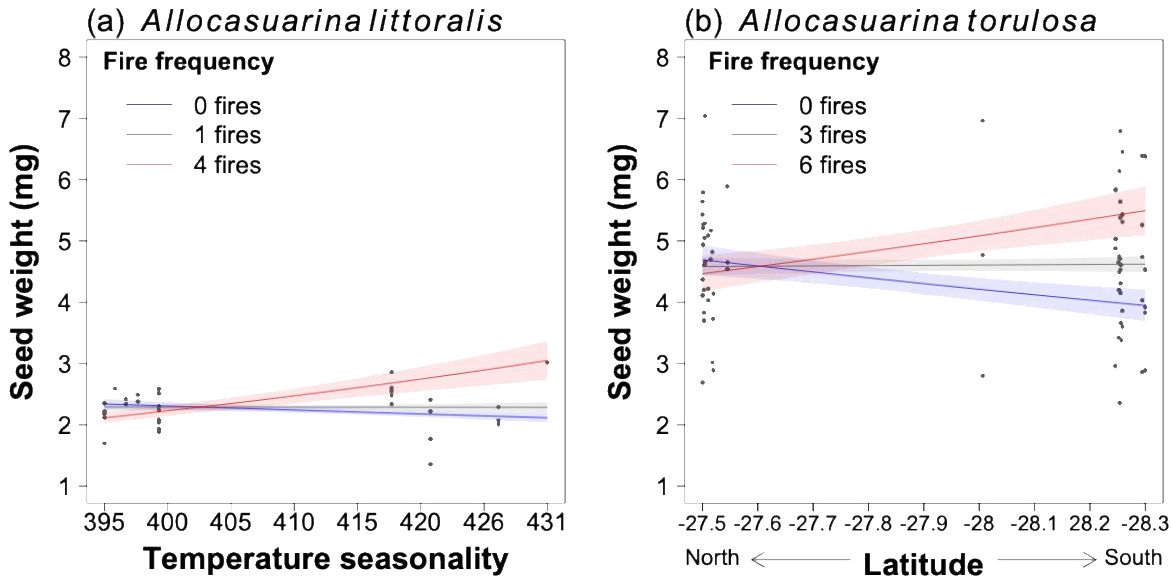

Figure 4 The estimated effect (and 95% confidence intervals) of fire frequency on seed weight in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. (a) In *Allocasuarina littoralis*, seed weight was influenced by an interaction between fire frequency and temperature seasonality. (b) In *Allocasuarina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

Appendix S1

Fire history influences reproductive traits in congeneric food tree species for a dietary specialist cockatoo

Felicity E. Charles, Patrick T. Moss, Annabel L. Smith

Section S1: Germination experiment optimisation methods and results

Incubation temperature optimisation

Water in a ten-chamber thermal gradient bar (CSK Model CSK-TGB, Serial 3310; CSK Group, Wacol, Queensland, Australia) was heated to temperatures ranging between 4° 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° to 36°C with chambers differing by *ca.* 3° 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). A 'seed lot' was defined as the whole collection of seeds from an individual and a 'seed sample' was of 20 seeds from the seed lot of an individual. For each species three seed subsamples were placed in separate petri dishes, giving 600 seeds across the thermal gradient bar for incubation temperature optimisation. Incubation temperature optimisation tests were run for 28 days, as previous studies considered this sufficient time for viable seeds to germinate (Turnbull and Martensz 1982, Crowley and Jackes 1990). To determine optimal germination temperature, we plotted the proportion of seeds germinated

against the number of trial days. We selected the optimum temperature as the one where overall proportion of seeds germinated was high (i.e., 70-100% proportion germination) over the fewest days. Following the incubation test, a priori and post-hoc seed viability tests were conducted (described in the main document and below). Ungerminated, viable seed was considered to have been exposed to an unsuitable germination temperature.

Temperatures of 6° and 10°C slowed germination rates or stopped germination over the 28-day sampling period, and these temperatures were unsuitable (Fig. S1). Germination in *A. littoralis* was most consistent in chamber temperatures from 14° to 32°C (70-90%, Fig. S1a). Thus, 17°C was considered optimal for *A. littoralis*, as this chamber had the highest overall germination for two of the three individuals tested (85-95%, Fig. S1a). Germination in *A. torulosa* was similar at 17° and 20°C (85-90%, Fig. S1b). *Allocasuarina torulosa* germination was most consistent across the range of temperatures from 14° to 36°C. Thus, we selected 20°C as the optimal temperature, which was consistent with a previous study (Turnbull and Martensz 1982).

