Long-term population trends in critically endangered montane Proteaceae driven by pre-fire fruit crops and fire interval

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Abstract

Understanding temporal trends in the populations of threatened flora and how they respond in key demographic parameters to ecological processes are crucial for effective conservation management. We explore patterns of change in abundance over time, predictors of post-fire recruitment success (as measured by the ratio of post-fire seedlings to pre-fire adults) and lengths of juvenile period for four critically endangered obligate-seeder Proteaceae from the Stirling Range (Koi Kyenunu-ruff) in south-western Australia from long-term fixed quadrats and surveys of whole subpopulations. All subpopulations were impacted by one or more fire events over the monitoring period. *Banksia brownii* and *Persoonia micranthera* showed consistent decline across all subpopulations and through all fire events. *Banksia montana* and *Banksia anatona* showed variation in trends, with some subpopulations having seedling recruitment indicating potential for a degree of population recovery after the most recent fires, but with other subpopulations approaching extinction. The best predictor of greater post-fire recruitment was a larger pre-fire fruit crop, and where this information was not available, a longer preceding fire interval. Post-fire recruitment of *Banksia brownii* was lower on drier and more exposed topographic positions, providing evidence of directional post-fire reassembly towards putative climate refuges and indicating that climate change is an increasing pressure on populations. Juvenile periods of the four species were long in the context of the broader south-west Australian region, and together with the post-fire recruitment data, indicate that species recovery will be greater with multi-decadal fire intervals. Acquiring detailed population and demographic information through consistent long-term monitoring provided a strong basis on which to quantify responses to threats and prioritise recovery actions.

Keywords: Juvenile period, Obligate seeder, Persistent seed bank, Recruitment, Seedling:adult ratio, Serotiny, South-western Australia, Threatened flora, Time series data

Introduction

Monitoring programs for threatened flora typically aim to collect data that will inform ongoing conservation management through quantifying species responses to environmental change and to management interventions (Lindenmayer *et al.* 2022). Yet, despite the recognised importance of long-term population monitoring data (Lindenmayer *et al.* 2022), such datasets are uncommon. By its very nature, long-term monitoring data requires time to accumulate, and with time comes the inherent challenges of maintaining funding, staff turnover with loss of existing knowledge, risks of drift in monitoring methods and shifting priorities (Lindenmayer 2018).

Altered fire regimes are recognized as a key threatening process for many threatened flora in seasonally dry, fire-prone environments such as those found in Mediterranean climates (Coates and Atkins 2001; Burgman *et al.* 2007). Key demographic data collected through monitoring programs can contribute to explaining the population-level consequences of burning and help define fire management. These include: (i) the time since fire until the development of the capacity for persistence through fire events, either as individuals (resprouters) or as a population (obligate seeders) (immaturity-risk); (ii) the longevity of individuals and seed banks in the absence of fire (senescence-risk); (iii) the size of the population and seed bank; and (iv) the timing of recruitment in relation to fire events (Noble and Slatyer 1980; Bradstock and Kenny 2003; Keith *et al.*

2007). However, other factors may also contribute to the effects of any fire event on plant populations and to broader temporal trends. These include plant traits such as seed dispersal capacity, while processes associated with the specific fire event have the potential to override demographic effects, including interactions with other threatening processes (Noble and Slatyer 1980; Driscoll *et al.* 2024). Pre- or post-fire drought, for example, can result in recruitment failure even when an otherwise sufficient seed bank is present (Lamont *et al.* 1991). For many threatened flora, this information is not available and there is much to learn about what are the most important drivers of population recovery after fires, and what management interventions may be available to mitigate instances (potential or realised) of population decline.

The Stirling Range (Koi Kyenunu-ruff) is a hotspot for threatened flora in the Southwest Australian Floristic Region global biodiversity hotspot, where a flora of exceptional floristic richness and with high short-range endemism intersects with chronic and interacting threats (Department of Conservation and Land Management (DCLM) 1999; Gioia and Hopper 2017; Gosper *et al.* 2021). The most pressing threats to flora in the Stirling Range are a shared susceptibility amongst many of the dominant shrub taxa to plant disease (*Phytophthora* dieback) and short fire intervals, compounded by post-fire herbivory (Barrett and Yates 2015; Rathbone and Barrett 2017; Barrett *et al.* 2024) and in the context of ongoing regional declines in rainfall (Barrett *et al*. 2008; Delworth and Zeng 2014). To inform management of threatened flora in the Stirling Range, systematic monitoring commenced in 1997 and increased in scope over time in terms of both the range of species and subpopulations included, particularly in response to landscape-scale fire events in 2000, 2018 and 2019 - the latter during the

2019-20 'Australian megafires' (Barrett *et al.* 2009; Gallagher *et al.* 2023; Driscoll *et al.* 2024).

In this study, we compile long-term demographic data for four critically endangered, obligate-seeding Proteaceae of the Stirling Range, including abundance of individuals (mature and immature), reproductive output and post-fire seedling:parent ratios. We use these data to address the following questions:

- Do species show consistent trends of population change over time and between subpopulations, considering the demographic influence of fire-initiated recruitment events?
- Can measures of pre-fire plant reproductive output, topographic position and fire regime and event parameters predict post-fire recruitment success? and
- Do the co-occurring threatened flora have similar juvenile periods?

Methods

Study ecosystem and threats

The Stirling Range forms a unique environment in south-western Australia, being the only range with peaks high enough to support montane ecosystems (elevation to 1,100 m ASL), and a primarily quartzite geology geographically isolated from similar formations. The Stirling Range is also an old landscape, having been weathered to expose the current peaks. The combination of antiquity and unique environmental conditions has favoured the evolution of a flora with high species richness and exceptional levels of short-range endemism (Barrett and Yates 2015; Gioia and Hopper

2017; Gosper *et al*. 2021). Over 80 vascular plant taxa are endemic to the ~115,000 ha Stirling Range National Park (SRNP) that covers the entire range (DCLM 1999). The major vegetation associations are heaths and shrublands.

While the ecosystems of the Stirling Range have largely been spared from land transformation, two major threats are pervasive and have such substantial impact that 33 state and/or nationally listed threatened flora taxa occur within the SRNP. The soil-borne slime mould *Phytophthora cinnamomi*, which causes *Phytophthora* dieback, was inadvertently introduced at some time prior to 1974, but has since spread to infest >66% of the SRNP (Grant and Barrett 2003) in a mosaic of infested and uninfested vegetation. *Phytophthora* dieback causes high levels of mortality in many species, with ~36% of the flora of the SRNP having some degree of susceptibility (Shearer *et al*. 2004; Barrett and Rathbone 2018). Much of the higher elevations of the Stirling Range have been impacted by multiple fires over the last few decades (Barret and Yates 2015; Gosper *et al*. 2022). The flora has evolved with recurrent fires, but with a high proportion of obligate seeder species (Keith *et al*. 2002) and relatively long juvenile periods associated with low productivity at rocky and high elevation sites (Gosper *et al*. 2022), a significant portion of the flora is vulnerable to short fire intervals (Barrett and Yates 2015). Intervals in the threatened flora populations under study ranged from as low as 9 years (1991-2000) to greater than 47 years (from fire at an unknown time prior to 1972, to 2019). Post-fire drought and browsing by mammalian herbivores, particularly the indigenous quokka (*Setonix brachyurus*; a macropod), compounds the impact of these threats through reducing survival and growth of post-fire recruits (Rathbone and Barrett 2017; Barrett *et al*. 2024). Mitigation actions to address these threats in the Stirling Range include aerial application of the fungicide phosphite to reduce the impact of

Phytophthora and fencing to exclude mammalian herbivores (Rathbone and Barrett 2017; Barrett and Rathbone 2018; Barrett *et al*. 2024).

