

Does fire season impact post-fire seed predation of serotinous seeds?



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This report is provided to the Australian Flora Foundation in fulfillment of the conditions of the grant awarded to the author in 2020. This report presents the interim results from a study intended to be included in a PhD study conducted by Tom Le Breton between 2019 and 2023 on the impacts of changing fire regimes on plant species and their conservation.

The study was interrupted and seriously impeded by the COVID-19 pandemic, a possibility flagged in the initial project proposal. Due to personal matters and the demands of the thesis the project was not able to be completed. Additional experimental plots are being set up in Autumn 2024 to complete the project and a final report will be issued to the Australian Flora Foundation containing those results in late 2024.

The ideas, experimental work, results, analyses and conclusions presented here are entirely the author's own effort, except where indicated otherwise. This work is original.



Signature of author Tom Le Breton

Date: 30/04/24

Cover photo: *Banksia ericifolia* in a recently burned area in the Royal National Park, NSW, 2020. This large mature plant was killed by the fire.

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Abstract

Fire seasons are changing globally, conflicts with timing of life-history stages of plants may increase extinction risk. Increased exposure to post-dispersal seed predation is one mechanism for this, with species likely at greater threat in more seasonal rainfall regions. We compare seasonal variance in levels of post-fire, post-dispersal seed predation for serotinous Proteaceae across aseasonal and seasonal rainfall regions in the south-east and south-west of Australia respectively. We examined predation effects on two species of *Banksia*, one in each climate type. The experimental design consisted of seed cafes with four levels of seed-predator exclusion: open to all, ant exclusion, vertebrate exclusion and all excluded. Ten experimental blocks were laid out at random within recently burned areas in Autumn (spring was not possible due to challenges posed by COVID lockdowns). The number of seeds remaining were counted at four week intervals until all were taken or had germinated. We found strong evidence that vertebrates are the predominate seed predator of *Banksia* seeds in both systems, consistent with past studies. We also found some evidence that seeds were predated at a higher rate in the south-west seasonal rainfall sites compared to the south-east aseasonal rainfall sites. However, further data is required to confirm the accuracy of this observation. While our data are preliminary they indicate that post-fire, post-dispersal seed predation of serotinous *Banksia* seeds is significant, particularly in the south-west of the country. Our findings have implications for conservation of similar species and fire management in areas where they occur.

Introduction

Fire regimes are changing globally due to anthropogenic activity and climate change (Le Page et al. 2010, Bowman et al. 2014, Jolly et al. 2015). Altered fire regimes present a significant challenge for plant species adapted to a particular historical regime as they pose the risk of interrupting key life history processes, reducing opportunities for reproduction and recovery (Nolan et al. 2021). While, changes are occurring across all elements of the fire regime, changes to fire seasonality represent one of the strongest influences humans have had on fire regimes (Balch et al. 2017) as well as one of the most understudied (Miller et al. 2019; Tangney et al. 2022). Like changes to other elements of the fire regime, altered fire seasonality has the potential to result in population declines or an overall increase in species extinction risk (Gill & Bradstock 1995; Miller et al. 2019). To conserve plant species, it is crucial to understand the threats that they face. There is therefore a need to better understand how altered fire seasonality may be negatively impacting native plant species.

Plant phenology, like fire seasonality, is driven by abiotic factors (e.g. temperature and rainfall), typically in annual cycles, with key life-history events timed relatively predictably throughout the year. Any anthropogenic changes to fire seasonality may therefore result in misalignments of abiotic conditions with key life-history events which can pose a threat to plant species (Ooi et al. 2004, Collette & Ooi 2017). The consequences shifting fire seasonality may be highly complex, and seasonality has many direct and indirect effects on plant species. Eight key mechanisms have been identified via which fire seasonality may negatively impact plant populations (Miller et al. 2019; Keith et al. 2020). These range from pre-fire factors like propagule and energy availability, to post-fire factors relating to seedling establishment and growth (Miller et al. 2019). One of these mechanisms, post-fire seed survival, may be influenced by fluctuations in seed predator activity (Orrock et al. 2015; Miller et al. 2019) which may result in up to nine times higher rates of seed mortality (Bond 1984). The effects of post-fire seed predation are predicted to differ depending on species fire response, seed release strategies and climate types (Miller et al. 2019).

