

# Lack of fire rather than pollinator absence may drive population decline in the critically endangered *Banksia conferta* (Proteaceae)

Stephen A. J. Bell<sup>A,\*</sup> , Nigel Hunter<sup>B</sup> and Andrew Steed<sup>B</sup>

For full list of author affiliations and declarations see end of paper

**\*Correspondence to:**

Stephen A. J. Bell  
Conservation Science Research Group,  
School of Environmental and Life Sciences,  
University of Newcastle, Callaghan,  
NSW 2308, Australia  
Email: [stephen.bell@newcastle.edu.au](mailto:stephen.bell@newcastle.edu.au)

**Handling Editor:**

Grant Wardell-Johnson

**Received:** 25 November 2021

**Accepted:** 25 July 2022

**Published:** 16 August 2022

**Cite this:**

Bell SAJ *et al.* (2022)  
*Australian Journal of Botany*, **70**(5), 372–383.  
doi:[10.1071/BT21143](https://doi.org/10.1071/BT21143)

© 2022 The Author(s) (or their employer(s)). Published by CSIRO Publishing.

This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC BY-NC-ND).

OPEN ACCESS

## ABSTRACT

**Context and aim.** Stands of the critically endangered *Banksia conferta* in north-eastern New South Wales show low recruitment and were examined to elucidate whether pollinator absence or fire history best explained this. **Methods.** Motion-detection cameras were deployed at three sites to identify potential pollinators, and age structure within stands and past follicle production were assessed through tree measurements and follicle counts. **Key results.** In total, 691 fauna-triggered image sequences were recorded between June and December 2019. Six mammal and 10 bird species were detected, but only 10 of these were observed probing inflorescences. White-cheeked Honeyeater and Sugar Glider combined comprised 66% of all fauna interactions, and of all 400 *Banksia* probes, 45% were from White-cheeked Honeyeaters and 18% were by Sugar Gliders. Different size structures of *B. conferta* were evident at each site, consistent with older and younger populations post-fire. Significantly more *Banksia* individuals (5×) were present at the younger site, likely governing pollinator composition through interspecific competition within pollinator guilds, and past follicle production was also greater here. **Conclusions.** Pollinator absence is not the cause of low recruitment in this population, and current stand structure and follicle production reflect past fire history. The three sites differed in their dominant fauna foragers, suggesting that *B. conferta* is a pollinator-generalist. Birds appear to operate as the key pollinating species during the day but are replaced by small mammals at night. Follicle production is higher in younger post-fire plants. **Implications.** The absence of fire from older populations for over 55 years is of concern, and population decline seems likely without fire intervention.

**Keywords:** *Banksia*, Honeyeaters, mammals, pollinator, population decline, recruitment, threatened, wildfire.

## Introduction

Understanding the ecology of threatened species aids effective long-term management (Scheele *et al.* 2018), and appreciation of the role of pollinator networks and fire are key management objectives in many species (Brown *et al.* 2017; Carbone *et al.* 2019). Identifying the balance between managing habitat for pollinators and all other co-habiting species and ecological processes, while also ensuring optimal fire-related recruitment conditions for a target taxon can be problematic, yet without this knowledge some species may undergo insidious decline (Driscoll *et al.* 2010; McLauchlan *et al.* 2020). For example, the removal of fire disturbance from habitats in which plant species require this for vital life stages can expedite population decline and result in local extinction (Gill and Bradstock 1995; Keith 1996), and high-frequency fire events may exhaust seed reserves or progressively weaken plants and similarly cause species loss (Keith 1996; Gallagher *et al.* 2021). Fire impacts on habitat for pollinators can also be dramatic, resulting in temporal shifts in fauna populations while recovery occurs, followed by a return to the structural habitat elements required for pollinators (Potts *et al.* 2003; Brown *et al.* 2017; García *et al.* 2018).

Pollination in the woody shrubs and small trees comprising *Banksia* (Proteaceae) appears uncomplicated because of their large and showy inflorescences, highly sought after by nectivorous fauna at peak flowering for their copious nectar. Despite this, several studies have shown low rates of seed production in this genus (Collins and Rebelo 1987), irrespective of high visitation rates by pollinators (Vaughton 1988; Carthew 1993a). Pollination in *Banksia* can be enacted either through vertebrate (mammal, bird) or invertebrate (insects) interactions, including flying (Carthew 1993b; O'Rourke *et al.* 2020) and non-flying mammals (Carpenter 1978; Goldingay *et al.* 1991; Hackett and Goldingay 2001; Wooller and Wooller 2001, 2002, 2003; Thavornkanlapachai *et al.* 2019), and birds (Ramsey 1988; Carthew 1993b; Krauss *et al.* 2009, 2018; Llorens *et al.* 2012). Several *Banksia* species are suspected of being pollinated by multiple faunal groups (Hopper 1980; Evans and Bunce 2000; Wooller and Wooller 2002), with such species commonly being referred to as pollinator-generalists (Saffer 2004). Field observations suggest that birds are the most common visitors to *Banksia* flowers, but in some cases, flower morphology may favour insects (Sedgley *et al.* 1993) over vertebrates, and those emitting strong-scented nectar at anthesis tend to attract mammals (Carpenter 1978; Whelan and Burbidge 1980).