Study species and population monitoring methods

All four study species are listed as critically endangered under Australian and Western Australian legislation and were subject to detailed long-term monitoring as they are thought to be at high risk of extinction. Sampling methods varied between species and subpopulations within species, according to feasibility based on the size and extent of subpopulations at the start of the monitoring program.

Banksia montana

Banksia montana (Stirling Range Dryandra; Proteaceae) is a long-lived serotinous obligate seeding shrub restricted to the Eastern Stirling Range Montane Heath and Thicket ecological community. The species is susceptible to *Phytophthora* (Shearer *et al*. 2013) and has a relatively long juvenile period (time to 50% of individuals flowering) of > 10 years (Barrett *et al*. 2008, 2009). Searches to locate and count all individuals in all four extant subpopulations (Bluff Knoll, East Bluff, Isongerup and Pyungoorup) have been conducted near-annually since 1997.

The ratio of post-fire seedlings to pre-fire adults (seedling:adult ratio) was calculated for all available combinations of fire event, preceding fire interval and subpopulation. This resulted in 11 unique combinations from the four subpopulations and three fire

events (2000, 2018 and 2019) over the period of population monitoring, with preceding intervals ranging from 9 to >50 years.

Inflorescence and infructescence counts were measured mostly annually on tagged individuals of two cohorts: (i) the 10 individuals of the 1991 cohort at Bluff Knoll from 2001 onwards; and (ii) the entire seedling population (>250 individuals) of the 2018 and 2019 cohorts across all subpopulations over the period 2021-2024. These data were used to calculate the proportion of the sampled individuals in a specific age cohort that were reproductively mature (flowering and/or fruiting).

Banksia brownii

Banksia brownii (Feather-leaved Banksia; Proteaceae) is a long-lived serotinous obligate seeding shrub that occurs in both the Eastern Stirling Range Montane Heath and Thicket and Montane Mallee Thicket ecological communities in the Stirling Range, as well as in lowland locations to the south of the SRNP. The species has very high susceptibility to *Phytophthora* and the Stirling Range subpopulations have a relatively long juvenile period (time to 50% of individuals flowering) of > 10 years (Barrett *et al.* 2008, 2009). Three time series of changes in the abundance of *B. brownii* are available from fixed quadrats, differing in fire history and location: (i) three 10 × 10 m quadrats at Mt Hassell burnt in 1996 and 2019 sampled in 2006, 2020, 2021, 2022 and 2025 (Mt Hassell 10 × 10s); (ii) eight 5 × 2 m quadrats at Mt Success burnt in 2000 sampled from 1997 to 2004; and (iii) thirty-eight 5 × 5 m quadrats at Yungermere burnt in 2019 sampled 2019 to 2025 (Yungermere 5 × 5s).

Attainment of reproductive maturity, defined as evidence of flowering or fruiting, was collected from three time series: (i) 28 tagged plants at Mt Hassell of the 1996 fire cohort that were monitored from 2003 to 2010; (ii) 10 tagged plants at Yungemere of the 1991 fire cohort that were monitored in 2003; and (iii) 211 tagged plants at Yungemere of the 2019 cohort monitored from 2020 to 2025.

Seedling:adult ratios were calculated at the quadrat level for the Yungermere 5 × 5s and Mt Hassell 10 × 10s, both of which burnt in 2019 with preceding fire intervals of 28 and 23 years respectively.

Banksia anatona

Banksia anatona (Cactus Banksia; Proteaceae) is a long-lived serotinous obligate seeding shrub that occurs in the Montane Mallee Thicket ecological community of the SRNP. It has very high susceptibility to *Phytophthora* and a moderately long juvenile period (time to 50% of individuals flowering) of ~6 years (Barrett *et al.* 2008, 2009). Five time series of changes in the abundance of *B. anatona* are available from fixed quadrats: (i) five 5 × 5 m quadrats at Ellen Track sampled from 2002 to 2025 in an area burnt in 1991, 2000 and 2018 (Ellen 5 × 5s); (ii) five 4 × 4 m quadrats at Ellen Track sampled from 2000 to 2025 in an area burnt in 1991 and 2018 (Ellen 4 × 4s); (iii) four 4 × 4 m quadrats sampled from 1999 to 2012 in an area south-east of Ellen Peak burnt in 1991 and 2000 (SE Ellen 4 × 4s); (iv) three 5 × 5 m quadrats sampled from 2020 to 2025 south-east of Ellen Peak in an area burnt in 2018 (SE Ellen 5 × 5s); and (v) six 5 × 5 m quadrats at Mt Success sampled from 2020 to 2024 in an area burnt in 1991, 2000 and 2019 (Mt Success 5 × 5s).

Attainment of reproductive maturity was collected for: (i) all 58 individuals of the 2000 cohort in the Ellen Track 5 × 5s from 2002-2018; (ii) for 120 individuals of the 2018 cohort in 10 × 10 m quadrats at Ellen Track (part of a fencing experiment described in Barrett *et al*. 2024, but only including data from unfenced plots here) sampled 2019-2025; (iii) 50 individuals of the 2018 cohort in and adjacent to the SE Ellen 5 × 5s from 2020-2025; and (v) 586 individuals of the 2019 cohort in the Mt Success 5 × 5s from 2020-2024.

Seedling:adult ratio was calculated at the quadrat level for the following combinations of subpopulation, fire event and fire history: (i) Ellen Track 5 × 5s (described above) burnt in 2000 with a 9 year fire interval and in 2018 with an 18 year fire interval; (ii) Ellen Track 4 × 4s burnt in 2018 with a 27 year interval; (iii) SE Ellen 4 × 4s burnt in 2000 with a 9 year interval; (iv) six 5 × 5 m quadrats at Mt Success burnt in 2019 with a 19 year interval; (v) sixteen 10 × 10 m quadrats at Ellen Track burnt in 2018, half with a 27 and half with a 18 year interval.

