Population Ecology of Two Endemic, Fire-sensitive, Blue Mountains *Banksia* Taxa (Proteaceae) in Response to Fire

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Banksia penicillata (northern Blue Mountains) and *Banksia paludosa* subsp. *astrolux* (Southern Highlands) occur in small, isolated populations and occasionally as isolated individuals. We undertook a field study of both species to better understand their population ecology in relation to fire. Both are large, serotinous, fire-sensitive shrubs with plant-stored seedbank and a relatively short lifespan (<50 years); both were impacted by the severe December 2019 fires. Recruitment is generally fire-related, but some recruitment also occurs in the absence of fire.

At a landscape-scale, populations of *Banksia penicillata* occupy dry sandstone ridgetops, providing variable protection from major fires, with occasional intergenerational long-distance seed dispersal establishing populations of variable duration in sites which do not usually act as fire refugia. *Banksia paludosa* subsp. *astrolux* has similar responses, but generally smaller populations and more restricted range. Although some plants have been reported as surviving the 2019 fire in nearby rocky ridgetop refugia, all plants were killed in our study populations and seedling recruitment has not replaced all pre-fire occurrences, despite 18 years since the previous fire.

Using a precautionary approach, and in the context of a rapidly changing climate, we recommend that both species would benefit by having populations of varying fire histories and ages >15 years old across the landscape, including some sites with fire intervals >30 years, to provide increased opportunities for distance-dispersal and establishment of new fruiting populations. Applying IUCN threatened species criteria, there is a strong case for listing *Banksia paludosa* subsp. *astrolux* as Endangered and *Banksia penicillata* as Vulnerable.

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KEY WORDS: *Banksia penicillata*, *Banksia paludosa* subsp. *astrolux*, fire ecology, fire refugia, life cycle, long distance dispersal, population dynamics, serotiny.

INTRODUCTION

Banksia species (Proteaceae) feature in many ecological studies, including nutrient uptake on low nutrient soils, pollinator interactions, and plant community responses to fire (Gill 1981; Hammill et al. 1998; Myerscough et al. 2000). They are characteristic components of woodland and heath vegetation on low nutrient sand and sandstone soils in eastern Australia and are particularly prominent in the Sydney region where fire is a prominent part of the ecosystem (Hammill and Tasker 2010; Myerscough et al. 2000). Some *Banksia* species respond to fire by resprouting from basal lignotubers and/or epicormic shoots (resprouters); others are killed by fire (fire-sensitive seeders), to be replaced by seedling recruitment from winged seed released post-fire from woody cones (infructescences), a condition known as serotiny (Lamont et al. 2020). According to Lamont et al. (2020), serotiny confers fitness benefits when fire return intervals are between age to reproductive maturity and the plant lifespan.

Depending on the species, seeds may be released spontaneously, annually, or periodically (e.g., *Banksia integrifolia* subsp. *integrifolia*), when cones are broken off the stem or when a stem dies. In most Sydney species, however, a substantial proportion of seed is retained on the adult plant and ultimately released following burning. No soil-stored seedbank or post-release dormancy has been reported (Myerscough et al. 2000). Because of their general abundance in shrubby sclerophyll vegetation, *Banksia* species are often important markers in post-fire recovery studies where counts of annual growth bursts can be used to measure duration of post-fire periods (Cowling and Lamont 1985; Wills 2003); loss of fire sensitive species can demonstrate the impact of fires at short time intervals (Bradstock and O'Connell 1988; Bradstock et al. 1997; Gallagher et al. 2021). For fire-sensitive species, a mass recruitment event following fire provides the next generation. *Banksia ericifolia* may take 8–10 years to build up an adequate canopy seed store for self-replacement, so that minimum fire-free intervals of this duration or longer are needed to maintain populations (Bradstock and O'Connell 1988; Jenkins et al. 2005); successful germination and seedling establishment require patches of bare soil.

Banksia penicillata (A.S. George) K.R. Thiele is a conspicuous but rare shrub up to 7 m tall, occurring in small local populations in the upper and northern Blue Mountains, particularly on the Newnes Plateau north of Lithgow. Though first collected in 1897, it was only described in 1981, first as *Banksia conferta* var. *penicillata* and then as *Banksia conferta* subsp. *penicillata* (George, 1981), before being recognised as a distinct species, *Banksia penicillata*, in 2000. Published knowledge on *Banksia penicillata* is limited to the taxonomic descriptions (George 1999; Harden 2002) and brief ecological summaries. It is a fire-sensitive, non-lignotuberous, serotinous, seeder shrub (Benson and McDougall 2000).

Banksia paludosa subsp. *astrolux* A. S George, named in 1986, is a morphologically similar and related taxon, restricted to a small area in the Southern Highlands (Wingecarribee Shire), about 60 km south of the most southern known occurrences of *Banksia penicillata* (Fig. 1). It is a fire-sensitive, non-lignotuberous, and generally ridgetop-associated taxon, up to 5 m tall, with similar morphology and ecology to *Banksia penicillata*, in contrast to the smaller, lignotuberous, *Banksia paludosa* subsp. *paludosa*, which is variably associated with wetland areas.

Banksia penicillata and *Banksia paludosa* subsp. *astrolux* are the least well-known of the Sydney region *Banksia* taxa. Neither are currently listed as threatened but *Banksia penicillata* has previously been classed as 3RC- (ROTAP; Briggs and Leigh 1995), and subsequently proposed as IUCN conservation status of Least Concern (Bell 2008). The conservation status of *Banksia penicillata* and *Banksia paludosa* subsp. *astrolux* is currently being assessed.

This paper describes a field study of aspects of the ecology and population dynamics of *Banksia penicillata* and *Banksia paludosa* subsp. *astrolux* in response to fire, based on observations prior to 2013 and targeted field surveys in the Blue Mountains area in 2018–2021, a period including 2019, the driest year on record, culminating in extensive bushfires affecting populations of both species in late 2019. In 2020, annual rainfall across the study area was above average; La Niña became established during September 2020 and reached moderate strength by the end of the year (BOM Annual Climate Statement 2020; www.bom.gov.au/climate/current/annual/aus/), and rainfall has remained high to date (June 2021).

We discuss the role of long-distance dispersal in the observed distribution of both species, comprising isolated populations and individuals, and the threats to the species from more frequent drought and fire with projected climate change. We discuss our observations of both of these two fire-sensitive taxa in the context of their very different geographical ranges in the Blue Mountains.

DISTRIBUTION

The first collections of *Banksia penicillata* were made by R.T. Baker in 1897 in the Coricudgy Range, and R.T. Cambage in 1906 near the Wolgan River. Current Australian Virtual Herbarium (AVH) specimen records represent ~35 locality records for *Banksia penicillata* within an area bounded by Lee Creek and Wollemi Creek in the north and northwest, south through Mt Coricudgy to Dunville Loop, and Cyrils Rocks to Green Gully (Glen Davis), and the Baal Bone Gap area, then across the Newnes Plateau (main concentration of sites) from Glowworm Tunnel to Marrangaroo, and scattered locations east to Culoul Range and Mt Irvine, and at Leura (one site with three patches of plants) ~20 km further south (Fig. 1). The geographic range of *Banksia penicillata* is ~130 km north-south and 70 km east-west. Elevations range from 400 m (Culoul Range) and 550 m (Glen Davis) to 1050 m at the Glowworm Tunnel. Annual rainfall ranges 800–1300 mm. Using IUCN criteria, Extent of Occurrence (EOO) for *Banksia penicillata* is 5967 km^2 (Vulnerable), while Area of Occupancy (AOO) is 312 km^2 (Endangered) (T. Auld pers. comm.).