Fire is an important ecological process in the life history of many *Banksia* species, where it is often necessary to promote seed release from an infructescence and permit new recruitment (George 1981; Lamont *et al.* 2007). A long absence of fire may consequently threaten the persistence of such fire-dependent species in an area (Gill and McMahon 1986; Gill and Bradstock 1995; Lamont *et al.* 2007), and to manage for this, an understanding of species-specific seed production and plant longevity is paramount (Gosper *et al.* 2013). Seeds in *Banksia* are either released spontaneously over a short time span ('non-serotinous') or are retained unopened in the crown until fire ('serotinous'). In some cases, differing site conditions in populations of the same species display different levels of serotiny (Whelan *et al.* 1998; Lamont *et al.* 2020), and this can affect habitat-management strategies for different populations of these species.

*Banksia conferta* is a serotinous critically endangered shrub or small tree that in New South Wales (NSW) occurs only in Coorabakh National Park (NSW Scientific Committee 2007). Widely disjunct populations are also present in the Lamington Plateau, Mount Barney and Glasshouse Mountains regions of south-eastern Queensland (George 1981, 1999; Harris *et al.* 2007), where the species is listed as vulnerable under Queensland legislation. Although reportedly non-lignotuberous and likely killed by fire events (George 1999; Griffith 2005), NSW populations are known to resprout from a plate-like lignotuber (Bell 2017), which can develop into a bulbous mass beneath the ground surface. Flowering occurs over winter, with inflorescences opening florets

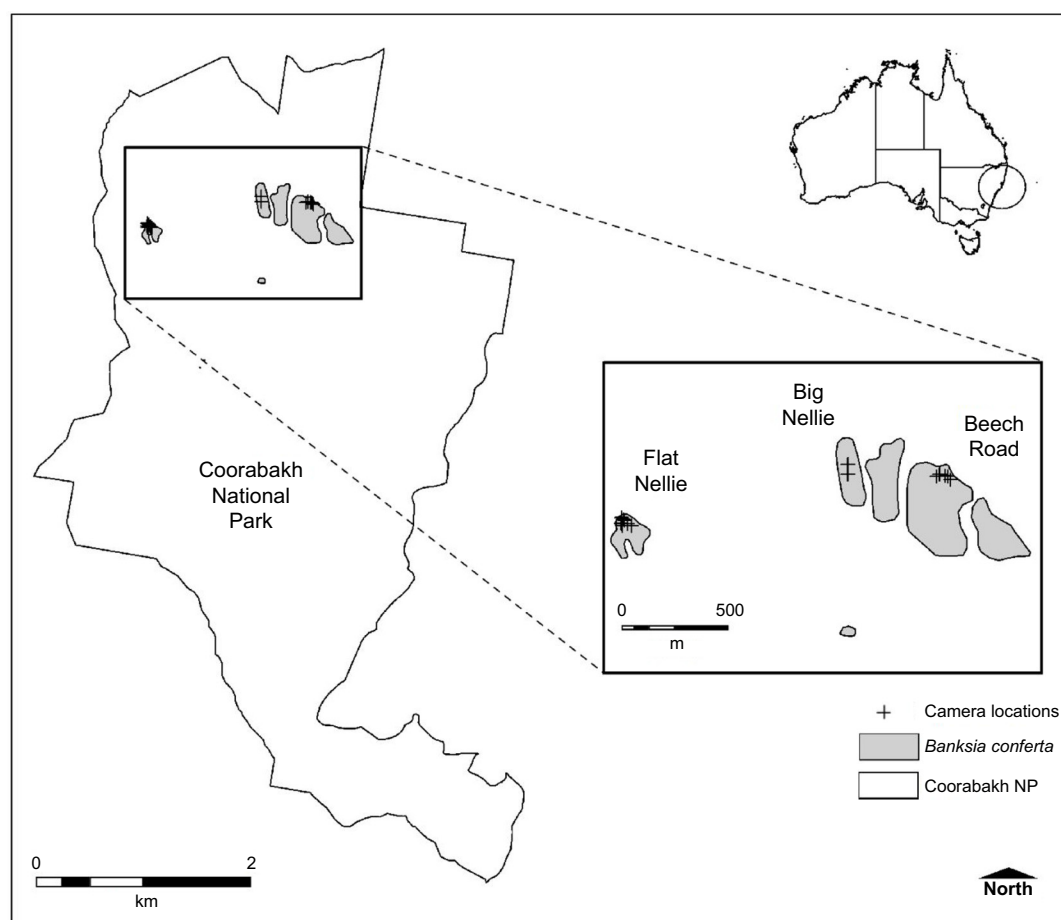
bottom-to-top, and, just prior to anthesis, a strong musky 'wet towel' odour is released (becoming sweeter at anthesis) during prolific flowering events (pers. obs.). Key pollinators in NSW populations are unknown, although Eastern Pygmy Possums are thought to play an important role in Queensland (Harris *et al.* 2007), and, elsewhere, other *Banksia* species are favoured dietary foods of this small arboreal possum (Turner 1984, 1985; Bladon *et al.* 2002; Tulloch and Dickman 2006; Harris *et al.* 2014). *Banksia conferta* flowers possess attributes indicative of vertebrate pollination (Sedgley *et al.* 1993; Ladd *et al.* 1996), and together with the presence of a strong odour at anthesis suggest mammalian pollination to be important.