Persoonia micranthera

Persoonia micranthera (Small-flowered Snottygobble; Proteaceae) is an obligate seeding shrub with a soil-stored seed bank that is restricted to the Eastern Stirling Range Montane Heath and Thicket ecological community. It is susceptible to *Phytophthora* and aerial cankers, while juvenile period is not known (Barrett *et al*. 2008). Four time series of changes in the abundance of *P. micranthera* are available, two from fixed quadrats and two from a sample of tagged individuals. The quadrat time series were: (i) five 5 × 3 m quadrats at Bluff Knoll burnt in 2000 and 2018 sampled from 2002

to 2025; and (ii) six 5 × 2 m quadrats at Isongerup burnt in 2000 and 2018 sampled from 1997 to 2025. 50 individuals of the 1991 fire cohort at Bluff Knoll were monitored from 2001 to 2014, and 23 individuals of the 1991 cohort at East Bluff were monitored from 2001 to 2017, recording individual status as alive or dead and whether individuals had become reproductively mature (evidence of flowering or fruiting).

Statistical analysis

Trend data was plotted for all species, using total counts across all subpopulations (*B. montana*), converting quadrat counts to plant density (remaining species) or changes in the number of live tagged individuals (one time series in *P. micranthera*). For analysis of both trend and seedling:adult ratio data, the number or density of pre-fire individuals, and infructescences where relevant, were taken from post-fire surveys of burnt stags and cones if there were no pre-fire data within the two years preceding fire.

The predictors included in models for seedling:adult ratio varied between species based on the type of sampling (total population or quadrats), the distribution of recruitment events across years and populations (i.e. rainfall could only be included if sampled recruitment events spanned fires in multiple years), and whether data was available pre-fire infructescences. In all species, subpopulation, which usually referred to occurrences on different peaks, was included as a random effect.

For *B. montana*, where data were of the form of total population counts, predictors were: (i) rainfall in the year following fire; (ii) number of pre-fire adults (log transformed to address outliers); (iii) mean number of pre-fire infructescences (log-transformed) and (iv) preceding fire interval. For *B. brownii*, where data were of the form of quadrat-based

263 counts, predictors were: (i) topographic position of quadrat, as categorical factors of
264 either gully (southerly and south-easterly drainage lines), ridge (minimum altitude of
265 600 m asl, slopes just below main ridgelines), or spur (southerly and south-easterly
266 ridges coming off main ridges, below 600 m a.s.l); (ii) pre-fire infructescence density; (iii)
267 pre-fire adult density; and (iv) preceding fire interval. For *B. anatona*, where data were of
268 the form of quadrat-based counts, predictors were: (i) rainfall in the year following fire;
269 (ii) pre-fire adult density; and (iii) preceding fire interval. Rainfall was taken from the
270 closest weather station at Amelup (station 010502;
271 https://www.bom.gov.au/climate/data/index.shtml), although as this station is in the
272 lowlands and outside of the SRNP the values would only be a proxy for the survey
273 locations.

274 Linear mixed models were constructed for seedling:adult ratio, including the random
275 effect of subpopulation and the remaining terms as fixed factors. The analyses used the
276 *lme4* package (version 1.1-38; Bates *et al.* 2015), with *lmerTest* (version 3.1-3;
277 Kuznetsova *et al.* 2017) used to provide significance tests for the model, and *emmeans*
278 (version 2.0.1; Lenth and Piaskowski 2025) to provide pairwise tests between levels of
279 topographic position. Analyses were conducted in *R* (version 4.5.2; R Core Team 2025).
280 Inspection of a Q-Q plot and the residuals against fitted values indicated it was
281 appropriate to log transform ($\log_{10}$ (x+1)) seedling:adult ratio to meet assumptions of
282 normality and variance in all cases. For visualisation, univariate relationships between
283 key predictors and seedling:adult ratio were plotted.

284 Juvenile period was explored by plotting the proportion of the live individuals
285 sampled that were reproductively mature against age (number of winters after fire) and

fitting a linear regression using *Sigmaplot* (version 10.0; https://grafiti.com/sigmaplot-detail/).

Results

Banksia montana

Fire events had substantial impacts on the population of *B. montana*. The fire in 2000, which burnt parts of three out of four subpopulations with preceding intervals ranging from 9 to >35 years, initiated a dramatic decline in both total population size and number of mature plants (Fig. 1a), from a point at the start of monitoring of over 130 individuals to just over 50. Some plants in all subpopulations affected by the 2000 fire did not get burnt, and along with the remaining unburnt subpopulation, these mature plants formed the bulk of the total population over the period between 2001 and 2017. Notably, there was minimal recruitment following the 2000 fire, and few of that cohort survived past 2010. The trajectory of the population over the inter-fire period was for a gradual decline to less than 50 individuals, with incremental mortality of mature individuals outpacing incorporation of the few inter-fire recruits and the 1991 cohort into the mature population.

All extant *B. montana* individuals were killed by fires that burnt all subpopulations in either 2018 or 2019, with the result that no mature individuals existed in the wild through to 2023. Unlike the 2000 fire, these fires (especially 2018) initiated a substantial recruitment event totalling over 1250 seedlings. The juvenile population has since been declining sharply with a handful reaching reproductive maturity.

Over the period of monitoring there has been a striking difference in the performance of the four subpopulations. Through to 2018-9, the four subpopulations each supported a meaningful proportion of the total population (Fig. 1b). However, after the fires in 2018 and 2019, two of the subpopulations have declined to near extinction, while one subpopulation has become numerically dominant.

The linear mixed model explained nearly 70% of the variation in seedling:adult ratio (mostly from fixed effects), with mean infructescences per pre-fire individual the only significant predictor (Table 1). Higher seedling:adult ratios were associated with more infructescences in the pre-fire adult cohort (Fig. 3a).

There was an essentially linear increase in the proportion of the population that was reproductively mature until all surviving individuals had flowered by age 21 years (from the 1991 cohort) (Fig. 4a). The most precocious individuals of *B. montana* of the 2018 cohort began flowering at 5 years after fire, although only <1% of individuals reached reproductive maturity at this age. The metric of juvenile period when half of individuals were reproductively mature was reached at ~14 years.

Banksia brownii

Fires resulted in the death of all individuals in all subpopulations and monitored quadrats and initiated post-fire recruitment, noting that at the quadrat scale some quadrats that had individuals pre-fire did not have recruits establish post-fire, while individuals recruited in new areas where there were no adults pre-fire. Like *B. montana*, rates of recruitment after the 2000 fire, with a preceding interval of 9 years, were extremely low (Fig. 2a). In this case, post-fire juvenile density was substantially lower

331 than the pre-fire population density. The two monitored subpopulations impacted by
332 the 2019 fire with preceding fire intervals of 23 and 28 years, did have recruit density
333 exceed pre-fire adult density, but density of juveniles is rapidly declining.

334 Each of topographic position, density of pre-fire adults and density of pre-fire
335 infructescences were significant predictors of the post-fire seedling:adult ratio (Table
336 1). A lower seedling:adult ratio occurred on spurs compared to gullies and ridges (Fig.
337 3d). A higher seedling:adult ratio was associated with lower pre-fire density of adults but
338 greater density of pre-fire infructescences (Fig. 3b, c).

339 The first individuals were reproductively mature at 6-8 years of age, depending on
340 subpopulation and cohort. The metric of juvenile period when half of individuals were
341 reproductively mature was reached at ~12 years (Fig. 4b).