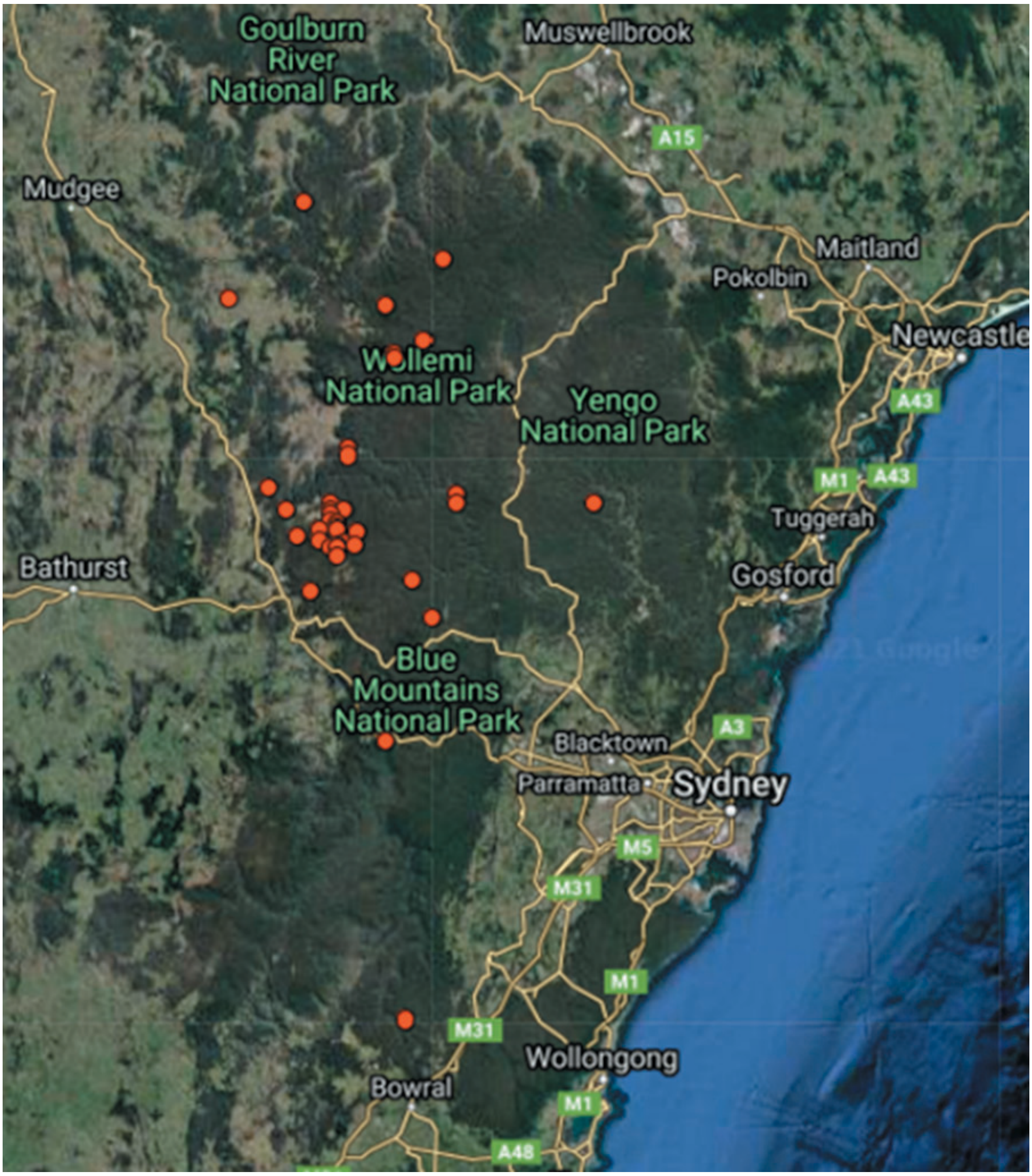

Figure 1. Australian Virtual Herbarium records for *Banksia penicillata*. The western cluster is on the Newnes Plateau and the most easterly record shown is an incorrectly located Culoul Range collection which should be in Wollemi National Park (NP) west of the Putty Road. The most southerly record shown (north of Bowral) represents *Banksia paludosa* subsp. *astrolux* in Nattai NP northwest of Hilltop.

Banksia penicillata grows in dry sclerophyll open forest, woodland and occasionally, montane heath, and is restricted to small populations on sandstone cliffs or steep slopes and around rocky outcrops according to Harden (2002). Recorded occurrences are all on the extensive Triassic Sandstone plateaus of the Sydney Basin, mostly in Wollemi, Gardens of Stone and Blue Mountains national parks (part of the Greater Blue Mountains World Heritage Area) or Newnes State Forest. These sites have remained essentially undisturbed in European times; the low nutrient sandstone soils and rugged terrain (characteristic of Old Climatically Buffered Infertile Landscapes (OCBILs; Hopper 2021)) being unsuitable for

European agriculture, before their values as national parks and wilderness were recognized.

Banksia paludosa subsp. *astrolux* is known from a small number of ridgetop occurrences in woodland on Triassic Hawkesbury Sandstone plateaus of the Sydney Basin, between 450 m and 700 m elevation, in a small area near Hilltop and Balmoral in the Southern Highlands (Wingecarribee Shire) (Fig.1). Recorded occurrences of *Banksia paludosa* subsp. *astrolux* are mostly in Nattai National Park, part of the Greater Blue Mountains World Heritage Area. Using IUCN criteria, EOO is 55.15 km^2 (Critically Endangered), while AOO is 20 km^2 (Endangered) (T. Auld pers. comm.).

METHODS

In October 2019 we collected data on the population structure of *Banksia penicillata* for sites in the upper Blue Mountains (Fig. 2, Table 1), including on the Newnes Plateau, near Mt Wilson and at Leura. At that time, some of the populations (upper Marrangaroo Creek catchment, Newnes Plateau) had been burnt previously in 2013 (State Mine Fire) and we were interested in the impact of that fire on survival, growth, and population structure. Two months later, in December 2019, the Gospers Mountain Fire burnt all of our study populations, with the exception of the Leura site. In April and December 2020 and March 2021 we made post-fire visits to most of our sites to record population responses to the fire. A summary of the sites and populations is given in Table 1. Using NSW National Parks and Wildlife Service and Forestry Corporation of NSW fire history maps, which identify boundaries of individual fires, we confirmed fire histories in the areas containing our study sites; however, due to a range of topographic and other factors, this does not mean that all areas within individual fire boundaries are burnt (Table 2).

At each site, plant height and basal stem diameter for 10–20 individuals were measured, and any population size/age classes noted. The particular pattern of *Banksia* growth allows an estimate of plant age by counting annual growth spurts (section of branch between the most recent terminal bud and the previous annual terminal bud along individual branches) and assuming they represent single annual growth increments. This is commonly done with other *Banksia* species (Cowling and Lamont 1985; Wills 2003); however, it is important to include an allowance for at least one year for seedling establishment, in addition to counts of annual growth spurts. Not every branch tip grows each year, and it is worth checking this by comparing the pattern of recent years' growth for a number of nearby shoots. Age was estimated, using the above method, with reference to a known garden specimen of 26 years growing in shallow unfertilized soil in Katoomba. The plant was approximately 6 m high and 6 m wide, the youngest (most recent) cones with fertile follicles were ~5–6 years old, all consistent with our field observations. Our estimates of plant ages using the above technique were subsequently checked against years since previous fire in our studied populations.

Dead adult plants were counted in each burnt population where there was still evidence, post-fire, of stem and branch remains and where it was feasible to survey the entire population. This was not possible for either of the Marrangaroo Creek populations (MCN and MCS) where all plant remains were combusted, and the solitary plant at Birds Rock West was not relocated. It was also not possible for Birds Rock North or three of the four Mt Wilson populations due to population size and topographic complexity.

In the field, ages of mature and immature cones were estimated by counting growth spurts back from the crown edge along stems in a range of populations, from large (Birds Rock North) to small (Junction Swamp three plants). More vigorous stems extending upwards and laterally in the crown were selected.

Seedlings numbers under plants at various sites were counted in compass quadrats for evidence of any seedling microhabitat preferences, and the distance from the crown edge to the most distant seedling (putatively from that plant) was recorded as a measure of potential localised population expansion over time.

In June 2021 we surveyed five populations of *Banksia paludosa* subsp. *astrolux*, near the Nattai and Starlight trails in Nattai National Park, northwest of Hilltop, and one population at nearby Balmoral in Bargo State Conservation Area, all burnt in December 2019 in the Green Wattle Creek Fire. All these populations were previously burnt in a large 2001-2002 fire. Recent fire history for these sites was confirmed from NSW National Parks and Wildlife Service fire history maps. Dead adult plants were counted in each population. Because of the small size of all studied populations, we estimated the population area and age of individual plants, and for selected plants, we counted the number of mature cones per plant, age of youngest (most recent) mature cones per plant and estimated the number of open follicles on burnt cones, and the number of surviving seedlings per plant or population.