One group in which recruitment may be particularly sensitive to post-fire seed predation are serotinous species, such as *Banksia*, which retain their seeds in the canopy and release them after fires (Cowling & Lamont 1987; Miller et al. 2019). Serotinous species tend not to have seed dormancy and so rely on being released at a time when conditions are or will soon be suitable for germination. Being released too early in the year leaves seeds exposed to seed

predators for longer periods of time as they wait for the next germination season (Bond 1984). In relatively stable temperate environments where rainfall occurs year round timing should have less impact on the success of post-fire recruitment. However, in seasonal environments where rainfall is constrained to certain times of year fires at different times of year may lead to reduced recruitment success and have long term impacts on species populations and demographics. For species which rely on their canopy-stored seed bank for post-fire regeneration, obligate seeders, failure to recruit from released seeds can result in the local extinction of populations (Gill & Bradstock 1995).

Serotinous *Banksia* species in Australia are important components of many ecosystems in the south-east and south-west of the country. However, the regions have significant differences in their climates. In the south-east the heath and woodlands where *Banksia* frequently occur have an aseasonal rainfall regime that is generally quite consistent within and between years. While the south-west has a highly seasonal rainfall regime that sees the majority of rainfall occur in the winter. Both however, are experiencing pronounced shifts in their fire seasonality seeing increases in the occurrence of prescribed fire in shoulder seasons of autumn and spring due to the need for hazard reduction and the protection of human lives and assets (McCaw 2013; Clarke et al. 2019). Studies are increasingly showing negative impacts of altered fire seasonality in both these regions through a range of mechanisms (Millet et al. 2019) including post-fire predation of serotinous seeds following release from the canopy seed bank. However, the role and effect of seed predation following fires at different times of year is understudied.

To address this and to determine the degree to which rainfall seasonality influences post-fire seed predation we sought to undertake a series of seed removal experiments in both climate types and following both autumn and spring fires. The aims of this study are to:

1. Measure levels of post-dispersal seed predation for Proteaceae species with canopy-stored seed banks, following fires in different seasons.
2. Compare seasonal variance in levels of seed predation across seasonal and aseasonal rainfall regions.

By answering these questions we hope to better understand the risks associated with fire in different seasons for serotinous species such as *Banksia* to both inform better management actions and assessment of the risks posed to species persistence under different fire management regimes.

Methods

Study species

We conducted this study on two species of *Banksia*. The south-east species, *Banksia ericifolia*, is an obligate seeding, serotinous shrub to small tree that grows in heath and woodland across the coast and ranges of New South Wales. While it has corky bark, it lacks a lignotuber and is fire-killed, relying on seed released from follicles post-fire to recruit and replenish the population (Zammit & Westoby 1987; Jenkins et al. 2010). The south-west species, *Banksia menziesii*, unlike *B. ericifolia* is a resprouting serotinous species, that has both a shrubby form and a tree form and grows to different heights across its range due to an aridity gradient (Lamont et al. 2007). The species distribution occurs primarily on the coastal plain in banksia woodland on deep sandy soils. Despite being a resprouter, *B. menziesii* can experience moderate levels of mortality after being burnt particularly in the north of its range where the smaller plants grow and are more likely to be fully consumed (Lamont et al. 2007). As a result, the species has been observed to be declining in part due to recruitment below replacement levels (Lamont et al. 2007). So, while the two species have contrasting fire response strategies, successful recruitment remains vital to both and in both species is sensitive to post-fire seed predation.

Study regions

South-east study sites were located in the Royal National Park, south of Sydney (Fig. 1), in the Sydney Basin Bioregion (DAWE 2012). Vegetation across the park is highly varied but the study site was located in a mixture of heath and shrubby woodland on sandy soils and sandstone. Rainfall across the Sydney Basin Bioregion is largely aseasonal, with an annual average in the park of 1138 mm, peaking in March but occurring persistently throughout the year (BOM 2024a). The dominant fire season in this region is Summer, but fire management activities such as hazard reduction burning are often conducted in the shoulder seasons (March-May or August-October) and occasionally in winter if conditions allow (Clake et al. 2019).