342

343 *Banksia anatona*

344 The SE Ellen subpopulation of *B. anatona* monitored over the period 1999-2012 showed
345 a catastrophic decline in density after being burnt in 2000, following on from a previous
346 fire in 1991 (Fig. 2b). The two subpopulations at Ellen Track monitored since 2000/2002
347 gradually declined in plant density over the inter-fire period though to 2018. Post-fire
348 recruitment in both these subpopulations after the 2018 fire resulted in greater post-fire
349 density than pre-fire density, but post-fire density was greater by several orders of
350 magnitude in the subpopulation that had slightly higher pre-fire density and longer fire
351 interval (burnt in 1991 and 2018, compared to 1991, 2000, 2018). Recruit density after
352 the 2019 fire at Mt Success was the greatest recorded at any site, but was highly
353 variable and is rapidly declining, as is recruit density at SE Ellen after the 2018 fire.

Seedling:adult ratio was affected by fire interval (Table 1), with a lower ratio associated with short (<10 years) intervals (Fig. 3e). Unlike *B. montana* and *B. brownii*, random subpopulation effects contributed a substantial proportion of the variation explained by the model.

A linear model was a reasonable representation of the relationship between the proportion of the sample that was reproductively mature and time since fire. The first individuals were reproductively mature at 4-7 years of age, depending on subpopulation and cohort. The metric of juvenile period when half of individuals were reproductively mature was reached at ~12 years (Fig. 4c).

Persoonia micranthera

Fires resulted in the death of all individuals in monitored quadrats. Recruitment occurred in most monitored quadrats post-fire, but not all in the first winter post-fire. In all monitored fire events, new individuals germinated and recruited through at least the first five years post-fire (Fig. 2c). Across both subpopulations monitored, there was a strong overall declining trend in population density with time, shown through both a lower post-fire peak in density and a lower extant population density at the time of fire. Similar, or even more severe declines, were observed in monitoring of tagged individuals over time in different combinations of subpopulation and fire cohort. The 1991 cohorts at East Bluff and Bluff Knoll declined from 23 to 0 live individuals over the period 2001-2017 and from 50 to 11 individuals from 2001-2014, respectively (Fig. 2d). Neither of these cohort-subpopulation combinations had any successful recruitment after being burnt in 2018.

The first of the monitored individuals in the 1991 cohort reached reproductive maturity at 10 years since fire. Beyond 10 years, there was an essentially linear increase in the proportion of the population that became reproductively mature through to about 20 years, by which time all or nearly all of the surviving individuals had reproduced (Fig. 4d). The metric of juvenile period when half of individuals were reproductively mature was reached at ~14 years.

Discussion

Temporal population trends

Two of the four monitored critically endangered Proteaceae of the Stirling Range – *B. brownii* and *P. micranthera* - appear to be undergoing chronic decline, with reduced numbers in subpopulations with each successive fire event and multiple extinctions either at the subpopulation or at all monitored quadrats within subpopulations. In contrast, there was variability among fire event and subpopulation combinations in long-term trends in *B. montana* and *B. anatona*. For both these species, there were some subpopulations that had substantially elevated levels of recruitment after fire in 2018 or 2019 compared to the numbers of plants that existed pre-fire, although other subpopulations have declined to near extinction over the whole monitoring period. Sharp declines in the juvenile cohorts arising from the 2018 and 2019 fires have occurred, as are typical in obligate-seeder species through density-dependent thinning (Harvey *et al.* 2011). However, density-independent causes of mortality, through *Phytophthora* dieback and a drying climate, may be compounding density-dependent effects (Crouchet *et al.* 2019). Nevertheless, it is plausible that as recruits of *B.*

400 *montana* become reproductively mature over coming years the total number of mature
401 *B. montana* individuals may approach that at initial monitoring in 2000, indicating some
402 small degree of population recovery.

403 Poor recruitment after the 2000 fire – which is clearly apparent compared to
404 recruitment after the 2018 and 2019 fires (Fig. 1, 2) – occurred in each of *B. montana*, *B.*
405 *brownii* and *B. anatona*. Indeed, no post-fire recruitment occurred at all in the areas
406 burnt in 2000 with a 9-year interval in *B. montana* (Barrett and Yates 2015). In cases of *B.*
407 *brownii* and *B. anatona*, which also had prior fire intervals of 9 years, the quadrat-level
408 density also declined to near zero in some subpopulations. However, there were also
409 low rates of recruitment after the 2000 fire in two *B. montana* subpopulations with
410 preceding intervals exceeding 25 years. This suggests that a short fire interval was not
411 the only contributing factor to poor recruitment after the 2000 fire. The other processes
412 in addition to fire interval that may have contributed to variation in recruitment rates
413 with different fires are not known, but may include variation in seed banks (beyond that
414 attributable to interval) in relation to plant size and vigour. The potential explanation of
415 poor post-fire rainfall resulting in high seedling mortality (Lamont *et al.* 1991) has little
416 evidence to support it, as 2001 rainfall was greater than in first year post-fire for the
417 2018 or 2019 cohorts (at the closest weather station, Amelup; station 010502,
418 https://www.bom.gov.au/climate/data/index.shtml). A more rapid and thorough field
419 campaign to locate and fence recruits at the cotyledon stage the first spring after the
420 more recent fires compared to 2001-2 could also contribute to these differences.
421 Survey effort does not seem a good explanation for low number of recruits in
422 subsequent years after 2000, however, as recruits become conspicuous as they grow.

All subpopulations and age cohorts in *P. micranthera* have exhibited a consistent declining trend over time and across multiple fire events. Whilst it is plausible that there may be multiple process at play in causing the declines, the consistently high levels of mortality of live plants seems likely to be a contributing factor. *P. micranthera* has longevity over decadal time scales and seed input into the seed bank would be expected to occur over a prolonged period. Observations of plant health have noted limb dieback progressively causing necrosis and death, which are symptoms not associated with *Phytophthora* dieback, thus suggesting another cause. Investigation of the interaction between climate-induced stress and pathogens may be one fruitful avenue of inquiry (Yates et al. 2021). Since the 2018-19 fires, more extensive surveys are consistently noting healthier, larger plants in wetter micro-habitats compared to the sites monitored in this paper. Intriguingly, the threatened *P. hirsuta* in NSW also exhibited symptoms of dieback from an unknown cause in recruits after the 2019-20 megafires, with higher incidence of dieback perhaps associated with fire severity and changed soil conditions (Andres *et al.* 2022).

For *P. micranthera*, and to a lesser degree in *B. brownii*, declines in plant density at the scale of long-term monitored quadrats could be being partly offset by observations of post-fire recruitment after the 2018-19 fires in areas where there were no pre-fire plants. Reassembly of community composition at the plot scale after fire events is a well-known process in ecosystems dominated by obligate-seeding species (Thuiller *et al.* 2007). A priority for future research is to test whether post-fire recruitment in *P. micranthera* and *B. brownii* is largely random within the bounds of seed dispersal capacity (such as in lottery models; Chesson and Warner 1981), or directional in response to specific threats. In the case of *B. brownii*, the analysis of seedling:adult

ratio indicates that some topographic positions are proving more favourable for contemporary recruitment compared to where recruitment occurred in the past. Spurs, which are putatively more exposed and drier, were less suitable for contemporary recruitment, suggesting a role for the well-documented recent and ongoing decline in regional rainfall (Delworth and Zeng 2014).