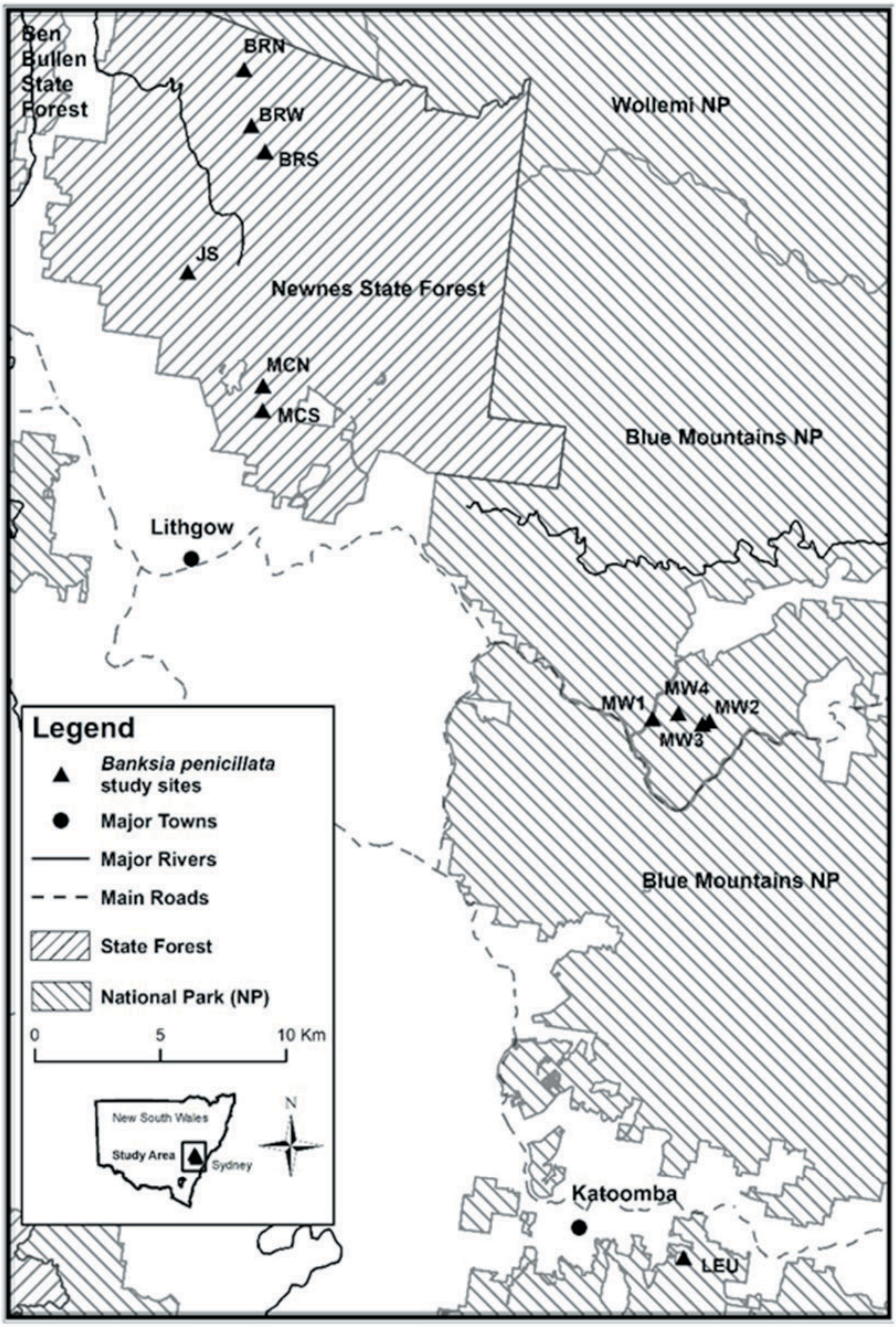

Figure 2. Location map of *Banksia penicillata* study sites. BRN = Bird Rock North, BRW = Bird Rock West, BRS = Bird Rock South, JS = Junction Swamp, MCN = Marrangaroo Creek North, MCS = Marrangaroo Creek South, MW = Mt Wilson, LEU = Leura.

Table 1. Summary of *Banksia penicillata* study sites, showing population sizes and conditions in 2019 pre-fire and 2020 post-fire, and character (refugial or non-refugial site).

Sites - north to south (Coordinates: GDA94, Zone 56)	**Population size and condition 2019, pre-fire**	**Population condition 2020, post-fire**	**Site character**
Birds Rock North (BRN); E237871, N6310708, 1038 m. Newnes State Forest	Many large old plants about 35 years old; >2 ha; no sign of recent fire; last fire possibly 1984	Partly burnt Dec 2019, many large plants survived among rocks with variable canopy scorch; seedling recruitment under dead plants or plants with partial canopy scorch	Woodland; rocky spur on ridge with pagodas; refugial site
Birds Rock West (BRW); E238147, N6308543, 1180 m. Newnes State Forest	Single plant 50 mm stem diameter, 3.5 m high, possibly 15 years old; possibly distance dispersal recruitment early 2000s	Burnt Dec 2019, not found 2020	Open forest; non-refugial site
Birds Rock South (BRS); E238719, N6307421, 1116 m. Newnes State Forest	Single plant 13 years old, with many seedlings; possible distance dispersal recruitment	Burnt Dec 2019; post-fire seedling recruitment (73) under and outside canopy of dead plant	Woodland, non-refugial site
Junction Swamp (JS); E235500, N6302450, 1175 m. Newnes State Forest	Single ~ 38-year-old plant and two 19-year-old plants recruited under canopy edge	Burnt Dec 2019; all adult plants dead with seedling recruitment under dead plants and outside canopy edge	Open forest; non-refugial site
Marrangaroo South (MCS); E238580, N6297563, 1136 m. Newnes State Forest	Extensive cohort of juvenile plants (4–6 years old) from post Oct 2013 fire recruitment; remains of dead mature, 22–25-year-old plants possibly recruited post-fire following an unrecorded fire in the early 1980's; <0.5 ha	Severely burnt Dec 2019, all plants dead, no remains of mature plants, no seedlings	Open forest; non-refugial site
Marrangaroo North (MCN); E238593, N6298522, 1109 m. Newnes State Forest	Location of previously extensive population of mature plants prior to the 2013 fire; >2 ha. Not visited between the 2013 and 2019 fires	2 dead juvenile plants, 4–6-year-old, recruited post the 2013 fire. Severely burnt Dec 2019, all dead, no remains of old adult plants, no seedlings.	Open forest; non-refugial site
Mt Wilson Road (MW1); E253607, N6285695, 951 m. Blue Mountains National Park	Multi-aged stand; 0.5 ha; single large ~30-year-old plant with younger adults 8–11 years old adjacent, recruitment in absence of fire; and widespread 15–19-year-old adult cohort, presumably also recruited in absence of fire	Burnt Dec 2019; all dead, except for the single 30-year-old original plant near the road with incompletely scorched canopy (subsequently died). Abundant seedling recruitment under dead plants 2 months post-fire	Ridgetop Woodland; non-refugial site
Mt Wilson East Powerline Access Trail end (MW2); E255809, N6285585, 864 m. Blue Mountains National Park	Population of 16–23-year-old plants; 1 ha; established post 1994 fire	Burnt Dec 2019, all adults dead, seedlings present Nov 2020	Woodland; rocky ridge end/ cliff-top; possible variably refugial site

Table 1 continued

Sites - north to south (Coordinates: GDA94, Zone 56)	**Population size and condition 2019, pre-fire**	**Population condition 2020, post-fire**	**Site character**
Mt Wilson East Powerline Access Trail site 2 (MW3); E255530, N6285493, 859 m. Blue Mountains National Park	Population of 16–23-year-old plants; 1 ha; established post 1994 fire	Burnt Dec 2019, all adults dead, seedlings present Nov 2020	Woodland; rocky ridge end; possible variably refugial site
Mt Wilson East Powerline Access Trail (MW4); E254622, 6285859, 920 m. Blue Mountains National Park	Single 23-year-old, isolated plant, 4 m high; established post 1994 fire by distance seed dispersal or single surviving seedling from previous plant(s)	Burnt Dec 2019, plant dead, seedlings present Nov 2020	Woodland; non-refugial site
Leura - Inspiration Point (LEU). Patch 1- E254801, N6264897, 863 m; Patch 2 - E254822, N6264974, 860 m; Patch 3 - E254811, N6265255, 911 m. Blue Mountains National Park	3 close populations of 33–36-year-old plants, with some smaller 10–15-year-old plants recruited in absence of fire before thick litter had accumulated. Area 100 m^2 + 600 m^2 + 30 m^2. Possibly an unrecorded fire event in the early 1980s initiated recruitment of oldest plants from a previous population	Site remains unburnt. Old plants remain healthy; no sign of seedlings; dense litter	Woodland; rocky ridge end; possible refugial site

RESULTS

Banksia penicillata

Population structure and ecology

Although Harden (2002) noted *Banksia penicillata* is a "shrub to 4 m", we found some individuals up to 7 m tall with a main trunk and broad crown of multiple branches, a structure evidently formed at an early stage of growth, probably within ~5 years of germination (Fig. 3). Width of crown spread was up to 7 m, depending on local population density and light availability, as branchlets with greater light availability were more vigorous (Fig. 4). In more exposed open heath (often on skeletal sandy soils) rather than woodland vegetation, similarly aged mature plants were shorter and branched at or near ground-level to form dense, dome-like shrubs, with basal stem diameters comparable to similar age, taller plants growing in more protected woodland or open forest sites, with stem diameters up to 280 mm (Fig. 5). We found no evidence of any lignotuber development and no sign of any resprouting consistent with lignotuber or basal regrowth. We found several plants with new shoots on existing lower trunks after crown scorch, but probably a local response to variable fire intensity.

Determination of plant age and longevity

The predominating episodic recruitment of plant cohorts was evident. We found that our annual growth spurt counts as a measure of plant age, correlated with stem basal diameter (R^2=0.89), was also an index of accumulating biomass (Fig. 6) and correlated with time since last fire, where known (assuming all recruitment was post-fire). Although both indices were variable, counts of annual growth bursts, and basal diameter measures together gave a good indication of population age class distribution.

We estimated the oldest plants we observed were 35–40 years old (Birds Rock North and Leura); plants had shed lower branches but showed continuing new apical growth and could not be considered moribund, though the continued apical growth made the whole branch top-heavy and liable to collapse. For populations burnt in the 2019 fires, all plants with

Table 2. Confirmed fire histories of *Banksia penicillata* study sites, with years since previous fire in brackets. Blank cells indicate no recorded fire.