Heat shock 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 in comparison to an untreated control. Heat shocks tests were conducted at 80°, 95°, 110°, 125°, and 150°C for durations of 0.5, 1, 2, 5 and 10 minutes. Three individual seed lots with a large quantity of seeds were used. These tests indicated that temperatures over 100°C were, in most cases, sufficient to kill loose seeds (Fig. S2). We selected 80° and 95°C for heat shock temperatures in the full factorial experiment (Fig. S2).

Heat shock optimisation tests showed consistently high germination in both species at 80°C, but variable germination responses between species as temperature and duration increased (Fig. S2). In *Allocasuarina littoralis*, the lethal temperature threshold was between 110° 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 the number of seeds germinating at this temperature reduced: 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° 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° to 105°C, as only seeds exposed to short durations at 110°C germinated (Fig. S2b). Exposure times of 5 minutes at 80° and 95°C produced consistently high germination, which was similar or greater than that of the controls. Therefore, we selected a 5-minute exposure time at 80° and 95°C for both species for heat shock in the main experiment.

Smoke exposure optimisation

Allocasuarina species produce dense leaf litter, which has an allelopathic effect on other plants (Buehler 2010, Ahmed et al. 2019). As such, we expected smoke responses in our study species could be strongly tied to smoke from their own leaf litter, rather than smoke more generally. To test this hypothesis, we conducted aerosol smoke tests to compare germination responses to smoke from *Allocasuarina torulosa* leaf litter material and 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 seed sample of 20 seeds was placed in a petri dish on an approximately 10 cm high shelf inside the smoke chamber. Nine seed samples were tested in a given smoking session. Between smoking session, all smoke was released from the chamber, before exposing new seed samples, to maintain a similar amount of smoke across individuals. We tested smoke exposures of 5, 10, and 20 minutes for each seed sample. 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.

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 in main document). 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 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.

Section S1 References

Ahmed, T. A., A. A. Elezz, and N. H. Al-Sayed. 2019. Dataset of allelopathic effects of *Casuarina equisetifolia*-L leaf aquatic extract on seed germination and growth of selected plant crops. Data in Brief **27**:104770.

Buehler, C. P. 2010. Soil modification and potential allelopathy: an investigation into how the invasive *Casuarina equisetifolia* L. (Australian pine) modify their environment. Mississipi State University, Mississipi, United States of America.

Callister, K. E., S. K. Florentine, and M. E. Westbrooke. 2018. An investigation of the soil seedbank and seed germination of perennial species in belah (*Casuarina pauper*) woodlands in north-west Victoria. Australian journal of botany **66**:202-212.

Crowley, G. M., and B. R. Jackes. 1990. Germination characteristics in tropical provenances of *Allocasuarina littoralis* and *A. torulosa*. Forest ecology and management **35**:227-238.

Keeley, J. E., and W. J. Bond. 1997. Convergent seed germination in South African fynbos and Californian chaparral. Plant ecology **133**:153-167.

Turnbull, J. W., and P. N. Martensz. 1982. Aspects of seed collection, storage and germination in Casuarinaceae. Australian Forest Research **12**:2810249.