South-west study sites were located in the Yeal Nature Reserve, north of Perth (Fig. 1), in the Swan Coastal Plain Bioregion (DAWE 2012). Vegetation in this region is primarily Banksia woodland on deep, sandy soils, the canopy consists of medium-sized trees dominated by various *Banksia* species and occasional sclerophyllous species (Tangney et al. 2022). The climate is warm Mediterranean, characterised by hot, dry summers and cool, wet winters with

rainfall being largely constrained to the winter months. The average annual rainfall at Gingin Airport (on the edge of Yeal NR) is 611 mm, 80% of which falls between May and September (BOM 2024b). Fire is typically constrained to summer, however, prescribed fires for hazard reduction are often conducted in shoulder seasons, spring and autumn (McCaw 2013; Densmore & Clingan 2019).

In both regions sites were selected opportunistically following the occurrence of prescribed burns in autumn and spring where they occurred in the right habitat.

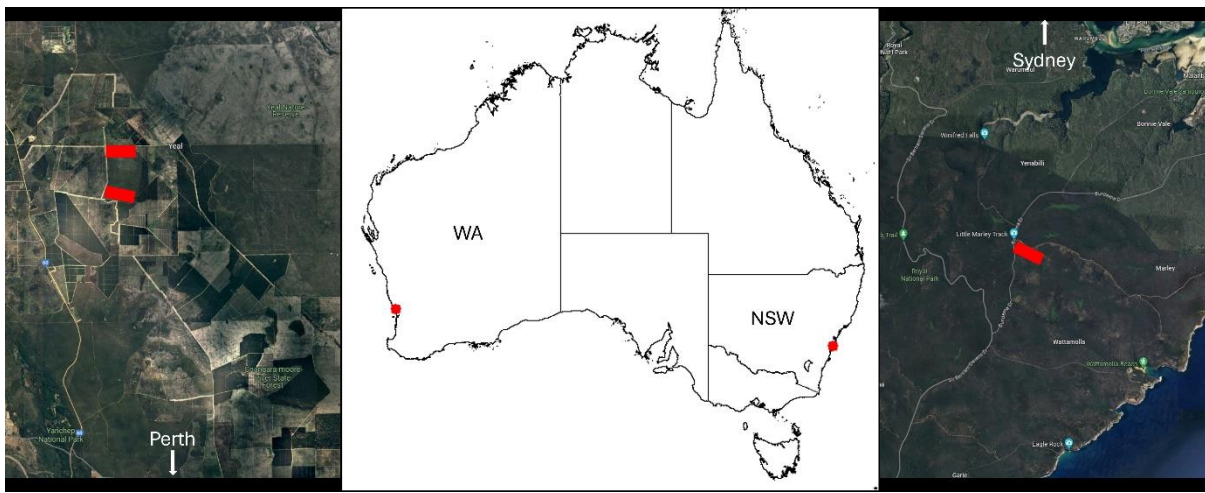


Figure 1. Map of the location of south-east (right) and south-west (left) study sites in Australia. Study sites are in red. The left and right maps are of the relative locations of the study sites within their local contexts, these maps are indicative only and not to scale.

Seed collection

Cones of both species were collected from the vicinity of the study sites and seeds extracted manually. Cones were first heated in an oven at 80 °C until the follicles began to open (c. 45 minutes). Seeds were then extracted from follicles using tweezers and the wing removed. Mouldy seeds were disposed, and the remaining healthy seeds were counted and stored at 15 °C and 15 rh.

Experimental design

The experimental design consisted of seed cafes set up in 10 replicate blocks of four treatments which comprised four treatments (Fig. 2). Blocks were 1 m² quadrats, with one treatment in each quadrant. In each treatment a 5 cm high piece of 90 mm diameter PVC piping was placed in the centre of the quadrant, 40 cm apart from one another. The pipes were

hammered into the ground until half (2.5 cm) remained above ground. Ten seeds of the study species were scattered evenly on the soil surface within each pipe.