***Banksia penicillata* sites - north to south**	**Confirmed fire year**						
	2019 Gospers Mountain Fire	**2013 State Mine Fire**	**2004/05 Sunnyside Ridge Fire**	**2002/03 Wollemi Complex Fire**	**1993/94[1]**	**1984[2]**	**1979/80[1]**
Birds Rock North site	yes (35)[3]	no	no	no	no	?[3]	
Birds Rock West site	yes	no	no	no	no		
Birds Rock South site	yes	no	no	no	no		
Junction Swamp site	yes	no	no	no	no		
Marrangaroo sites (2)	yes (6)	yes	no	no	no		
Mt Wilson sites (6)	yes (25)	no	no	no	yes (14)	no	yes
Leura sites (3)	no	no	no	no	no	no	no

1 Extensive fire. 2 Localized fire. 3 Forestry Corporation fire maps show the 1984 fire as two very small fires just south of the Birds Rock North population, but plant ages suggest a fire through this population at about that time.

Figure 3. Young 30 cm high *Banksia penicillata* in woodland, Newnes Plateau, 27 Oct 2019, showing early branch structure development. Photo: Ian Baird

Figure 4. Old, vigorous *Banksia penicillata* parent plant (4.5 m high x 6 m wide) in non-refugial woodland site, on the edge of the Mt Wilson Rd population, 23 Oct 2019, before the 2019 fire which ultimately killed it and the entire adult population. Photo: Ian Baird

Figure 5. Unburnt, old, dense, low, and spreading *Banksia penicillata* among rocks on spur end (refugial site) in full sun, Birds Rock North population, Newnes Plateau, 08 May 2020. Photo: Ian Baird

total crown scorch were killed, but where topographic features, such as a protective rock formation was adjacent (e.g., Birds Rock North), fire behaviour was often modified, leaving some plants unburnt or with only partial crown scorch. After partial crown scorch, growth continued from unaffected crown apices.

Episodic recruitment

Based on our observations, *Banksia penicillata* will release seed in response to a range of fire intensities, thus promoting recruitment, providing there is an adequate seed source (Figs 7–10).

In addition to seedling recruitment following fire, we found evidence of recruitment in the absence of fire in a number of sites. Prior to the 2019 fire, the Junction Swamp population comprised one old plant with two younger, but mature plants recruited under the outer crown edge in the absence of fire (Fig. 11). At the Leura site there were plants of a range of ages present indicating some recruitment in the absence of fire before a dense litter layer had become established. Similar observations were made in the larger Mt Wilson and Birds Rock North populations.

In our Marrangaroo Creek South population, when surveyed in 2019, all living plants had a range of size and branching forms with 1–5 years growth and had clearly recruited in the previous six years, as a result of an intense fire in October 2013 (State Mine Fire). A few plants had first inflorescences by this time, but no fertile cones had yet developed. The seed source was clearly the plants existing pre-2013-fire; their dead trunks still survived six years later (in 2019) but by then had lost all their cones and most branches (Fig. 12). There was dense juvenile establishment under some old dead plants, but very little under others, presumably indicating local variation in the immediate soil/litter microhabitat conditions and/or variability in pollination and seed set among plants.

Based on their size and number, the old pre-2013-fire plants appear to have been a more or less single-aged cohort, probably up to ~25 years (basal stem diameter 110–210 mm; 18–25 growth spurts); indicating recruitment from a similar fire event in the early–mid-1980s. Although Forestry Corporation fire maps do not record a fire at that time, observations of a fire in ~1980 in the adjoining Farmers Creek and Paddys Creek catchments (D. Benson pers. obs.) indicate that this fire could have also burnt into the adjoining upper Marrangaroo Creek catchment.

The Marrangaroo Creek South site was subsequently burnt by the 2019 Gospers Mountain Fire; a year later (November 2020), no evidence of the previously recorded *Banksia* population could be found, either of seedlings or burnt dead stems or

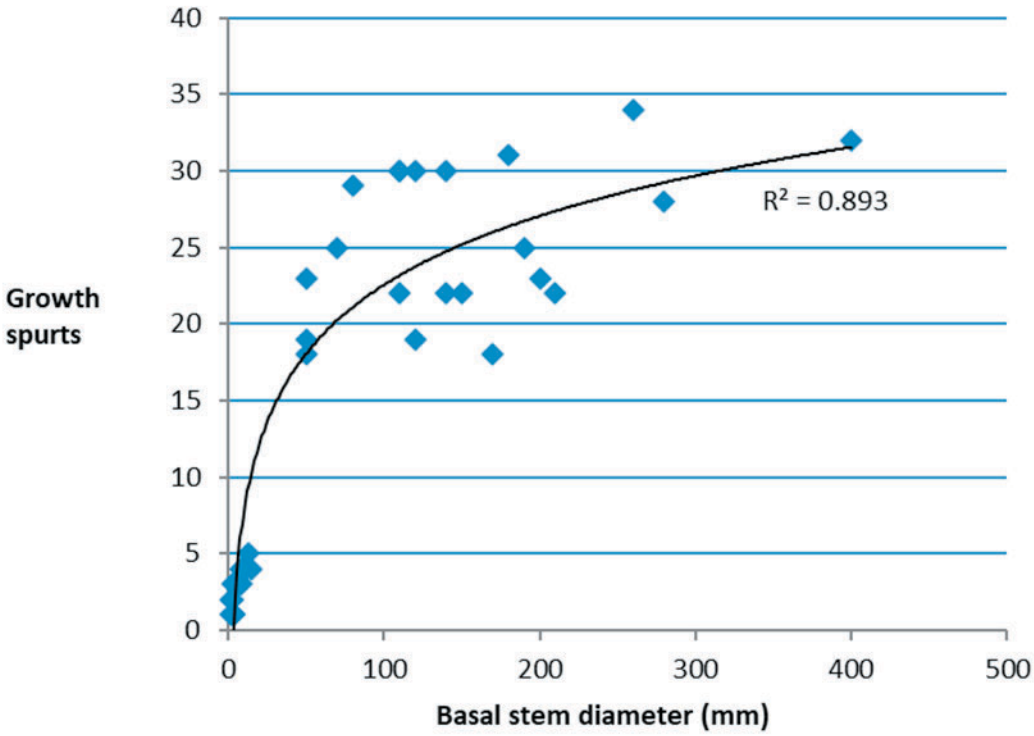

Figure 6. Relationship between number of growth spurts, interpreted as a measure of plant age (years), and basal stem diameter in *Banksia penicillata*.

Figure 7. Old unburnt *Banksia penicillata* (Fig. 4) with abundant cones and old inflorescences; mature unopened cones centre foreground, Mt Wilson area, 23 Oct 2019. Photo: Ian Baird

Figure 8. *Banksia penicillata* cones with open follicles, Mt Wilson area, 15 Mar 2021, showing impact of a high intensity fire on the cones. Abundant seedlings below. Photo: Ian Baird

Figure 9. *Banksia penicillata* on rocky spur, killed by high intensity 2019 fire, with seedlings below, Mt Wilson area, 24 Feb 2021. A formerly dense, 2.5 m high, dome-shaped plant growing in full sun. Photo: Ian Baird

Figure 10. Dense, +/- even-aged stand of young *Banksia penicillata* in non-refugial open forest habitat, 23 Apr 2020, northwest of Galah Mountain, Newnes Plateau. Population killed by the 2019 fire (previous fire 2001-2002 Wollemi Complex Fire), followed by abundant seedling recruitment, with no evidence of previous parent plants of the standing dead cohort. Photo: Ian Baird

Figure 11. (A) Canopy edge of old, previous, 2019-fire-killed *Banksia penicillata* parent; (B) two pre-2019-fire recruits (now dead) on outer canopy edge; and (C) post-2019-fire seedling recruit clusters among fallen burnt cones, suggesting seed release from fallen cones on ground in this instance, Junction Swamp population, Newnes Plateau, 8 Dec 2020. Photo: Ian Baird

cones, confirming our prediction that the 6-year-old cohort would be locally eliminated because of its immature state, despite its extensive pre-fire size.

The extensive Marrangaroo Creek North population, observed prior to the 2013 State Mine Fire, was not revisited until November 2020 (after both the 2013 and 2019 fires), by which time, the entire population appeared to be eliminated; the only evidence of the former population being two, dead 4–6-year-old plants (identified from dead leaves) which presumably recruited from seed after the 2013 fire.

Seedling establishment

Post-fire visits in November 2020 to other sites burnt in 2019 (Mt Wilson, Birds Rock South and North, Junction Swamp) showed death of parent plants (but not all at Birds Rock North), but seedling establishment had occurred beneath adult crowns. Seeds fall or blow into the open ash beds and post-fire surface litter to germinate and establish with subsequent rainfall (Fig. 13). Seedlings were recorded as early as 2 months post-fire and were concentrated under adult crowns, but numbers and densities were variable.