The decline to near extinction in some subpopulations of all monitored species has presumably resulted in a loss of genetic diversity, at least from the wild. Subpopulations of *Banksia* spp. occurring on separate peaks of the Striling Range harbour unique genetic diversity (Coates *et al.* 2015). Seed collections made before 2018-9 from the near-extinct subpopulations, and progeny from these collections growing in two seed production area translocations not on the Stirling Range (Barrett *et al.* 2024), likely act as a reservoir for some of the genetic diversity lost from the wild (Coates *et al.* 2015). The multiple occurrences of substantial subpopulation declines and extinctions emphasise the value of making conservation seed collections of threatened flora (Cochrane *et al.* 2007).

Juvenile period

This study confirmed previous work describing a relatively 'long' juvenile period (in the context of south-western Australia, being >10 years; Shedley *et al.* 2018) in serotinous obligate-seeding flora of the montane portions of the Stirling Range (Barrett *et al.* 2009; Gosper *et al.* 2022). Common metrics of juvenile period (Burrows *et al.* 2008; Gosper *et al.* 2013) were reached for all species over the range of ~12-14 years, when half of individuals were reproductively mature, and 24-28 years (2 × when half of individuals

are mature). Juvenile period metrics were reached soonest in *B. anatona* and *B. brownii*, of which some subpopulations occur at lower elevations than any populations of *B. montana* and *P. micranthera*. The low productivity of the montane Stirling Range, with winter temperature limitations and skeletal soils, likely explains the relatively long juvenile period lengths (Gosper *et al.* 2022). Increasing aridity with climate change may further extend juvenile periods in coming decades, perhaps counteracted somewhat by increasing temperatures (Enright *et al.* 2015; Gosper *et al.* 2022).

There was a protracted period, often in the order of about 10 years, over which individuals of the monitored subpopulations reached reproductively maturity. This suggests that over the initial years of seed accumulation a small percentage of the population will be contributing the bulk of the genetic material present in the seed crop, which has implications for conservation seed collections and fire management.

The use of juvenile period to delineate acceptable fire interval bounds (Bradstock and Kenny 2003; Gosper *et al.* 2013) for *P. micranthera* is complicated by four factors. First, high levels of mortality in monitored populations suggest that rates of seed input into the seed bank from a post-fire cohort are likely to peak relatively soon after the juvenile period is reached, as the increasing proportion of the population being reproductive with increasing age is offset by declining live plant density (Fig. 2d). There are currently insufficient data to determine when the point of maximum post-fire seed production is reached. Second, there is a lack of knowledge on the longevity of seed stored in the soil, which could inform over what period the persistent seed bank could potentially support post-fire recruitment after decline or loss of the above-ground population. Amongst other *Persoonia* there appears to be substantial variation in seed

493 bank longevity (Auld *et al.* 2000; Ayre *et al.* 2009). Third, the extent to which viable seed
494 may persist, ungerminated, through fire events is poorly understood, noting that there
495 appears to be some capacity for this in *P. micranthera* with recruitment in monitored
496 quadrats after the 2000 fire when only juvenile plants were present pre-fire (although
497 seed dispersal cannot be discounted). Bet-hedging post-fire germination responses
498 have been recorded in other *Persoonia* (Ayre *et al.* 2009). Fourth, it is unknown whether
499 inter-fire recruitment (i.e. beyond the lagged recruitment that occurs in the first 5 or so
500 years after fire; Fig. 2) can be a significant demographic process for *P. micranthera*,
501 although there is no observational evidence for this to date.

502

503 *Maximising post-fire recruitment*

504 The quantity of pre-fire infructescences was a significant predictor of post-fire
505 seedling:adult ratio in both species where these data were available (Table 1). Indeed, it
506 was a stronger predictor than fire interval, which was not a significant predictor in
507 models where infructescence data were available but was where infructescence data
508 were not available. The lesser importance of fire frequency was somewhat surprising
509 given the clear relationship between plant age and reproductive maturity (Fig. 4) and the
510 emphasis on interval in determining tolerable fire intervals for obligate-seeding flora
511 (Bradstock and Kenny 2003; Gosper *et al.* 2013). It is worth noting that the range of fire
512 intervals for which ratio data were available was limited for *B. brownii*, with no short (9-
513 year) intervals, as existed in the *B. montana* and *B. anatona* datasets. However, a
514 dramatic decline in the abundance of *B. brownii* with a nine-year fire interval has been
515 documented previously (Barrett and Yates 2015).

We interpret these findings as indicating that while fire interval, as it relates to juvenile period (immaturity risk) and senescence risk, can provide a proxy for the bounds in which recruitment in serotinous obligate seeders is possible, it is not always the best metric for predicting post-fire outcomes. Direct measures of plant performance (such as pre-fire fruit crop in this study), which admittedly has greater resourcing implications for data collection, provided a better-performing alternative. Pre-fire fruit crop size provides a direct mechanistic link to post-fire recruitment through quantifying the size of the seed bank available for post-fire germination. It also allows for variability in fruit crops with the same fire interval due to factors impacting fruit production such as resource availability (Enright *et al.* 2015; Gosper *et al.* 2022). Subpopulations in resource poor positions or growing over periods of poor rainfall that have a smaller fruit crop may be more vulnerable to local extinction through another fire event.

The partial decoupling of metrics of post-fire plant recovery from interval has mostly frequently been associated with differences in productivity – such as in precipitation, temperature or gross primary productivity – over both time and space (Enright *et al.* 2014; Enright *et al.* 2015; Gosper *et al.* 2022; van Dongen *et al.* 2023). The role of factors such as inter- and intra-specific competition, variation in levels of herbivory with fire events and between species, and interactions with plant pathogens and pollinators have received less attention, but likely also contribute to variation in fruit crops for a given fire interval and are worth investigating.

Management actions that enhance reproductive output could maximise species persistence and recovery for a given fire interval, although options appear limited and

mostly involve intensive intervention. Reduction in herbivore impact through mammal exclusion fencing, for example, has led to greater growth and seedling survival in co-occurring threatened flora (Barrett *et al.* 2024), which could plausibly flow through to greater reproductive output. Artificial provision of water has resulted in higher rates of germinant survival in experimental manipulations and more rapid attainment of reproductive maturity in plant translocations (Lamont *et al.* 1991; Monks *et al.* 2023; Barrett *et al.* 2024). Generally, however, regularly applying sufficient water to remote, mountain top populations would be extremely challenging logistically and from a resourcing perspective and may have interactions with disease, herbivory and competitors. Similarly, local reductions in the density of competing plants may maximise reproductive output in target species in natural ecosystems but requires testing.