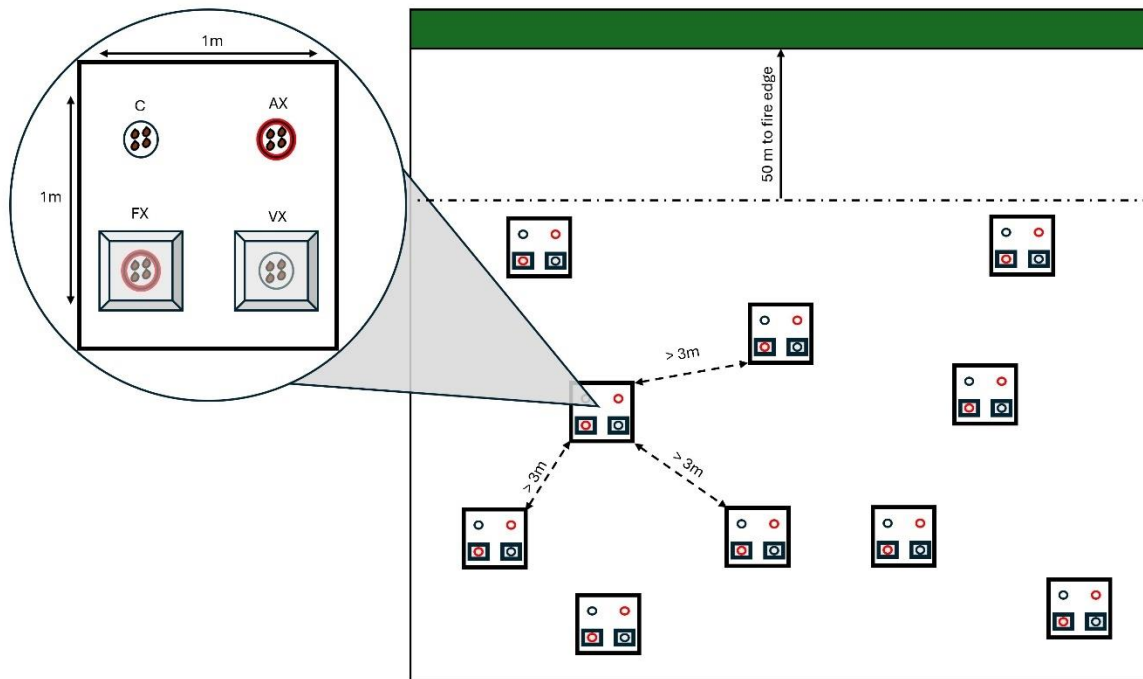


Figure 2. Seasonal seed predation experimental design and sampling replication. Ten experimental blocks (1 x 1 m) were established with each consisting of four treatments: an open control (C), ant exclusion (AX), vertebrate exclusion (VX) and full exclusion (FX), excluding both ants and vertebrates. Sites were located at least 50 m from the edge of the burned area and blocks were randomly located at least 3 m from one another.

All treatments shared the same basic design as the open control (C) treatment, which consisted only of the PVC pipe as a procedural control with no other obstructions to prevent invertebrates or vertebrates from accessing the seeds. The invertebrate, or ant, exclusion treatment (AX) was achieved by painting the outer rim of the pipe with insect glue (TAD All-Weather Insect Trapping Adhesive). The glue is colourless, odourless, non-repellent and insecticide free, and traps insects, preventing them from reaching the seeds, remaining effective for months. The vertebrate exclusion treatment (VX) consisted of a 10 x 30 x 30 cm cage made of mouse wire mesh with 10 mm gaps placed over the pipe and secured using fence hold downs. Finally, a full exclusion treatment (FX) incorporated both the insect glue painted onto the pipe and the cage placed over it.

Experimental blocks were deployed opportunistically within one month of the occurrence of any fire that occurred in the study regions during Autumn or Spring. Fires were monitored through alerts from state agencies responsible for implementing hazard reduction burning and responding to wildfires. Due to the unpredictability of wildfires and the weather and logistical constraints on prescribed fire this could only be done opportunistically, and we were unable to have the same experimental start date for all sites. Blocks were placed at least 50 m from the fires edge and the spatial configuration of the blocks was random with at least 3 m between each block to reduce the likelihood that the discovery of one block would lead to the discovery of others. Once sites were established, experimental blocks were revisited and seeds counted once a month until all seeds had been removed, consumed or germinated.

Autumn sites were established in May 2021 in the south-east ($n = 1$), and in June 2021 in the south-west ($n = 2$). Both were established within one month of prescribed fires that had consumed all of the understory and all or most of the canopy in the heath-woodland habitats. Due to the onset of COVID lockdowns an additional site was unable to be established for the south-east in NSW and no spring sites were able to be established. Furthermore, the lockdown meant monitoring was only possible for the first 4 weeks of the south-east experiment while the south-west sites in WA were able to be monitored for the full length of the study.