The highest number of seedlings counted under crowns (n=13) was 178 beneath a 35-year-old plant (16 seedlings/m^2). Overall average density was 63 seedlings/plant (3.7 seedlings/m^2). There was no obvious relationship with crown size or plant age with our limited sampling of a few relatively isolated plants, though seedling numbers were greatest under larger plants. Distribution of seedlings under the dead crowns of 13 plants, over different sites, showed highest average numbers (25) in the southwest quarter, with smaller but similar average numbers in the other three quarters (12–13), though there was considerable site variation (highest in northwest at Junction Swamp).

Occasional isolated seedlings occurred beyond the crown, generally no more than about 5 m from the edge, though distances of up to 20 m were recorded, indicating the generally limited local dispersal.

Flowering and fruiting

Flowering takes place in autumn. Likely dominant pollinators are birds and mammals as in other *Banksia* species. Pollination appears to be adequate with

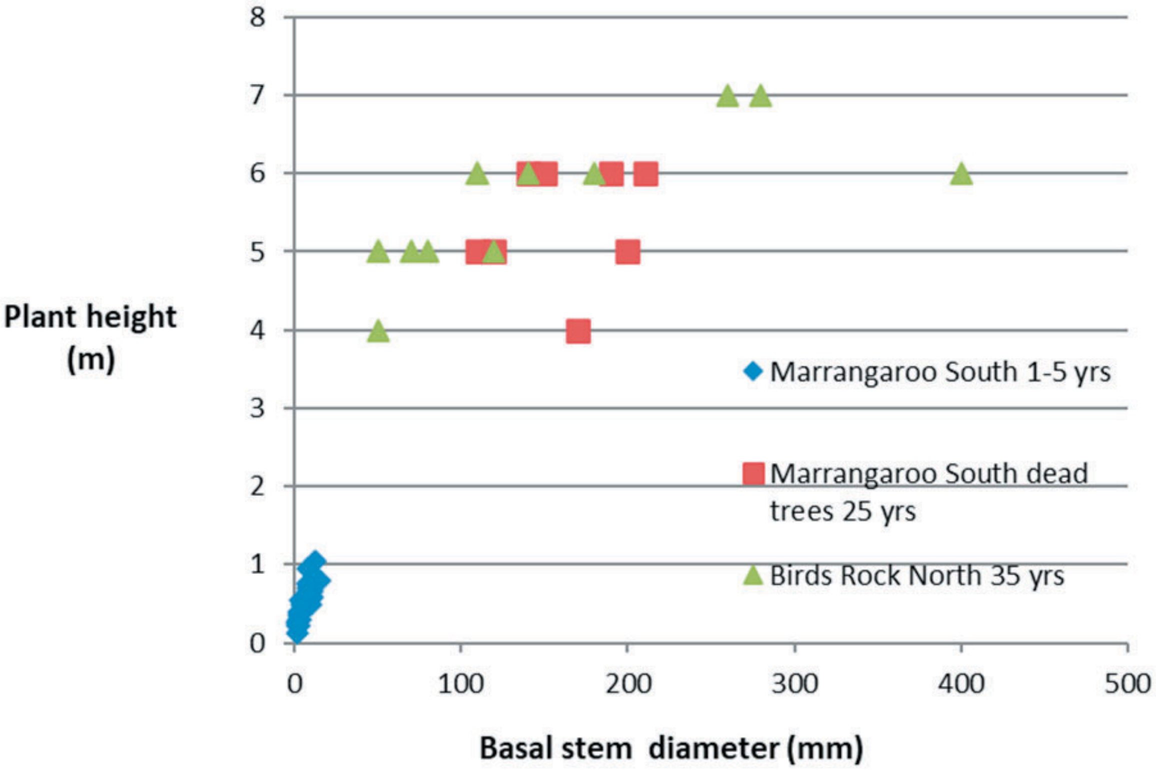

Figure 12. *Banksia penicillata* - Plant height/stem diameter clusters showing episodic recruitment for populations at Marrangaroo South and Birds Rock North.

Figure 13. *Banksia penicillata* seedlings, post 2019 fire, Birds Rock North population, Newnes Plateau, 8 May 2020. Photo: Ian Baird

mature fruits recorded in the large populations and, also often on isolated plants.

An initial, but rare, early inflorescence was noted on a <6-year-old plant (Marrangaroo Creek South population, subsequently burnt). Production of first mature fruits on juveniles may take a further 2 years. On mature plants, fertile cone numbers on young, up to 5-year-old shoots are low, but increase to a maximum on 6–10-year-old branches (Table 3). Older branches carry fewer cones towards their bases, as cones are lost, deteriorate with age, or are predated by cockatoos. Older plants carry more cones than younger ones due to increased plant size as a result of increasing accrual of bifurcating branches increasing the overall number of cones held as they age. Plants appear able to produce fertile cones throughout their lives.

Old unburnt cones of *Banksia penicillata* at Leura retained some mature follicles at 16–25 years old, and old cones at this site often had open follicles and seed release, but onto ground with a thick litter layer unsuitable for seedling recruitment.

Seed Dispersal

The densest seedling establishment post-fire was under or near adult individuals, now defoliated and dead, resulting from local dispersal by gravity and wind following follicle opening after plant death. Seedlings associated with post-fire surface soil and litter movement indicate some local surface water movement of seeds. Concentrations of seedlings were observed in microhabitats associated with small depressions or other microtopographic features, including post-fire accumulated litter, and where there was a possible moisture/microhabitat benefit. At Birds Rock North some seedling establishment post-fire had occurred along an old vehicle track where overhanging plants had dropped seed, which were subsequently transported by water flowing down the track. Maximum observed dispersal from canopy edges of adult plants was 20 m.

Table 3. *Banksia penicillata* - Number of cones/plant (from 5 branches) by age class (i.e., growth spurts from shoot apex) for different-aged plants (arranged young – old). Age class with maximum number of cones in bold.

Site	Number of plants	Plant age (year)	Age class of growth spurts								Total cones/ plant
			1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	
Marangaroo South	All	<6	0	0							
Mt Wilson young plants	4	16–20	3.5	**9.2**	3.2	0					16
Junction Swamp young plants	2	19	2	**3**	2.5	0.5					8
Birds Rock North	1	26	3	**12**	3	0	0				18
Leura unburnt	4	29–31	0	2.5	4.8	**6.3**	3.3	1	0		18
Birds Rock North	3	34	1.6	**7.7**	5	0	0	0	0		14
Mt Wilson old plant	1	35	4	**11**	3	0	0	0	0		18
Junction Swamp old plant	1	39	0	**4**	2	0	0	0	0	0	6
Leura unburnt	1	38–40	0	2	**8**	3	2	1	0	0	16
Average			1.8	**6.4**	3.9	1.2	0.9	0.4			

Table 4. *Banksia paludosa* subsp. *astrolux* – Size, age, cone numbers and seedling numbers of all surveyed populations (Hilltop-Balmoral, 7 Jun 2021). Field estimated ages shown were later revised following confirmation of date of previous fire.

Population location	Plants (n)	Plant status	Estimated age (yrs)	Cones (n)	Seedlings (n)
Nattai trail	1	dead	13	0	0
Starlight trail	11	dead	13	3 (on two plants)	17
Starlight trail campsite	1	dead	13	0	0
Spur west of Starlight trail campsite	1	dead	13	2	11
	1	dead	13	5	82
Rock outcrop north of Starlight trail	6	dead	9–15	3 (on one plant)	12
Halls Rd, Balmoral	1	dead	15	10	~100 total
	1	dead	15	0	
	1	dead	15	1	
	1	dead	15	0	
	1	dead	15	1	
	1	dead	15	2	
	1	dead	15	1	
	1	dead	15	0	
	1	dead	15	0	
	1	dead	15	11	

Banksia paludosa subsp. *astrolux*

The Green Wattle Creek fire in December 2019 killed all of the *Banksia paludosa* subsp. *astrolux* we visited. This comprised 6 small clusters ranging 1–11 plants (Table 4), estimated to be aged 13–15 years old at the time of the fire. We postulated a previous fire in 2003-2004, subsequently confirmed to be in the summer of 2001-2002, indicating that our maximum age estimates based on counts of growth bursts in these plants were underestimates. Assuming that the oldest plants had germinated in 2002, maximum plant ages in these populations were thus 17–18 years, up to 4 years older than we estimated. This could perhaps be explained as a result of fire effects on branches making counts of growth bursts less accurate, or due to effects of the long drought periods reducing frequency or vigour of annual growth spurts, including in the initial year of establishment. The 17–18-year inter-fire period had allowed mature cones to develop on some plants in 4 of the 6 sites (Table 4). Age of the youngest (most recent) inflorescences was 4–6 years, and the age of youngest mature cones (with open follicles) was 6–8 years. Number of open follicles per cone was very variable and ranged from <10 to ~80.

All identified *Banksia paludosa* subsp. *astrolux* seedling establishment was within 5 m of the crown edge. Seedling numbers under and adjacent to crowns of standing dead plants was highly variable and related to the number of mature cones and total number of open follicles per plant (Fig. 14). Sites with few cones resulted in replacement numbers of seedlings at this stage (e.g., 3 cones on 2 plants, resulting in 17 seedlings), presumably due to the good seasonal rainfall. Two isolated plants and a proportion of plants in larger populations of up to 18-year-old plants had no observed cones or post-fire seedlings established (Table 4), and in the case of the two isolated single plant sites, resulted in post-fire extinction. In the Balmoral population (plants up to an age of 18), 4 of the 10 plants (all growing in close proximity) had no cones and no seedlings.