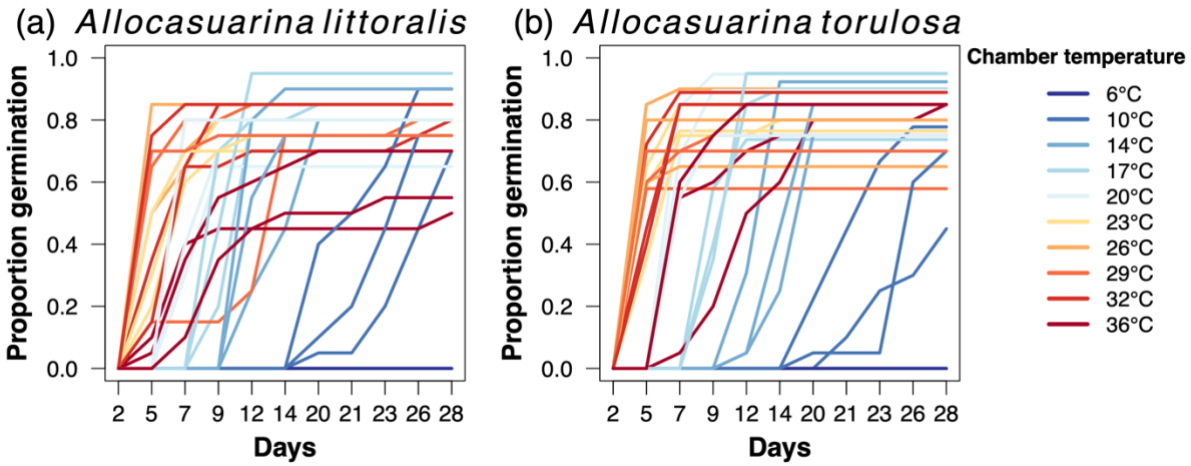

Figure S1 Cumulative proportion of seeds germinated along a thermal gradient bar ranging from 6° to 36°C for (a) *Allocasuarina littoralis* and (b) *A. torulosa*. No germination occurred in either species in chambers at 6°C. Optimal germination temperature was considered the point at which the majority of seeds had germinated within the shortest period of time. Optimal incubation temperatures for germination were determined to be 17°C for *A. littoralis* and 20°C for *A. torulosa*.

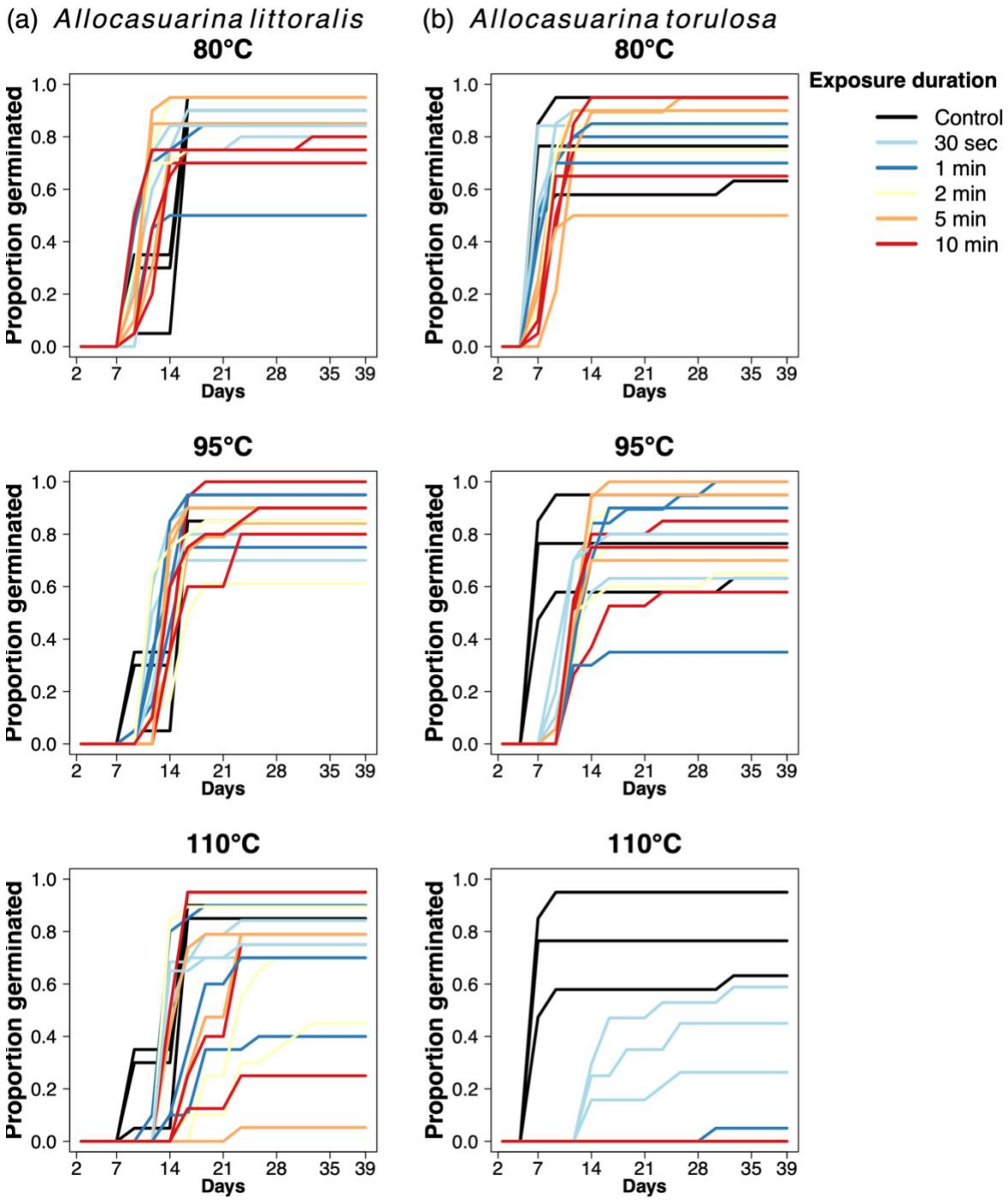

Figure S2 Cumulative proportion of seeds germinated in heat shock optimisation tests at 80°, 95°, and 110°C compared to a control (black) in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. A 5-minute exposure to 80° and 95°C for both species was considered optimal for heat shock in the main experiment.