Analysis

Data was analysed in R 4.3.1 (R Core Team 2024) using a generalised linear model (GLM) with a Poisson distribution in the base R stats glm function. The GLM tested the effects of two factors, treatment and climate, on the response variable, counts of seeds removed or consumed at 4 weeks. We chose to limit the length of the analysis to 4 weeks to account for the fact that the site in NSW was only able to be monitored for 4 weeks, while sites in WA were able to be monitored until all seeds had been removed or germinated (~3 months). Site replicates were too few ($n = 3$) to warrant including site as an additional random effect as this was effectively captured by climate. A one-way ANOVA was conducted using the *car* package (v 3.1-2) to test for the significance of the two fixed factors. Post hoc Tukey's HSD tests were conducted to assess differences among treatment levels and climate types using means and contrasts estimated in the emmeans package (v. 1.10.0, Lenth et al. 2021). This package was also used to calculate the effects size of each treatment and climate type.

Results

Seed predation

Seed predation was observed to occur in all treatment types and across both climate types during the study period with a tendency to occur when seeds were accessible to vertebrate seed predators and be higher at the seasonal climate sites (Fig. 3). Treatment influenced the number of seeds that were removed (GLM: d.f. = 3, $\chi^2 = 9.6$, $p < 0.05$). On average seeds were more likely to be removed in treatments that allowed vertebrate seed predation (open and ant exclusion) compared to treatments excluding vertebrates (vertebrate exclusion and full exclusion). Fewer seeds were removed at the aseasonal site, compared to the seasonal sites (GLM: d.f. = 1, $\chi^2 = 16.02$, $p < 0.001$) with four to ten times as many seeds being removed over the same period at the seasonal sites (Fig. 3).

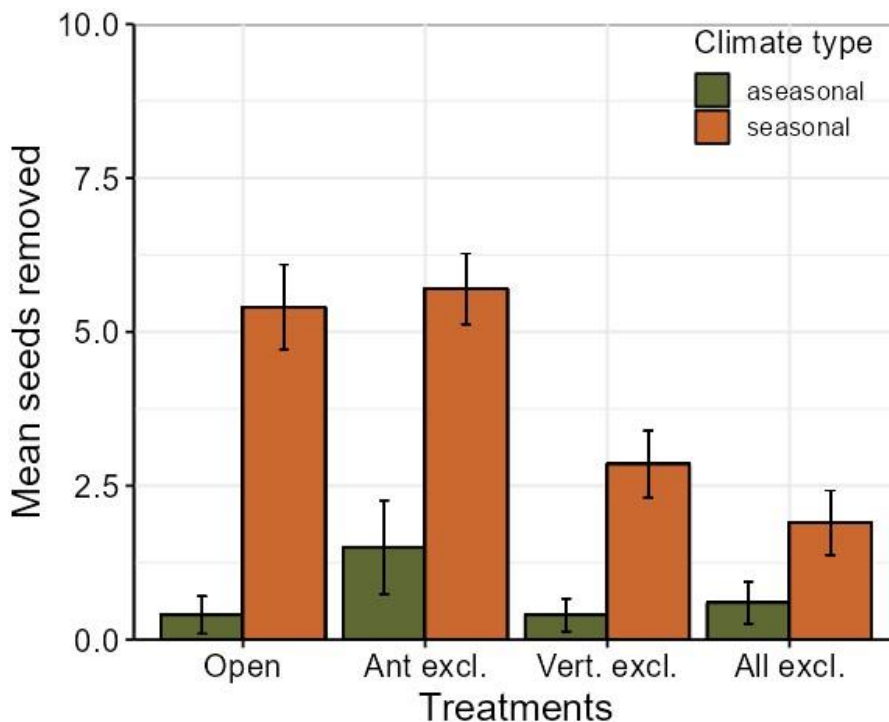


Figure 3. Mean number of *Banksia* seeds removed per treatment and climate type. Means averaged across sites within each climate type ($n_{\text{aseasonal}} = 2$; $n_{\text{seasonal}} = 1$) and replicates within sites ($n = 10$). Climate type corresponds to the region the sites were located in: south-east (NSW) = aseasonal, south-west (WA) = seasonal.

While treatment did influence the removal of seeds the effect of climate type was greater with larger differences observed between climate types than between treatments (Fig. 3). Pairwise comparisons reveal that regardless of climate type differences between treatments were only

observed between treatments that excluded vertebrates and treatments that did not (Table 1). Post-hoc tests did not find any evidence of differences within these two groups (Table 1).

Table 1. Effect sizes and pairwise means comparisons for four seed predation treatments.