DISCUSSION

Banksia penicillata and *Banksia paludosa* subsp. *astrolux* both occur as small, localized populations and sometimes as isolated single plants. Our observations

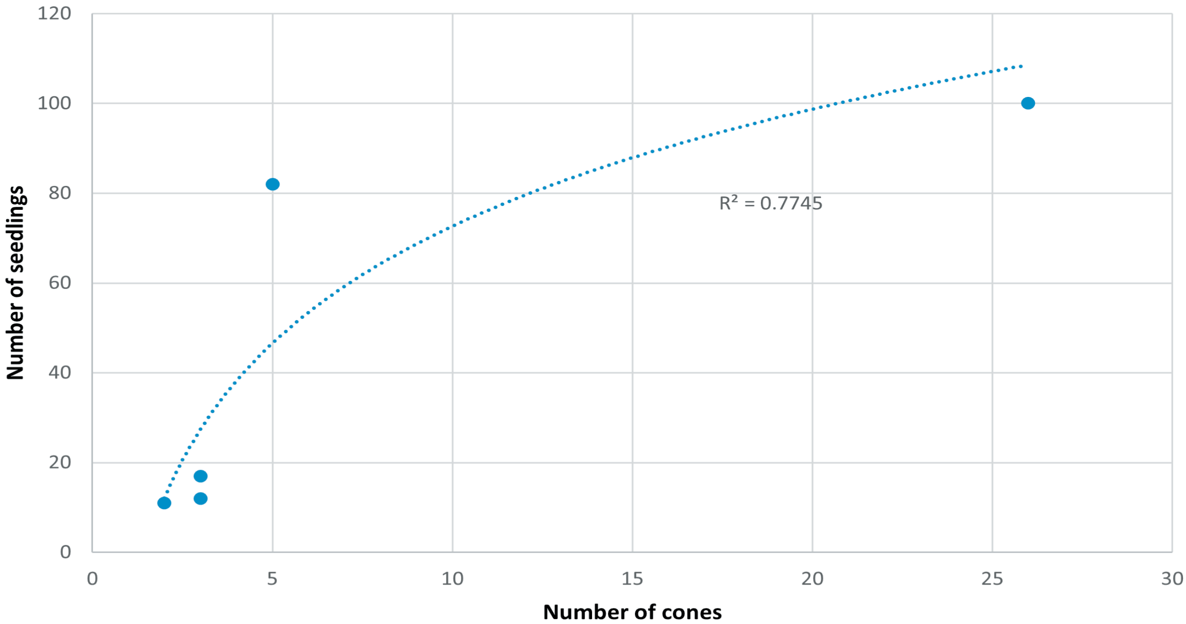

Figure 14. *Banksia paludosa* subsp. *astrolux* - Seedling recruitment related to the number of mature cones available.

confirm that both taxa are fire sensitive, seeder shrubs which typically regenerate through episodic post-fire seedling recruitment, following fire induced mortality of adult plants, but occasional recruitment also occurs in the absence of fire. Partial canopy death occasionally resulted from low intensity fire or competitor shading, resulting in continued apical growth of surviving branches, and unstable crowns. However, in the presence of ongoing stable conditions (and absence of fire or severe extended drought) we consider that these plants could live up to 50 years. Death is ultimately likely to be due to physical collapse of overextended, overburdened branches, in storms, or perhaps due to drought. Rare heavy snowfall events could contribute to plant collapse in some situations.

Population persistence requires appropriate fire-free intervals to develop adequate plant-stored seed banks. The distribution of populations and isolated plants of each taxa indicates long distance dispersal of seed or cones, and in addition to observations of some plants or populations surviving in rocky fire refugia, and recent extirpations of previously established populations in non-refuge areas, suggests that landscape-scale population dynamics of both taxa could be explained by a metapopulation model.

For both species, demographic patterns are consistent with mass establishment of seedlings following fire (Fig. 10), and assuming adequate rainfall, followed by rapid growth and gradual competition for light and resources, and gradual deterioration of weaker or slower growing individuals where canopies overlap (Fig. 15). Individual or widely spaced recruits may avoid competition and develop spreading canopies (Figs 4 and 16), though in sites with greater density the larger or more vigorous plants appear to remain dominant for life. Post-fire conditions of nutrient-enriched ash-bed and moderate to high light probably benefit seedling recruitment (Zammit and Westoby 1988) but the quick growth rate presumably requires adequate moisture. Habitat on ridges and plateaus makes rainfall the primary water source; no populations are associated with seepage or swamps. Likelihood of the timing of adequate rainfall following fire, and absence of any long-lived soil seedbank which outlives parent plants, may be factors limiting current distribution and abundance. However, the same applies to other co-occurring fire-sensitive *Banksia* species (*B. cunninghamii*, *B. ericifolia*) which are much more widely distributed and abundant across the region and raises the question as to why these two taxa are less abundant and more restricted in their distributions.

Long distance dispersal

The occasional isolated individuals of *Banksia penicillata* (across the Newnes Plateau, Mt Wilson) and *Banksia paludosa* subsp. *astrolux* recorded indicates that long distance dispersal occurs (Fig. 16). Long distance dispersal up to 2.6 km between dune

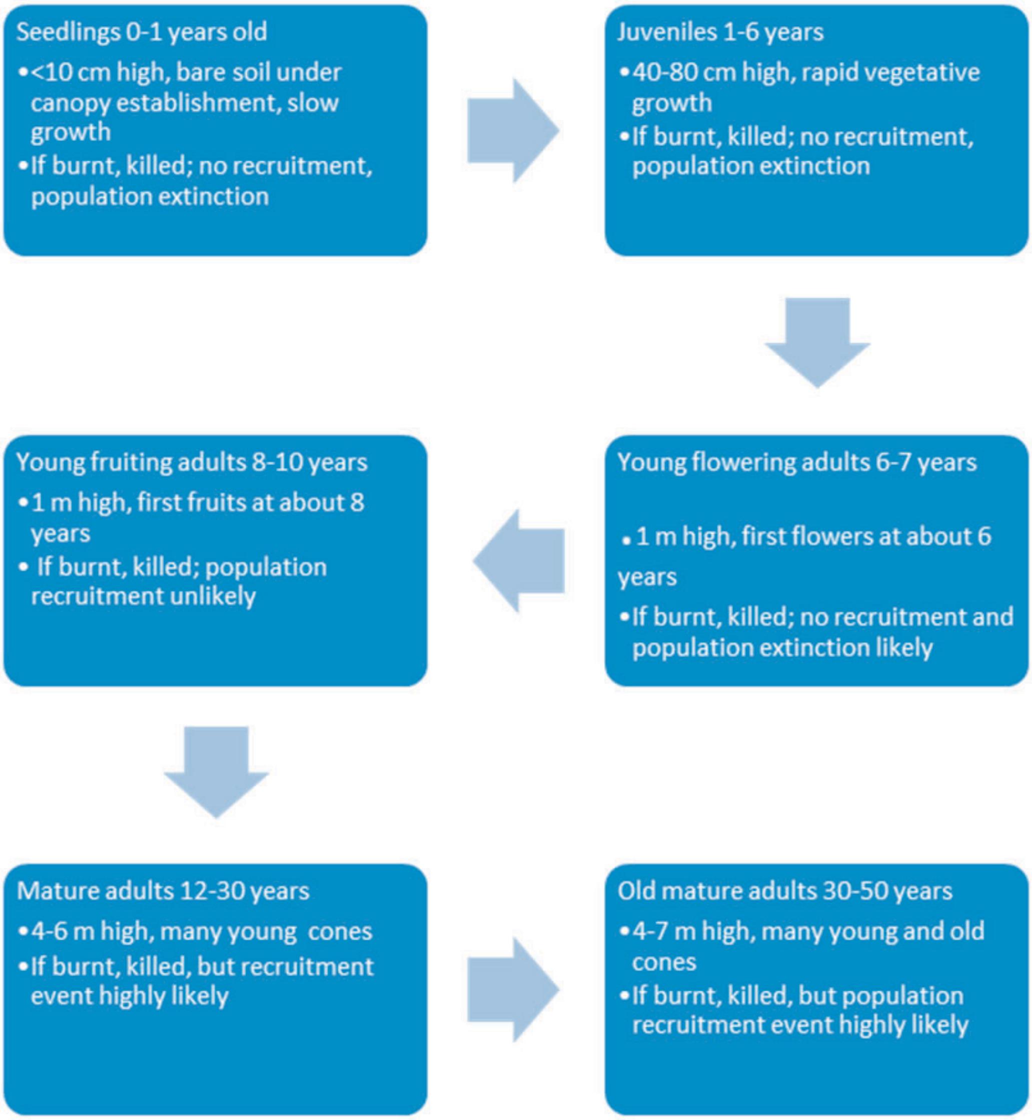

Figure 15. *Banksia penicillata* life stage summary from seedling to maturity with age, growth and reproduction events, and impact of fire on populations.

populations has also been recorded in southwestern Australia for co-occurring, fire-tolerant *Banksia attenuata* (He et al. 2009), and fire-sensitive *Banksia hookereana* (He et al. 2004), accounting for 5.5–6.8% of seeds, and broadly in the direction of seasonal winds.