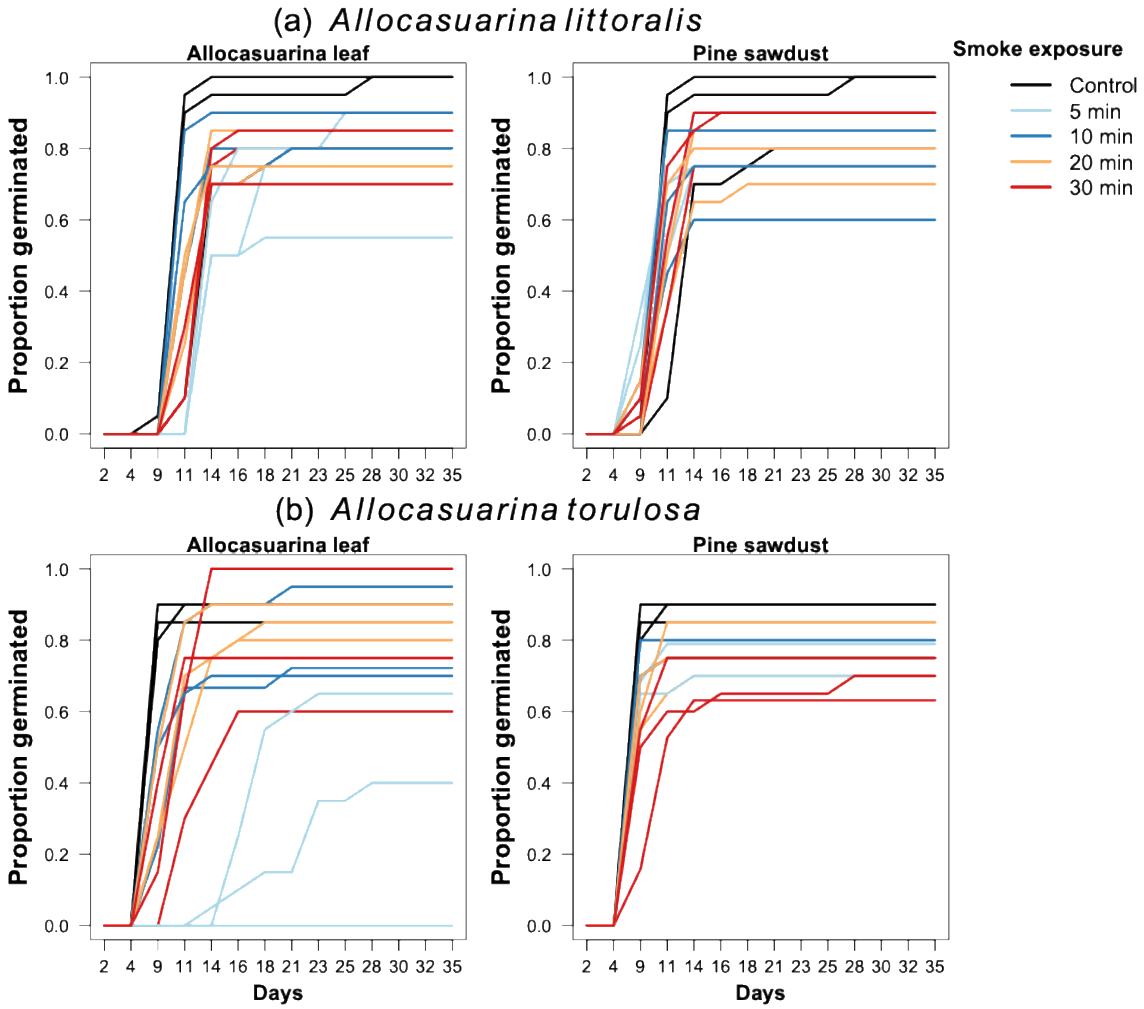

Figure S3 Cumulative proportion of seeds germinated after exposure to aerosol *Allocasuarina* leaf litter or pine sawdust derived smoke in (a) *Allocasuarina littoralis* and (b) *A. torulosa*. A 20-minute exposure to *Allocasuarina* leaf litter smoke for both species was considered optimal for smoke exposure in the main experiment.