Conclusion

Long-term monitoring of threatened flora populations and their demographic performance in the Stirling Range National Park has allowed investigation of temporal trends in abundance and provided information on juvenile period and factors associated with greater post-fire recruitment success, to inform ongoing conservation management. Two of the four species monitored are undergoing chronic decline, while the other two species show variation between subpopulations, with some showing signs of positive recovery after the most recent fires but others declining to near extinction. The four species had long juvenile periods in the context of the south-western Australia flora, and greater post-fire recruitment success was associated with

562 more abundant pre-fire fruit crops and/or longer fire intervals, indicating that multi-
563 decadal fire intervals will be required for the ongoing persistence of these species. One
564 species, *B. brownii*, showed landform-based reassembly after the most recent fires,
565 with greater post-fire recruitment in putatively more mesic contexts. With south-
566 western Australia experiencing recent and projected ongoing declining rainfall
567 (Delworth and Zeng 2014) and increasing temperatures as a consequence of climate
568 change, pressures on the threatened montane species under study are likely to
569 increase further. Juvenile periods can be expected to lengthen, total fruit crop size may
570 decrease, recruitment may become increasingly restricted to more mesic and
571 temperate topographic positions, and adult survival may be impacted through
572 interactions with plant disease (Enright *et al*. 2015; Giménez-Benavides *et al*. 2018;
573 Yates *et al*. 2021; Gosper *et al*. 2022).

574

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736 **Table 1.** Linear mixed model results for the ratio of post-fire seedlings to pre-fire adults.
737 Subpopulation was included as a random effect. * P < 0.05; ** P < 0.01; *** P < 0.001

738 ***Banksia montana***. Overall model performance: marginal r^2 = 0.65; conditional r^2 = 0.67,
739 RMSE = 0.32.

Fixed effects	Coefficient	Standard error	df	*t*
(intercept)	-0.356	2.89	4.65	-0.12
Rainfall in year following fire (mm)	-0.004	0.01	4.78	-0.54
Mean pre-fire infructescences	1.383	0.51	4.81	2.71*
Pre-fire adults	0.392	0.41	4.68	0.96
Fire interval (years)	-0.015	0.01	5.95	-1.10

740

741 ***Banksia brownii***. Overall model performance: marginal r^2 = 0.59; conditional r^2 = 0.59,
742 RMSE = 0.31. The topographic position of gully is the baseline against which the other
743 categorical topographic positions are compared in the analysis output.

Fixed effects	Coefficient	Standard error	df	*t*
(intercept)	1.496	1.23	11.3	1.22
Topographic position (gully vs ridge)	0.036	0.13	35.0	0.27
Topographic position (gully vs spur)	-0.489	0.13	34.3	-3.66***
Density of pre-fire infructescences	0.176	0.07	33.7	2.65*
Density of pre-fire adults	-1.101	0.30	35.0	-3.71***

Fire interval (years)	-0.015	0.04	9.6	0.73

Pairwise comparisons of topographic positions: Gully and Ridge ns; Gully > Spur**; Ridge > Spur**.

Banksia anatona. Overall model performance: marginal $r^2 = 0.29$; conditional $r^2 = 0.65$, RMSE = 0.32.

Fixed effects	Coefficient	Standard error	df	*t*
(intercept)	0.009	1.95	17.4	0.01
Rainfall in year following fire (mm)	0.001	0.01	18.7	0.21
Density of pre-fire adults	-0.573	0.32	35.5	-1.78
Fire interval (years)	0.037	0.01	27.8	2.53*

List of figures

Fig 1. Changes in the global population of *Banksia montana* over time, in the context of years in which fires affected some subpopulations (shown by red arrows – the 2000 fire impacted subpopulations at Bluff Knoll, Isongerup and East Bluff, and the fires in 2018 and 2019 cumulatively impacted all subpopulations): (a) total numbers of mature and juvenile *B. montana* individuals in all known subpopulations, since monitoring began in 1997. Note that data on mature (green bars, left axis) and juvenile (blue line, right axis) individuals are on different scales, and there are no monitoring data in 1998 and 1999; (b) total population size (mature and juvenile) and the contribution of the four subpopulations at five time points over the >25 years of monitoring data.

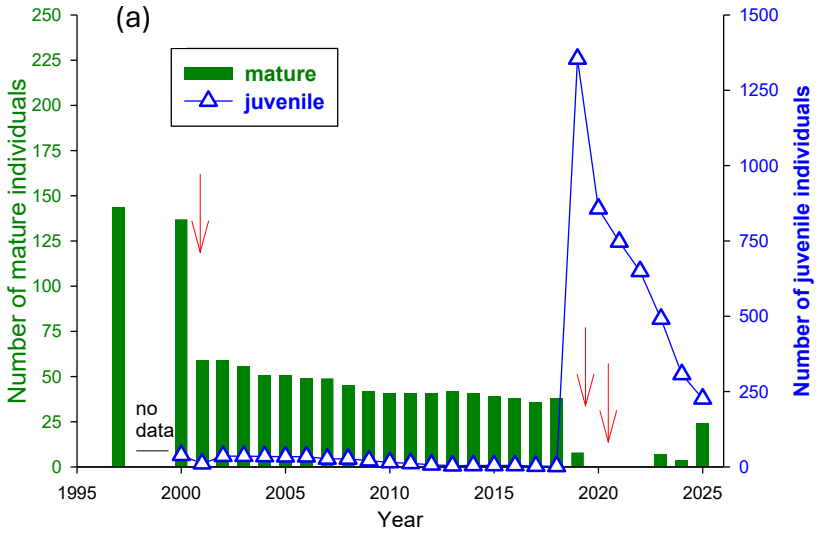
Fig. 2. Temporal trends in the density of threatened flora in the Stirling Range, in the context of years in which fires affected some subpopulations (shown by red arrows): (a) *Banksia brownii* from monitored quadrats (mean ± standard error); (b) *Banksia anatona* from monitored quadrats (mean ± standard error (negative only for ease of visualisation)); (c) *Persoonia micranthera* from monitored quadrats (mean ± standard error (negative only for ease of visualisation); ○, Bluff Knoll; ▲, Isongerup, both burnt in each of 2000 and 2018). The linear regression uses the five available post-fire population density maximum datapoints (larger symbol size ○ and ▲). Error bars are shown in one direction only for ease of viewing; (d) *P. micranthera* from monitoring tagged individuals that germinated after the 1991 fire from 2001 (time since fire of 10 years) onwards.

772 **Fig. 3.** Univariate relationships of significant predictors of the ratio of post-fire seedlings
773 to pre-fire adults (seedling:adult ratio) (Table 1). Note that seedling:adult ratio was log
774 transformed ($\log_{10}$ (x+1)) for analysis and is plotted here on a log scale. (a) mean pre-fire
775 infuctescences per plant in *Banksia montana* ($\log_{10}$ (x +1)); (b) pre-fire density of
776 infructescences in *B. brownii*; (c) pre-fire density of adults in *B. brownii*; (d) location in
777 different topographic positions (gully, ridge or spur) in *B. brownii*; and (e) fire interval in
778 *B. anatona*.