Two distance dispersal scenarios are most likely, either associated with storm or fire-storm conditions (anemochory) (for discussion, see Keith et al. 2020) or cockatoo dispersal (zoochory). For *Banksia* species in southwestern Australia, wind vortices ("willy-willies"), which are common after fire when seed is released, are most likely to be responsible for distance dispersal by picking up seeds from the open cones or ground and carrying them to several kilometres high before they drift back to earth in the direction of prevailing winds (He et al. 2004, 2009).

He et al. (2004) also suggested that because "post-fire cones are often damaged by black cockatoos, as the seeds are vulnerable in the open fruits, it is also possible that these granivores contribute to long-distance dispersal as well". Witkowski et al. (1991) recorded 10–20% cone removal by cockatoos for three co-occurring, serotinous, fire-sensitive *Banksia* species in southwestern Australia, while Groom and Lamont (2015), also in Western Australia, reported that damaged *Banksia prionotes* cones have been observed 250 m from the nearest possible parent, and pinecones have been dropped by black cockatoos over 1 km from the nearest plantation.

Figure 16. Solitary adult *Banksia penicillata* in woodland, Mt Wilson area, 2 Nov 2020, killed by moderate intensity 2019 fire, with abundant post-fire seedling recruitment. Note abundant dead but unburnt leaves. This plant probably recruited by long distance dispersal. Photo: Ian Baird

We have also recorded *Banksia penicillata* cones which have been predated upon, and seeds consumed by granivorous birds, most likely Yellow-tailed Black Cockatoos, *Calyptorhynchus funereus*, which also feed on other *Banksia* and woody fruited species (e.g., *Hakea* spp., *Pinus radiata*). These cockatoos are sometimes observed flying from food plants carrying pinecones and *Banksia* cones, when disturbed (I. Baird pers. obs., and C. Probets pers. comm.). Although the extent of their capacity for longer distance transport over kilometres is unknown, cockatoos have been observed in flight carrying cones above tree canopies in the Blue Mountains (I. Baird pers. obs.), and it is possible that an occasional cone is carried some distance by these birds before being dropped.

Our recorded Mt Wilson *Banksia penicillata* populations include six discrete populations (four discussed in this study) in the upper Bowen Creek catchment (between Mt Wilson Rd and Mt Charles fire-trail) aligned nominally in a west-east direction over a distance of 6 km (although additional populations north and south of this line may occur), suggesting the possibility of dispersal of seed by wind, but could also indicate some dispersal by cockatoos moving between their known *Banksia* foraging sites. These birds are long-lived and appear to maintain accurate memories of the locations of particular seasonal food resources over years.

While isolated populations or individuals of both *Banksia* taxa may result from an initial founder event, in some situations, isolated plants may indicate past populations where only one or a few post-fire recruits have survived on that occasion, e.g., the small Junction Swamp group of *Banksia penicillata* or the small groups of *Banksia paludosa* subsp. *astrolux.* Thus, depending on conditions, small, isolated groups may represent either expanding or contracting populations.

Landscape-scale population dynamics of *Banksia penicillata*

At the landscape scale, *Banksia penicillata* appears to exist as small core populations in more or less permanently occupied rocky fire refugia (Figs 5 and 17), with periodic expansion across larger areas of habitat, and subsequent contraction, in response to fire and climatic events. Populations range from extensive populations over hectares to isolated individual plants. Most populations are localised or clustered in characteristic ridge or spur habitats, with

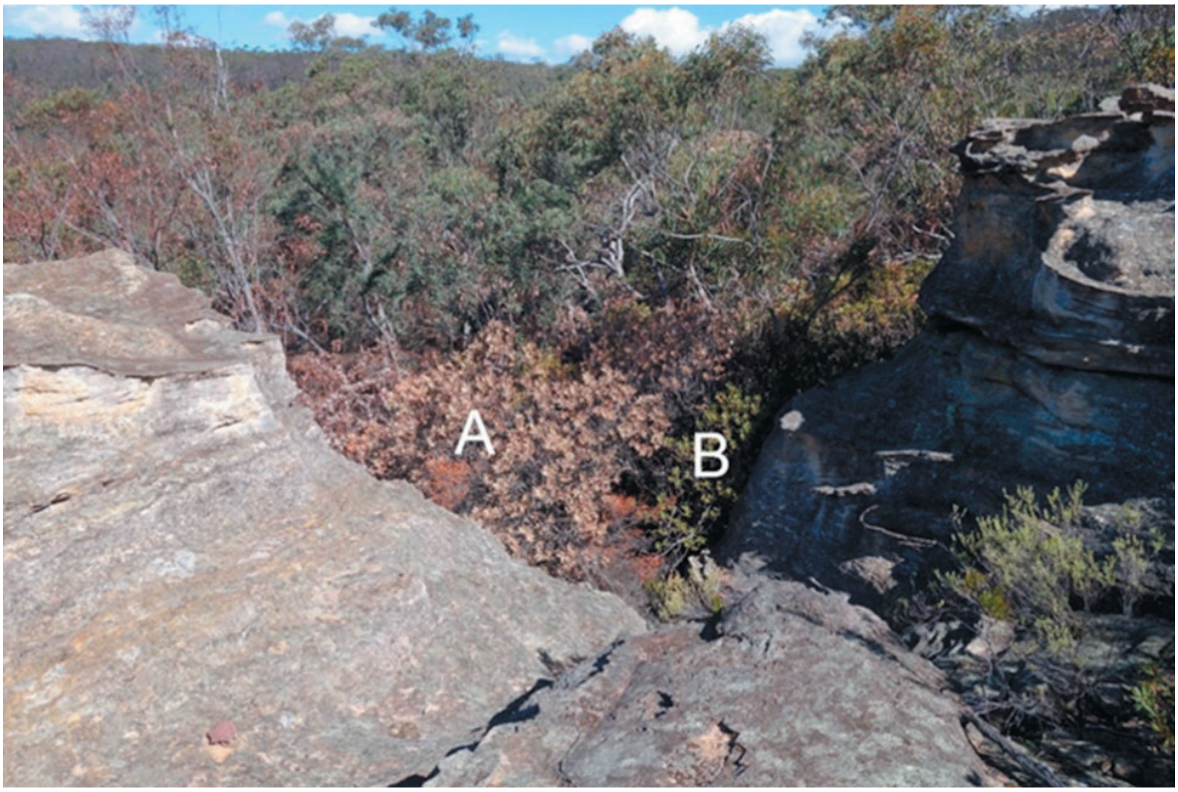

Figure 17. Crown-scorched (A) and unburnt (B) *Banksia penicillata* plants next to each other in refugial area among rocks, Birds Rock North population, Newnes Plateau, 8 May 2020. This site, although extensively burnt at varying intensities in 2019, provided partial or complete fire refugia for many plants. Photo: Ian Baird

relatively long distances separating some populations (e.g., ~20 km between Leura and Mt Wilson sites). Although we recorded seedlings established by local dispersal up to 20 m from parent plants post-fire, we speculate that seedlings could potentially disperse locally by wind or water for up to possibly 100 m in some situations.

Long distance seed dispersal events, however, contribute to establishment of populations of varying sizes and duration, vulnerable to inter-fire intervals less than the period required for the development of adequate plant-stored seed banks. Source populations also need adequate fire-free periods. The occasional occurrence of populations or isolated mature adults in woodland sites, not associated with rocky refugia, indicates that specific soil/habitat constraints are not a limiting factor as there appears to be plenty of suitable habitat available, and probably indicate seed dispersal by cockatoos or wind. Landscape-scale population dynamics appear consistent with a metapopulation model, based on long distance dispersal of seed. These observations suggest that metapopulation persistence in the landscape would benefit from having individual populations of varying post-fire ages, including some long unburnt core populations >30 years of age.

During our work, the impacts of two major fire events confirmed important parts of this model. Firstly, the extensive State Mine Fire in 2013 had killed all adult plants and triggered abundant germination, but the 2019 fire killed all juvenile recruitment in the two Marrangaroo Creek populations (North and South) before seed was set, extirpating these two populations. Secondly, the topographically complex cliff and pagoda rock habitat at Birds Rock North, associated with the ridgetop spur sites, did protect some of the older plants from being burnt in the 2019 fire (Figs 5 and 17), confirming this as a fire refugial site, even if in less protected parts of the site many older plants were killed. These 35-year-old plants, originating with a fire recruitment event (consistent with Forestry Corporation records of a 1984 fire nearby) had already benefitted from a long inter-fire period. We have observed additional likely refugial populations of *Banksia penicillata* in other cliff-face and pagoda rock habitats. Similarly, recent observations by Tony Auld (pers. comm.), of *Banksia paludosa* subsp. *paludosa* near our study sites in Nattai National Park, confirmed the presence of areas of rocky fire refugia where some plants survived, unburnt or only partly scorched.