Previous research hypothesised that for NSW populations of *B. conferta*, an absence of arboreal mammals and their pollinating services in the extensively logged former wood production forests of Coorabakh National Park may explain observed low follicle production (Bell 2017). An absence of records for the Eastern Pygmy Possum and other arboreal possums such as the Feather-tail Glider, Squirrel Glider and Sugar Glider (all known nectar feeders of other *Banksia* spp.) in fauna databases was postulated to correlate with an observed low abundance of the hollow-bearing trees they require (Smith 1973; Harris 2008, 2015). Although numerous records for Sugar Gliders (but few for the other three species) existed for surrounding areas, none was present within Coorabakh National Park. To test this hypothesis (i.e. that low follicle production was due to a dearth of mammalian pollinators), the present study conducted camera-trapping during the 2019 flowering season to document potential pollinators of *B. conferta*. Additionally, data on population size class (as a surrogate for plant age) and follicle presence (a measure of pollination) were examined against fire history to further investigate poor recruitment in this species. Specifically, this research aimed to determine whether an absence of arboreal mammals within flowering *Banksia* stands limits pollination and new recruitment, or, alternatively, whether stand structure as determined by fire history provides a better explanation for low seed production.

## Materials and methods

### Study area

Coorabakh National Park is positioned between the Lansdowne and Comboyne State Forests (part of the Lansdowne Plateau) and lies on the mid-northern coast of New South Wales, approximately 25 km north of the regional town of Taree (Fig. 1). Formerly part of Lansdowne State Forest and including the Big Nellie Flora Reserve, this 1800 ha national park conserves a range of rainforest, wet and dry sclerophyll forests, and minor areas of heath vegetation. Most of the reserve supports tall wet sclerophyll forests of *Eucalyptus pilularis*, *E. agglomerata*, *E. microcorys*, *E. saligna*,



**Fig. 1.** Known stands of *Banksia conferta* within Coorabakh National Park, showing camera locations at Flat Nellie, Big Nellie and Beech Road.

*Lophostemon confertus* and *Syncarpia glomulifera*, with subtropical rainforest dominated by *Ficus* spp., *Dendrocnide excelsa*, *Ceratopetalum apetalum* and *Archontophoenix cunninghamiana* in sheltered gullies (NSW National Parks and Wildlife Service 2007). Habitats supporting *B. conferta* are drier and often constrained to shallow soils on rock substrate (Redpath et al. 2008). A long history of logging has resulted in high volumes of even-aged trees throughout the park, with very few old-growth trees remaining.

The following three populations of *B. conferta* (at 450–480 m elevation) were investigated for potential pollinators: Flat Nellie, Beech Road, and Big Nellie. One of these (Flat Nellie) has shown abundant seed production in recent years, whereas the other two (Big Nellie and Beech Road) have displayed negligible seed production (Bell 2017). Four fire events have affected Coorabakh and populations of *B. conferta* over several decades, during 1957–59, 1963–65, 1990–92 and 2009–10. Study populations were last burnt 11 (Flat Nellie), 56 (Beech Road) and 63 (Big Nellie) years previously (Table 1). On its initial discovery in 2017, the Flat Nellie population was flowering (8 years post-fire),

**Table 1.** Habitat and fire history of study sites.

Location	Habitat	Known fires (type)
Beech Road	Open forest of <i>Eucalyptus agglomerata</i> , <i>E. notabilis</i> , <i>E. oreades</i> , <i>E. pilularis</i>	1964–65 (wildfire)
Big Nellie	Open forest of <i>Eucalyptus agglomerata</i> , <i>E. notabilis</i> , <i>E. pilularis</i>	1957–58 (wildfire)
Flat Nellie	Scrubby heath with scattered <i>Eucalyptus oreades</i> and <i>E. agglomerata</i>	1957–58 (wildfire) 2009–10 (wildfire)

Fire history data from the NSW SEED Portal (<https://www.environment.nsw.gov.au/research-and-publications/seed-data-portal>).

and in 2018 infructescences were recorded on plants from 1 m in height.