Treatment	Comparison	Effect size	P-value
Full exclusion	Ant exclusion	-1.076	<0.0001**
	Open control	-0.934	<0.0001**
	Vertebrate exclusion	-0.327	0.3496
Ant exclusion	Open control	0.141	0.6931
	Vertebrate exclusion	0.749	<0.0001**
Open control	Vertebrate exclusion	0.608	0.0008*

Effect size and means comparisons are based on contrasts between the Treatment and Comparison columns. P-values are derived from a post-hoc Tukeys Test.

* indicates statistically significant differences (<0.05)

** indicates highly statistically significant differences (< 0.01)

Discussion

Post-fire seed predation can be a significant challenge for serotinous species (Tasker et al. 2011) that release their canopy stored seed-bank after the passage of fire and which must then wait on or near the soil surface for conditions suitable for germination. Our preliminary results find strong evidence of post-fire seed predation for two species of *Banksia* across two climate types (aseasonal rainfall and seasonal rainfall) following autumn fires (Fig. 3). Predation in both climate types appears to be primarily driven by vertebrate seed predators as there was significantly more seed predation in treatments that allowed vertebrate predation compared to those that excluded it. More importantly, seed predation was much higher for the seasonal climate sites than for the aseasonal site. Suggesting that climate type and the distribution of rainfall throughout the year is influencing vertebrate seed predation pressure. While these results are preliminary, they suggest that our initial hypotheses that post-fire seed predation may shape seed fates for serotinous species differently under different climate types has some merit.

The dominance of vertebrates as seed predators for these large seeded serotinous species is consistent with past studies (Bond 1984; Cowling et al. 1990; Denham & Auld 2002; Tasker et al. 2011). Typically, the vertebrates predating seeds in these studies are small mammalian granivores (Bond 1984; Tasker et al. 2011). Both the Royal National Park in the south-east where the aseasonal rainfall site was located and Yeal Nature Reserve in the south-west of the seasonal rainfall sites are home to several species of native and introduced granivorous rodents known to consume *Banksia* seeds (Tasker et al. 2011; DAWE 2016). While some of these species may cache seeds it is unlikely that any of the removed seeds escaped and were able to germinate, while chewed remnants of seeds were observed at all sites. Ant predation also occurred and was not insignificant (particularly at the aseasonal sites), however, the lower rate of removal by ants is largely to be expected owing to the lack of reward structures on *Banksia* seeds such as nutritious arils that might otherwise encourage ants to take the seeds. The use of PVC pipe in our study to contain the seeds may be perceived as an obstacle to ants that may have artificially reduced their seed predation. However, we observed at least one instance of ants directly consuming seeds and several instances of ants exploring the interior of the PVC pipes where the seeds were contained.

The pattern of seed predation observed in the seasonal rainfall climate at the south-west sites is consistent with seasonal cycles in the region. The late autumn (May) fire that occurred falls within the seasonal window for fire (Miller et al. 2021) and is followed immediately by the wet winter. This is reflected in the fact that while seed predation rates were high ultimately some proportion of seeds escaped via germination. The high rate of predation may also reflect an increase in seed predator numbers or activity during the wet season when they are more likely to breed while water is available. This idea is consistent with continental scale patterns in seed predation that have observed seed predation is greater under higher evapotranspiration as the increased availability of water and food resources allows for population increases of seed predators (Orrock et al. 2015). This would suggest that the predation following the autumn fire in the west coast sites that would have occurred during the wetter winter should be higher than seed predation during the dry summer following a spring burn. Additionally, Miller et al. (2021) conducted a seed sowing experiment comparing the survival of seeds sown in autumn and spring in the same *Banksia* woodlands system as our study and found a 99% decrease in seedling survival when seeds were sown in spring compared to autumn. While they did not directly examine seed predation, it is likely that it plays a role in this higher rate of seed mortality as resources become increasingly scarce and seed predator populations that increased over the wet winter period attempt to persist through the dry summer.