779

780 **Fig. 4.** Juvenile period in threatened flora of the Stirling Range: (a) *Banksia montana*,
781 aggregating two longitudinal series: (i) the seedling cohort from all populations
782 recruiting after the 2018 and 2019 fires monitored from 2021-2024 (age range 3-6 years;
783 ▲); and (ii) tagged plants of the 1991 cohort at Bluff Knoll monitored from 2001 onwards
784 (10-21 years; ○); (b) *Banksia brownii*, aggregating three longitudinal series of tagged
785 plants: (i) the 2019 cohort at Yungemere monitored from 2020-2024 (age range 1-6
786 years; ▲); (ii) the 1996 cohort at Mt Hassell monitored from 2003-2010 onwards (age 7-
787 14 years; ○); and the 1991 cohort at Yungemere monitored in 2003 (12 years; ▪); (c)
788 *Banksia anatona* from four time series: (i) the 2000 cohort at Ellen track monitored from
789 2002-2017 (age range 2-17 years; ○); (ii) the 2018 cohort at Ellen track monitored from
790 2019-2025 (1-7 years; ▲); (iii) the 2018 cohort at SE Ellen monitored from 2020-2025 (2-
791 7 years; ▪); and (iv) the 2019 cohort at Mt Success monitored from 2020-2024 (2-5 years;
792 ▼); and (d) *Persoonia micranthera* from two time series of tagged plants recruiting after
793 the 1991 fire: (i) Bluff Knoll (age range 10-21 years; ○); (ii) East Bluff (10-25 years; ▲).

794



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797 Fig 1

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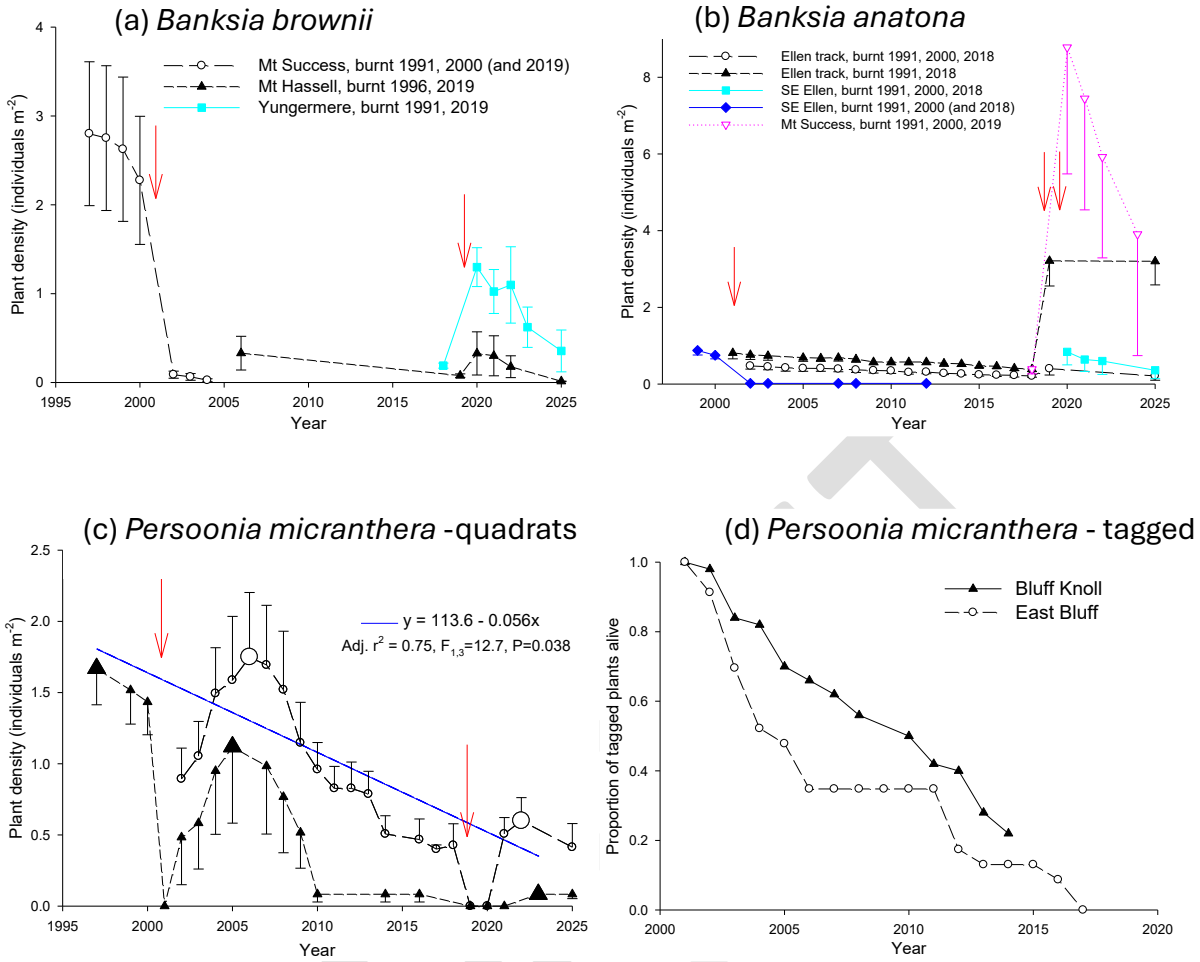
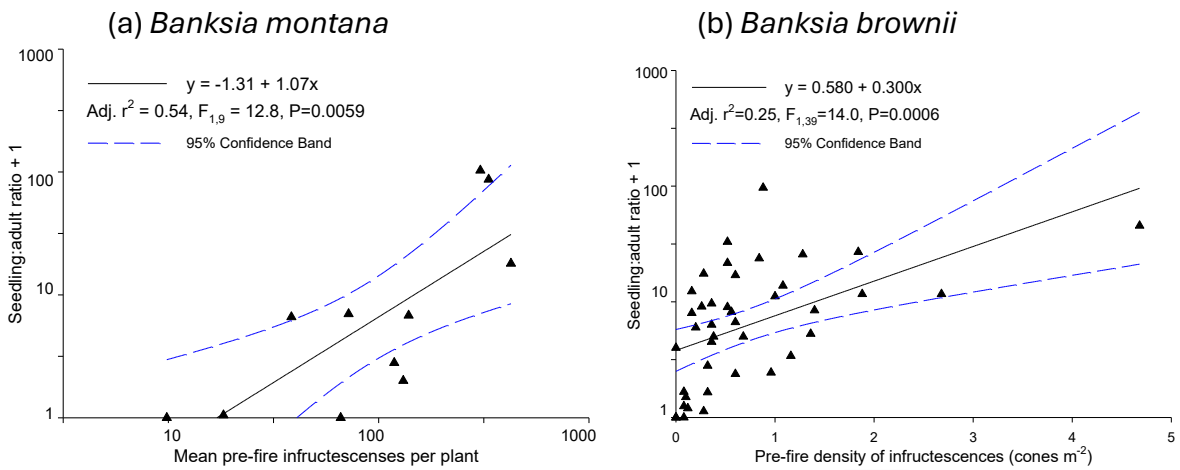