Conservation issues for *Banksia penicillata* and *Banksia paludosa* subsp. *astrolux*

Based on our *Banksia penicillata* observations of age to maturity of first cones and allowing at least several years for additional plant-stored seed to accumulate, a minimum fire interval >12 years should generally allow individual populations of this species to develop an adequate plant-stored seed bank for population viability. However, as a precautionary approach, in the context of a rapidly changing climate, for *Banksia penicillata* we also recommend, as an objective, a minimum fire interval >15 years, together with variable frequencies across the landscape, including maintaining some long unburnt sites >30 years of age. Increasing the recommended minimum fire interval increases likelihood of development of adequate plant-stored seed banks, successful post-fire recruitment, and distance seed dispersal events by cockatoos in between fires. The Extent of Occurrence (EOO) and Area of Occupancy (AOO) of *Banksia penicillata* (using IUCN criteria) suggests that there is a strong case for listing the species as Vulnerable under NSW State and Commonwealth legislation.

Banksia paludosa subsp. *astrolux* also occurs as small, localised populations and isolated, single, mature plants, and has a very similar seedling recruitment pattern, life cycle and population ecology. However, none of the sites we visited had provided fire refugia during the recent 2019 fires, all adult plants we observed were dead and seedlings at only 4 out of 6 surveyed sites provided potential replacement plants. The last inter-fire period of 18 years evidently resulted in only small populations, and although these have provided replacement seedlings in those 4 sites following the 2019 fire, a proportion of those populations, and two isolated single plants, produced no cones before the 2019 fire.

Evidence from *Banksia paludosa* subsp. *astrolux*, that two isolated plants and a proportion of plants in larger populations of up to 18-year-old plants had no observed cones or post-fire replacement seedlings (Table 4), suggests that 12 years is too low in this species. As a precautionary approach, we thus recommend a minimum post-fire interval >15 years to increase likelihood of development of adequate plant-stored seed banks, successful post-fire recruitment, distance seed dispersal events by cockatoos in between fires, and long-term persistence of established populations, as for *Banksia penicillata*. Additionally, variable fire frequencies across the landscape, and fire-free periods >30 years in parts of the landscape, would increase opportunities for establishment of occasional new populations, through long distance dispersal of seed or cones from established populations. Post-fire weather conditions (rainfall), however, are likely to be critical. All our observations of seedling establishment have been in most favourable conditions; a fire in 2018 associated with the 2019 drought may have resulted in much poorer establishment.

In a recent post-fire survey to assess the impact of the 2019 fires and conservation status of *Banksia paludosa* subsp. *paludosa*, Tony Auld (pers. comm.), however, recorded a number of plants surviving unburnt or partly scorched in rocky ridgetop fire refugia in Nattai National Park within 1 km of our nearest study populations. The EOO and AOO of *Banksia paludosa* subsp. *paludosa* are very small, but it is possible that additional unrecorded populations are present in more remote parts of Nattai National Park, Bargo State Conservation Area, or adjoining areas; some of these may also be associated with rocky terrain, providing variable fire refugia.

With a high likelihood of future increased drought and fire frequencies and considering its highly restricted EOO and AOO, there is a strong case for listing *Banksia paludosa* subsp. *astrolux* as Endangered under NSW State and Commonwealth legislation. In terms of current management our observations suggest, using a precautionary approach, that *Banksia paludosa* subsp. *astrolux* would benefit from having the next inter-fire period >25 years to allow the current small, much reduced, and vulnerable stands to develop adequate plant-stored seed banks, to provide adequate future post-fire recruitment and potential seed sources for distance dispersal.

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REFERENCES

Bell, S.A.J. (2008). Rare or threatened plant species of Wollemi National Park, central eastern New South Wales. *Cunninghamia* **10**, 331-371.

Benson, D.H. and McDougall, L. (2000). Ecology of Sydney plant species. Part 7b: Dicotyledon families Proteaceae to Rubiaceae. *Cunninghamia* **6**, 1017-1202.

Bradstock, R.A. and O'Connell, M.A. (1988). Demography of woody plants in relation to fire: *Banksia ericifolia* L.f. and *Petrophile pulchella* (Schrad) R.Br. *Austral Ecology* **13**, 505-518. doi:10.1111/j.1442-9993.1988.tb00999.x

Bradstock, R.A., Tozer, M.G. and Keith, D.A. (1997). Effects of high frequency fire on floristic composition and abundance in a fire-prone heathland near Sydney. *Australian Journal of Botany* **45**, 641-655. doi:10.1071/BT96083

Briggs, J.D. and Leigh, J.H. (1995). 'Rare or threatened Australian plants'. (CSIRO Publishing: Canberra).

Cowling, R.M. and Lamont, B. (1985). Variation in serotiny of three *Banksia* spp. along a climatic gradient. *Austral Ecology* **10**, 345-350. doi:10.1111/j.1442-9993.1985.tb00895.x

Gallagher, R.V., Allen, S., Mackenzie, B.D.E., Yates, C.J., Gosper, C.R., Keith, D.A., Merow, C., White, M.D., Wenk, E., Maitner, B.S., He, K., Adams, V.M. and Auld, T.D. (2021). High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity. *Diversity and Distributions* **27**, 1166-1179. doi:10.1111/ddi.13265

George, A.S. (1981). The genus *Banksia* L.f. (Proteaceae). *Nuytsia* **3**, 239-473.

George, A.S. (1999). *Banksia* (Proteaceae). In 'Flora of Australia'. pp. 175-251. (ABRS/CSIRO: Melbourne, Australia).

Gill, A.M. (1981). Adaptive responses of Australian vascular plant species to fires. In: 'Fire and the Australian Biota' (eds A.M. Gill, R.H. Groves and I.R. Noble) pp. 243-272. 'Australian Academy of Science: Canberra'.

Groom, P.K. and Lamont, B.B. (2015). Seed release and dispersal in southwestern Australia: Adaptations for survival. In: ''Plant life in southwestern Australia (eds P.K. Groom and B.B. Lamont). (DeGruyter Open: Warsaw, Poland).

Hammill, K. and Tasker, L. (2010). 'Vegetation, fire and climate change in the Greater Blue Mountains World Heritage Area'. (Department of Environment, Climate Change and Water NSW: Sydney).

Hammill, K.A., Bradstock, R.A. and Allaway, W.G. (1998). Post-fire seed dispersal and species re-establishment in proteaceous heath. *Australian Journal of Botany* **46**, 407-419. doi:10.1071/BT96116

Harden, G.J. (2002). 'Flora of New South Wales. Volume 2. Revised Edition'. (University of New South Wales Press: UNSW Sydney).

He, T., Krauss, S.L., Lamont, B.B., Miller, B.P. and Enright, N.J. (2004). Long-distance seed dispersal in a metapopulation of *Banksia hookeriana* inferred from a population allocation analysis of amplified fragment length polymorphism data. *Molecular Ecology* **13**, 1099-1199. doi:10.1111/j.1365-294X.2004.02120.x

He, T., Lamont, B.B., Krauss, S.L., Enright, N.J. and Miller, B.P. (2009). Long-distance dispersal of seeds in the fire-tolerant shrub *Banksia attenuata*. *Ecography* **32**, 571-580. doi:10.1111/j.1600-0587.2008.05689.x

Hopper, S.D. (2021). Out of the OCBILs: new hypotheses for the evolution, ecology and conservation of the eucalypts. *Biological Journal of the Linnean Society* **160**, 1-31. doi:10.1093/biolinnean/blaa160

Jenkins, M.E., Morrison, D.A. and Auld, T.D. (2005). Estimating seed bank accumulation and dynamics in three obligate-seeder Proteaceae species. *bioRxiv preprint*. doi:10.1101/001867

Keith, D.A., Dunker, B. and Driscoll, D.A. (2020). Dispersal: The eighth fire seasonality effect on plants. *Trends in Ecology & Evolution* **35**, 305-307. doi:10.1016/j.tree.2019.12.001

Lamont, B.B., Pausas, J.G., He, T., Witkowski, E.T.F. and Hanley, M.E. (2020). Fire as a selective agent for both serotiny and nonserotiny over space and time. *Critical Reviews in Plant Sciences* **39**, 140-172. doi:10.1080/07352689.2020.1768465

Myerscough, P.J., Whelan, R.J. and Bradstock, R.A. (2000). Ecology of Proteaceae with special reference to the Sydney region. *Cunninghamia* **6**, 951-1015.

Wills, T.J. (2003). Using *Banksia* (Proteaceae) node counts to estimate time since fire. *Australian Journal of Botany* **51**, 239-242. doi:10.1071/BT01074

Witkowski, E.T.F., Lamont, B.B. and Connell, S.J. (1991). Seed bank dynamics of three co-occurring banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and interfire establishment. *Australian Journal of Botany* **39**, 385-397. doi:10.1071/BT9910385

Zammit, C. and Westoby, M. (1988). Pre-dispersal seed losses, and the survival of seeds and seedlings of two serotinous seedlings of two serotinous *Banksia* shrubs in burnt and unburnt heath. *Journal of Ecology* **76**, 200-214. doi:10.2307/2260464