The lower rate of seed removal observed in the aseasonal site in the south-east contrasts somewhat the results of a previous similar study which also took place in the Royal National Park in similar habitat. Tasker et al. (2011) observed up to 77% seed removal over 7 days in their open/control treatment compared to the <10% removal observed on average in our study over four weeks. The reason for this is not entirely clear, vegetation types were comparable and our placement of experimental blocks at 50 m from unburnt vegetation was intermediate to the distances used in their study (10 m for their burnt-edge treatment and 100 m for burnt-interior). The species of *Banksia* used in the two studies did differ, however, their findings suggest that vertebrates are not picky about the seeds they eat. Perhaps tellingly, they note that the second trial they ran in autumn, as opposed to summer, had a much lower rate of seed removal than the summer trial. At a minimum this indicates that seed-predation is variable in this system though it may also indicate that it is reduced heading into the cooler months which would be consistent with the low rate of removal observed in our study.

Unfortunately, due to the exceptional circumstances of the COVID-19 pandemic this study was not initially able to be completed and even the trials that were undertaken were interrupted. Consequently, key components of the study are not able to be addressed including the comparison between spring and autumn burns and the conclusions we can draw are limited by the incompleteness of the aseasonal rainfall trial and lack of replication there. We are preparing to remedy this with two additional autumn trials to be run in 2024 followed by two spring trials in both the seasonal and aseasonal climates.

Beyond these larger logistical challenges there are some limitations of the study at present. The use of two different species and the differing suites of invertebrate and vertebrate seed predators in the seasonal and aseasonal climate types may be contributing to some of the differences we are observing in post-fire seed predation rates. However, with the exception of some shared invasive rodent seed predators (e.g. brown rats and house mice), there are no species in common across the two climate types, meaning that there are limited options to control for these differences. Replication across a broader suite of species in both regions may lead to more robust patterns and conclusions, however, even without the complications that arose during this study the level of replication required would have had to increase significantly to accommodate additional species.

Despite these challenges and limitations the results are illustrative of the significance of post-fire predation as a factor affecting recruitment of serotinous species in fire prone regions. The role of seasonality may not be clear but these preliminary results strongly suggest that while vertebrates are the dominant seed predator across both study regions, the predation pressure differs between the two. The inclusion of additional sites in additional seasons will allow us to better understand the nature and drivers of these differences and potentially inform management recommendations around the timing of fire for serotinous species.

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References

- Australian Bureau of Meteorology (2024a) Monthly rainfall averages Audley (Royal National Park) New South Wales. www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index. Accessed 03 Mar 2022
- Australian Bureau of Meteorology (2024b) Monthly rainfall averages Gingin Aero Western Australia. www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index. Accessed 03 Mar 2022
- Balch, J.K., Bradley, B.A., Abatzoglou, J.T., Nagy, R.C., Fusco, E.J. and Mahood, A.L., 2017. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences*, 114(11), pp.2946-2951.
- Bond, W.J., 1984. Fire survival of Cape Proteaceae-influence of fire season and seed predators. *Vegetatio*, 56(2), pp.65-74.
- Bowman, D.M., Murphy, B.P., Williamson, G.J. and Cochrane, M.A., 2014. Pyrogeographic models, feedbacks and the future of global fire regimes. *Global ecology and biogeography*, 23(7), pp.821-824.
- Bradstock, R.A., 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography*, 19(2), pp.145-158.
- Clarke, H., Tran, B., Boer, M.M., Price, O., Kenny, B. and Bradstock, R., 2019. Climate change effects on the frequency, seasonality and interannual variability of suitable prescribed burning weather conditions in south-eastern Australia. *Agricultural and Forest Meteorology*, 271, pp.148-157.
- Collette, J.C. and Ooi, M.K., 2017. Germination ecology of the endangered species *Asterolasia buxifolia* (Rutaceae): smoke response depends on season and light. *Australian Journal of Botany*, 65(3), pp.283-291.
- Cowling, R.M. and Lamont, B.B., 1987. Post-fire recruitment of four co-occurring *Banksia* species. *Journal of Applied Ecology*, pp.645-658.
- Cowling, R.M., Lamont, B.B. and Enright, N.J., 1990. Fire and management of south-western Australian banksias. In *Proceedings of the Ecological Society of Australia* (Vol. 16, pp. 177-183).
- Denham, A.J. and Auld, T.D., 2002. Flowering, seed dispersal, seed predation and seedling recruitment in two pyrogenic flowering resprouters. *Australian Journal of Botany*, 50(5), pp.545-557.
- Densmore, V.S. and Clingan, E.S., 2019. Prescribed burning in a mediterranean-climate region mitigates the disturbance by bushfire to a critical food resource for an endangered bird, the Carnaby's cockatoo. *Fire Ecology*, 15, pp.1-12.
- Department of Agriculture, Water and the Environment (DAWE) (2012) Interim Biogeographic Regionalisation for Australia, Version 7. Commonwealth of Australia, Australian Capital Territory.