(a) Banksia brownii
Mt Success, burnt 1991, 2000 (and 2019)
Mt Hassell, burnt 1996, 2019
Yungermere, burnt 1991, 2019
Plant density (individuals m-2)
Year
(b) Banksia anatona
Ellen track, burnt 1991, 2000, 2018
Ellen track, burnt 1991, 2018
SE Ellen, burnt 1991, 2000, 2018
SE Ellen, burnt 1991, 2000 (and 2018)
Mt Success, burnt 1991, 2000, 2019
Plant density (individuals m-2)
Year
(c) Persoonia micranthera -quadrats
y = 113.6 - 0.056x
Adj. r2 = 0.75, F1,3=12.7, P=0.038
Plant density (individuals m-2)
Year
(d) Persoonia micranthera - tagged
Bluff Knoll
East Bluff
Proportion of tagged plants alive
Year

Fig 2



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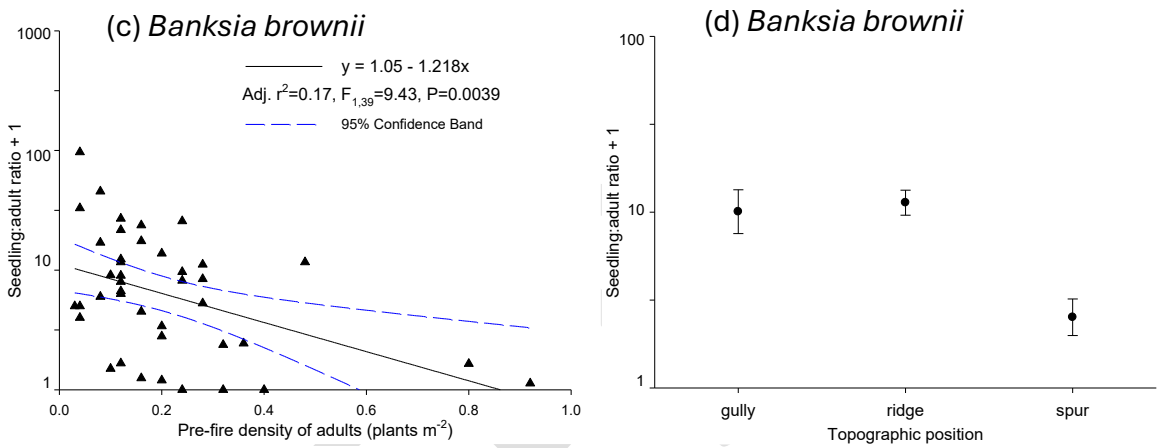

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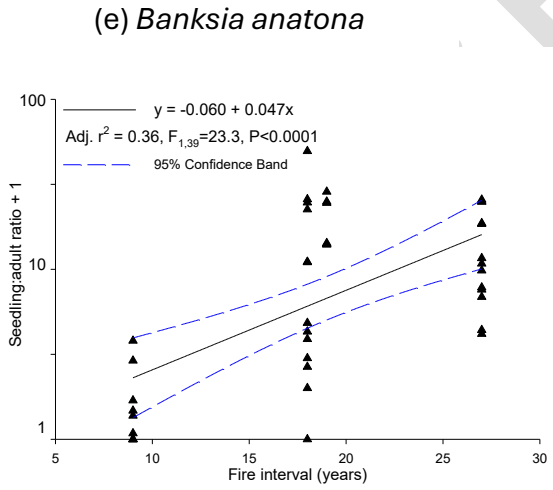


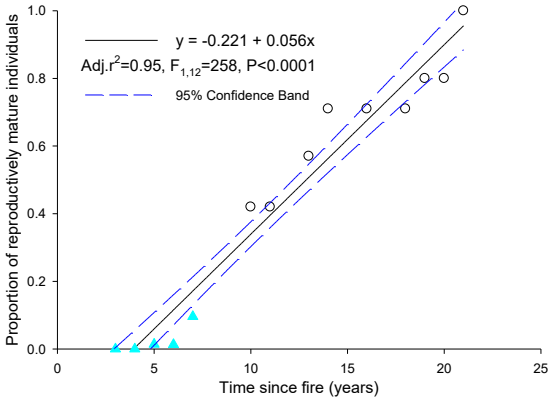
806

807 Fig 3

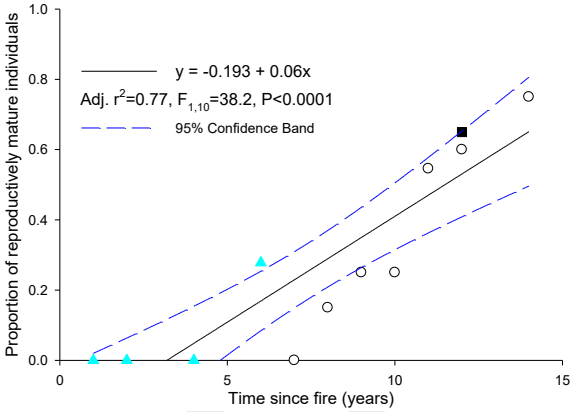
808

809

(a) *Banksia montana*



(b) *Banksia brownii*



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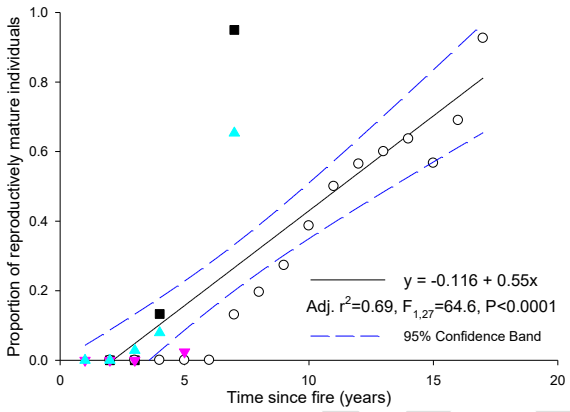
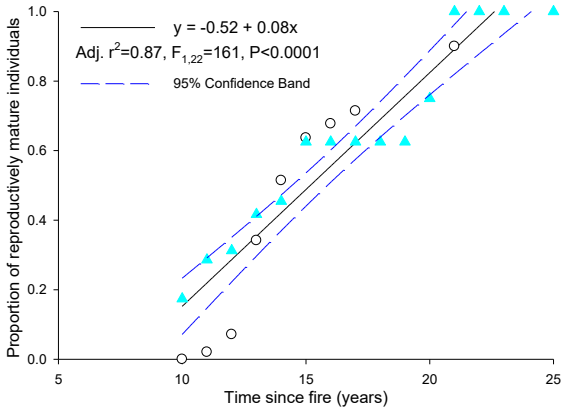
(c) *Banksia anatona*



(d) *Persoonia micranthera*



811

812 Fig 4