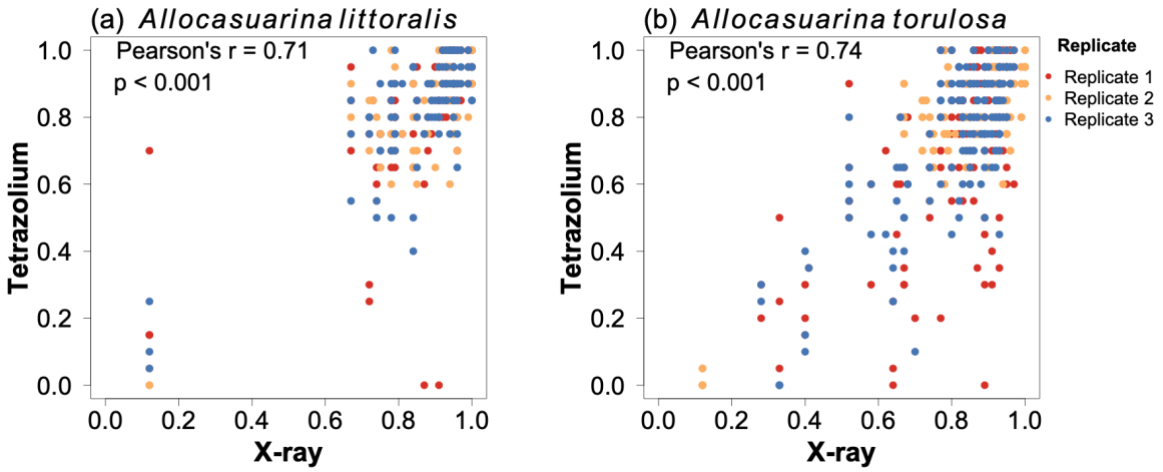

Figure S4 The relationship and correlation coefficient between seed viability rates across experimental replicates measured using pre-germination x-ray and post-germination 1% 2,3-5 triphenyl tetrazolium chloride for (a) *Allocasuarina littoralis*, and (b) *A. torulosa* individuals.

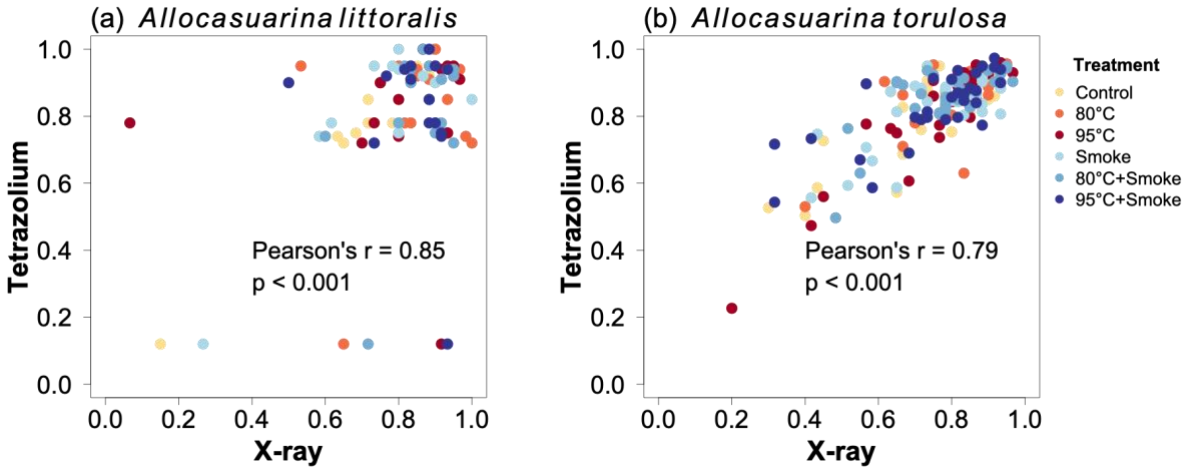

Figure S5 The relationship and correlation coefficient between seed viability rates across seed treatments measured using pre-germination x-ray and post-germination 1% 2,3-5 triphenyl tetrazolium chloride for (a) *Allocasuarina littoralis*, and (b) *A. torulosa* individuals.