Department of Agriculture, Water and the Environment (DAWE) (2016) Approved Conservation Advice (incorporating listing advice) for the Banksia Woodlands of the Swan Coastal Plain ecological community. Commonwealth of Australia, Australian Capital Territory.

Gill, A.M. and Bradstock, R., 1995. Extinction of biota by fires.

He, T., Lamont, B.B. and Pausas, J.G., 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews*, doi: 10.1111/brv.12544

Jenkins, M.E., Morrison, D.A. and Auld, T.D., 2010. Estimating seed bank accumulation and dynamics in three obligate-seeder Proteaceae species. arXiv preprint arXiv:1001.4914.

Jolly, W.M., Cochrane, M.A., Freeborn, P.H., Holden, Z.A., Brown, T.J., Williamson, G.J. and Bowman, D.M., 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, 6, p.7537.

Lamont, B.B., Enright, N.J., Witkowski, E.T.F. and Groeneveld, J., 2007. Conservation biology of banksias: insights from natural history to simulation modelling. *Australian Journal of Botany*, 55(3), pp.280-292.

Lenth RV, Buerkner P, Herve M, Love J, Miguez F, Riebl H, Singmann H (2021) Package “emmeans” v. 1.7.2. Iowa, United States of America: Department of Statistics and Actuarial Science, The University of Iowa.

Le Page, Y., Oom, D., Silva, J.M., Jönsson, P. and Pereira, J.M., 2010. Seasonality of vegetation fires as modified by human action: observing the deviation from eco-climatic fire regimes. *Global Ecology and Biogeography*, 19(4), pp.575-588.

McCaw, W.L., 2013. Managing forest fuels using prescribed fire—a perspective from southern Australia. *Forest Ecology and Management*, 294, pp.217-224.

Miller, R.G., Fontaine, J.B., Merritt, D.J., Miller, B.P. and Enright, N.J., 2021. Experimental seed sowing reveals seedling recruitment vulnerability to unseasonal fire. *Ecological Applications*, 31(7), p.e02411.

Miller, R.G., Tangney, R., Enright, N.J., Fontaine, J.B., Merritt, D.J., Ooi, M.K., Ruthrof, K.X. and Miller, B.P., 2019. Mechanisms of Fire Seasonality Effects on Plant Populations. *Trends in Ecology & Evolution*.

Mills, C.H., Gordon, C.E. and Letnic, M., 2018. Rewilded mammal assemblages reveal the missing ecological functions of granivores. *Functional ecology*, 32(2), pp.475-485.

Nolan, R.H., Collins, L., Leigh, A., Ooi, M.K., Curran, T.J., Fairman, T.A., Resco de Dios, V. and Bradstock, R., 2021. Limits to post-fire vegetation recovery under climate change. *Plant, cell & environment*, 44(11), pp.3471-3489.

Ooi, M.K., Auld, T.D. and Whelan, R.J., 2004. Delayed post-fire seedling emergence linked to season: a case study with *Leucopogon* species (Epacridaceae). *Plant Ecology*, 174(1), pp.183-196.

Orrock, J.L., Borer, E.T., Brudvig, L.A., Firn, J., MacDougall, A.S., Melbourne, B.A., Yang, L.H., Baker, D.V., Bar-Massada, A., Crawley, M.J. and Damschen, E.I., 2015. A continent-wide study reveals clear relationships between regional abiotic conditions and post-dispersal seed predation. *Journal of Biogeography*, 42(4), pp.662-670.

R Core Team (2021) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Tasker, E.M., Denham, A.J., Taylor, J.E. and Strevens, T.C., 2011. Post-fire seed predation: Does distance to unburnt vegetation matter?. *Austral Ecology*, 36(7), pp.755-766.

Tangney, R., Miller, R.G., Fontaine, J.B., Veber, W.P., Ruthrof, K.X. and Miller, B.P., 2022. Vegetation structure and fuel dynamics in fire-prone, Mediterranean-type *Banksia* woodlands. *Forest Ecology and Management*, 505, p.119891.

Zammit, C. and Westoby, M., 1987. Seedling recruitment strategies in obligate-seeding and resprouting *Banksia* shrubs. *Ecology*, 68(6), pp.1984-1992.