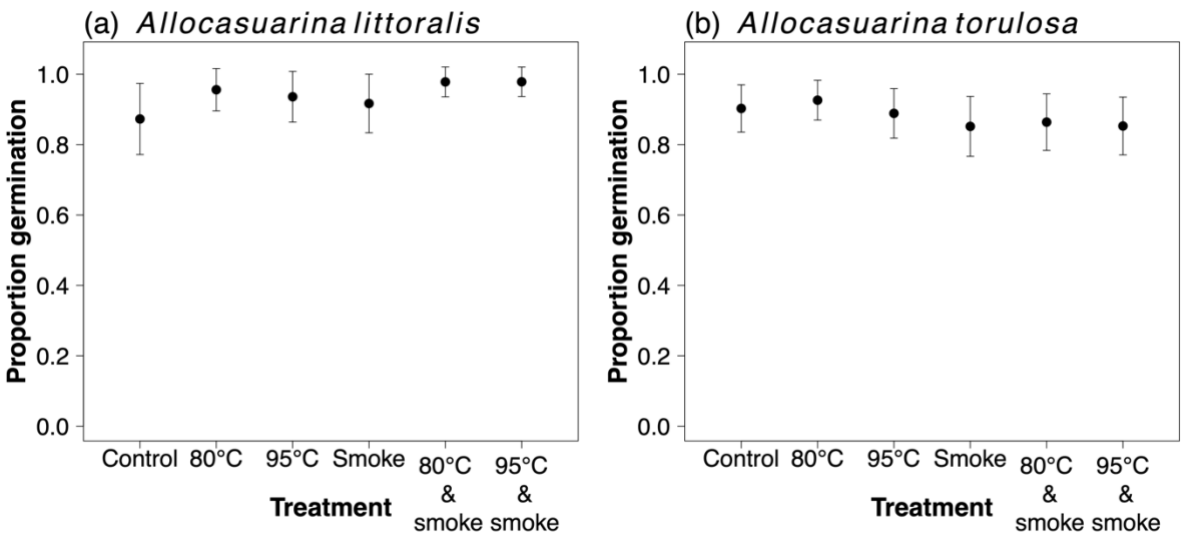

Figure S6 The estimated effect (and 95% confidence intervals) of seed treatments on proportion germination of (a) *Allocasuarina littoralis* and (b) *A. torulosa* from southeast Queensland, Australia. There was not a strong effect of seed treatment on germination rate in either species, with the null model ranked higher than any model containing the seed treatment term (see Table 2, main document).

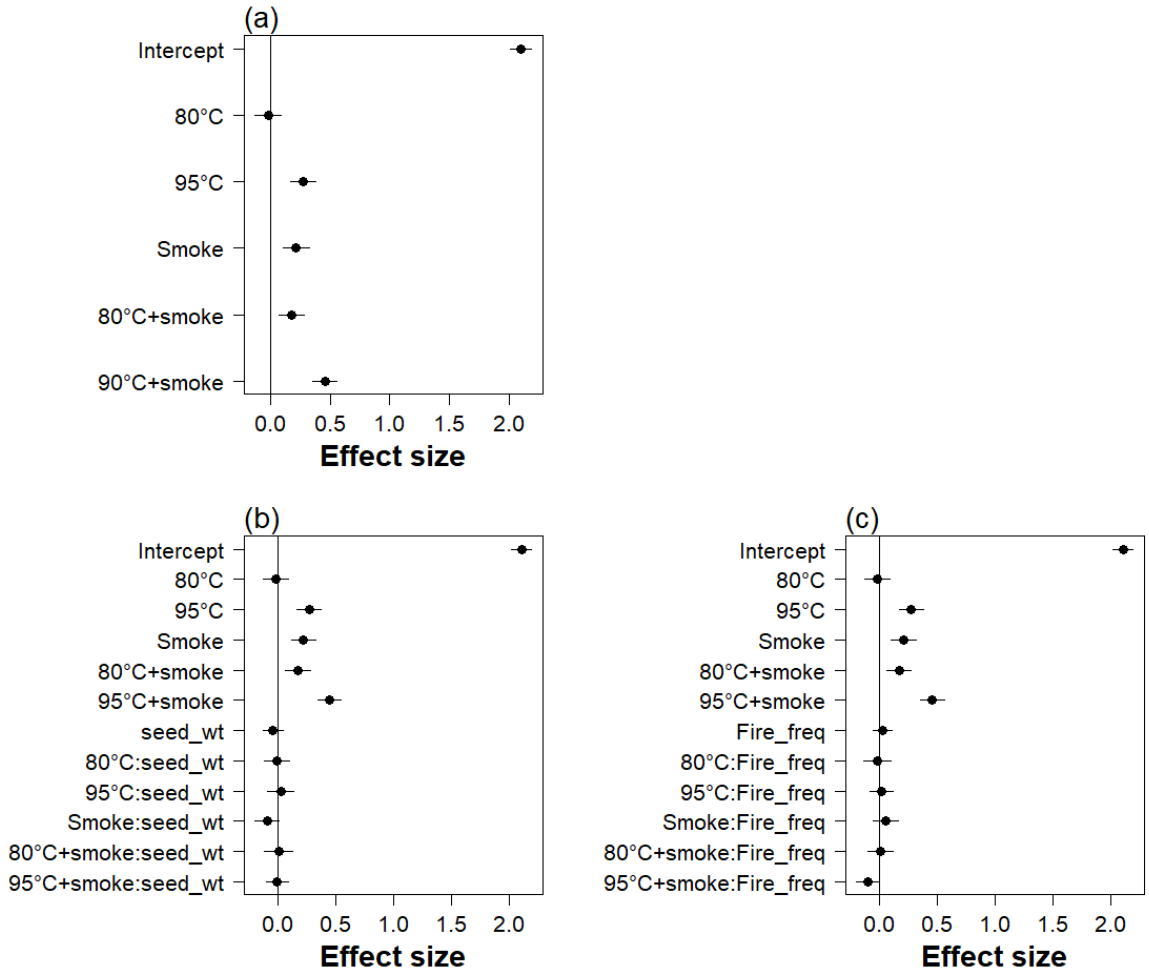

Figure S7 Effect sizes of coefficients (and 95% confidence intervals) for models examining time to 50% germination in *Allocasuarina torulosa*. Effect sizes were examined to determine the strength of effects for models including (a) treatment, (b) treatment × seed weight, and (c) treatment ×fire frequency.

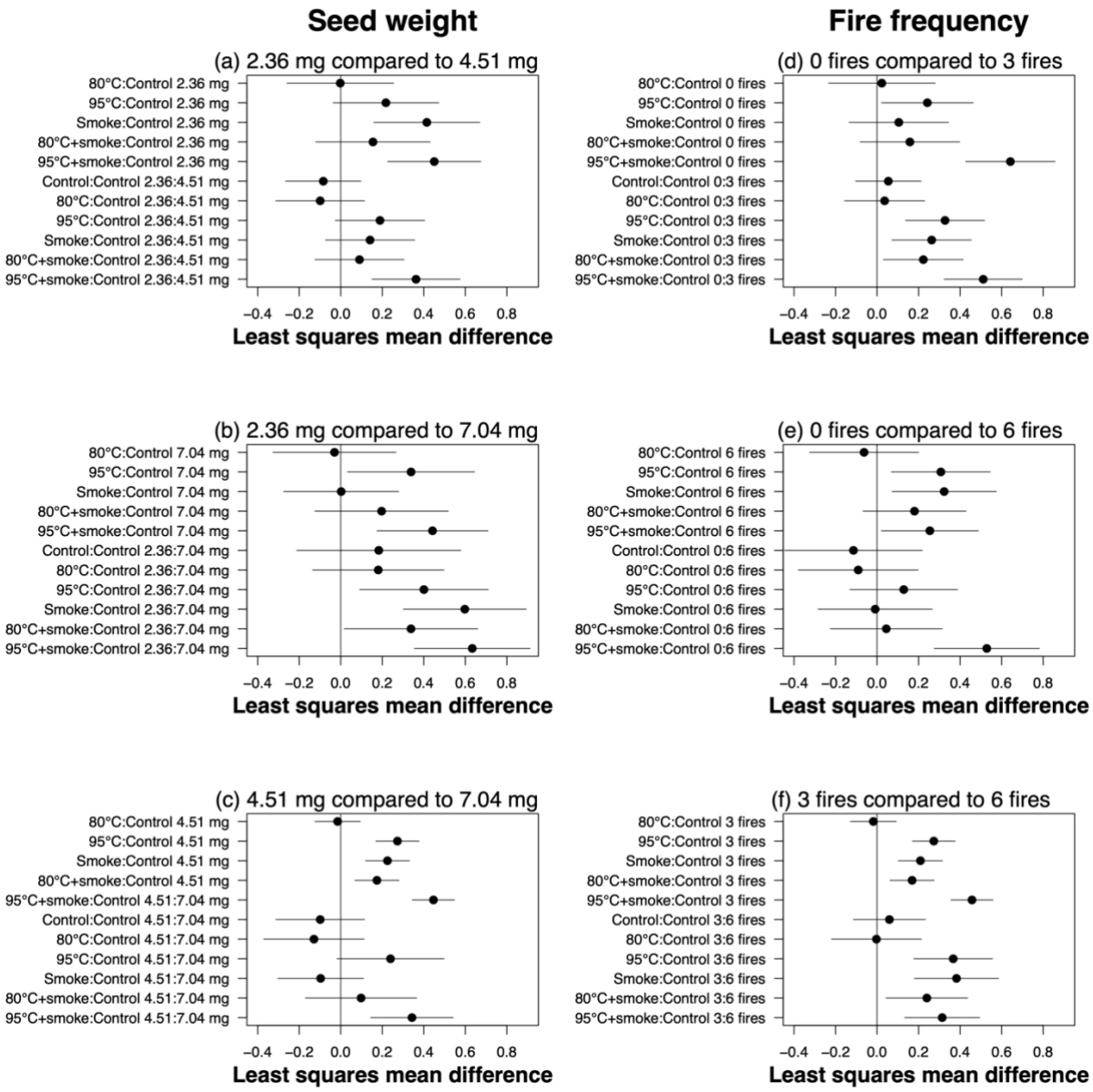

Figure S8 Least squares mean differences (and 95% confidence intervals) for models examining the effect of seed treatments compared to controls on time to 50% germination in *Allocasuarina torulosa*. Models included an interaction between treatment and (a-c) seed weight, or (d-f) fire frequency. To aid 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.

Table S1 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*. Models are ranked from lowest to highest AIC_c and the top-ranked models are shown in bold.

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

Table S2 Models used to examine the influence of fire frequency, time since fire, and environmental variation on population demographic structure in *Allocasuarina littoralis*. Models are ranked from lowest to highest AIC_c and the top-ranked models are shown in bold.

Fire metric	Demographic 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
	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
	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
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
	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
	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

Table S3 Models used to examine the influence of fire frequency, time since fire, and environmental variation on population demographic structure in *Allocasuarina torulosa*. Models are ranked from lowest to highest AIC_c and the top-ranked models are shown in bold.

Fire metric	Demographic 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	43.13	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

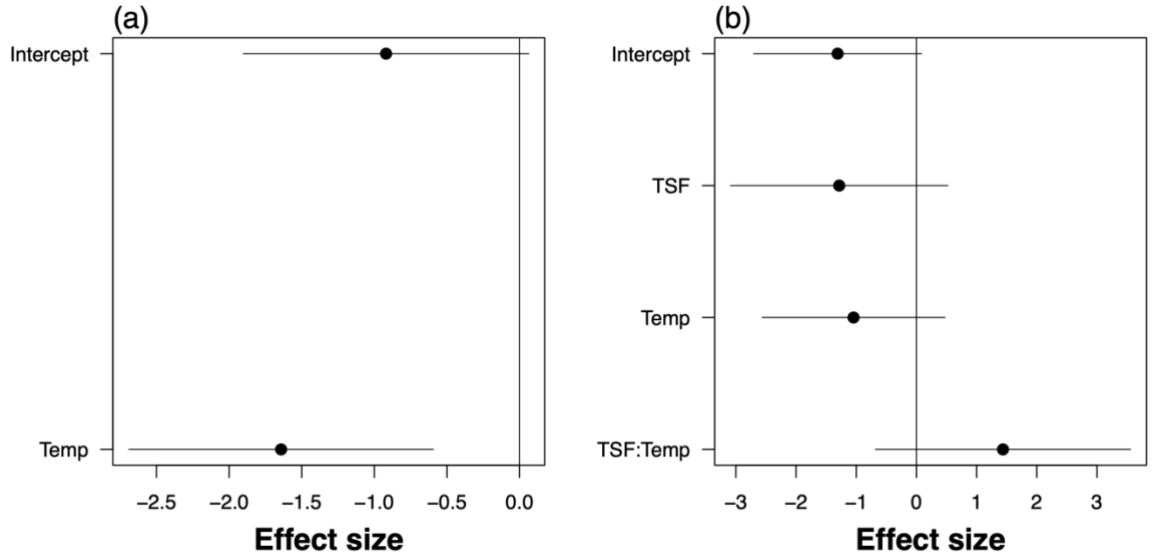

Figure S9 Effect sizes of coefficients (and 95% confidence intervals) for the influence of (a) temperature seasonality, and (b) temperature seasonality and time since fire (TSF) interaction on the proportion of recruits (i.e., seedlings and saplings) to mature individuals in *Allocasuarina torulosa*.