### Camera placement

Fourteen motion-detection cameras (Reconyx Hyperfire HC600) were installed within these three stands of *B. conferta* on 30 May 2019, including seven at Flat Nellie, five at Beech Road and two at Big Nellie (Fig. 1). These

focused on between 1 and 4 inflorescences each (nine at Beech Road, four at Big Nellie, 17 at Flat Nellie; 30 in total) and when triggered were programmed to fire three successive images in quick succession (approximately one every second), so that each trigger captured a three-image sequence. All cameras were positioned near *Banksia* inflorescences that were in late bud or had not yet reached full anthesis, to maximise chances of capturing fauna interactions. Most inflorescences within the populations had already attained or passed full anthesis, so targeting the last few remaining inflorescences would likely focus fauna activity here. One consequence of this may be that fauna behaviour observed was not representative of that occurring across the full flowering season; however, focusing survey effort on the last remaining inflorescences would ensure sufficient data capture for analysis.

### ***Banksia* size class, inflorescence density and follicle presence**

Within each site, single randomly placed belt transects (100 × 5 m) were sampled in 2020 (after the completion of camera trapping) to collect data on *Banksia* size classes, past flowering effort and successful production of follicles. To assess size class and past flowering, diameter-at-breast-height (DBH; later aggregated into six size classes) and height (to the nearest 0.5 m) of all individuals within transects were measured, and the numbers of current and old inflorescences on each individual were tallied. If present, seedlings and individuals less than breast height (1.6 m) were included in the lowest size class. Follicle presence was measured separately on 10 randomly selected *Banksia* individuals within each transect (with a required minimum of five inflorescences per individual), by counting the number of old inflorescences (irrespective of age) with and without follicles on each plant, assessed by feeling for protuberances beneath the retained filaments. In this context, follicle presence was used as an indicator of successful seed production, but the number of follicles per infructescence was not recorded and no attempt was made to quantify the seedbank.

### **Data analysis**

Camera-capture data were viewed on-screen to detect fauna interactions. All interactions were tabulated against date and time, and whether clear interest was shown in the target inflorescences (recorded as a 'probe'). Separate interactions within a short time period were differentiated if images captured the subject animal leaving or approaching the target; uncertain movements potentially comprising a single visit were combined and recorded as a single interaction. Univariate statistics were used to determine the most frequent faunal visitors for each site and to assess *Banksia* density, whereas a linear regression assessed *Banksia* structure (testing whether height could predict girth) and inflorescence abundance (testing whether height or girth could predict

flowering). An independent measures ANOVA was used to test for significance in relative follicle production among the three populations, with Tukey's HSD *post hoc* test being used to examine pair-wise comparisons.

## **Results**

### **Camera monitoring**

Cameras were triggered 691 times by fauna (3% of all images); all other images were presumably in response to wind events. Total fauna-triggered image spans varied for each camera, from 23 to 146 days ( $\bar{x}$  = 67, std = 51), and four cameras returned no fauna images. Although Camera 1 at Flat Nellie commenced recording on the 30 May 2019, it was a month later before the first fauna-triggered image was captured, and all collection finished in that camera by the 22 July. Three cameras (Camera 2 at Flat Nellie, and Cameras 10 and 11 at Beech Road) captured fauna interactions over a total period of 133 and 146 days. The months of June and July were the most active for interactions, corresponding to peak flowering in *B. conferta*, with the last fauna interactions on 24 October 2019.

### **Fauna visitation**

Six mammal and 10 bird species were captured interacting with *B. conferta* plants, with 10 species seen to probe inflorescences (Table 2). White-cheeked Honeyeaters and Sugar Gliders combined comprised 66% of all fauna interactions ( $n$  = 691), and of all 400 *Banksia* probes, 45% were from White-cheeked Honeyeaters and 18% from Sugar Gliders. Six fauna species (one mammal, five birds) interacted with inflorescences but did not probe flowers. Highest activity was seen at Flat Nellie (188 bird and 75 mammal probes), followed by Beech Road (77 bird, 77 mammal) and then Big Nellie (0 birds, 18 mammals).

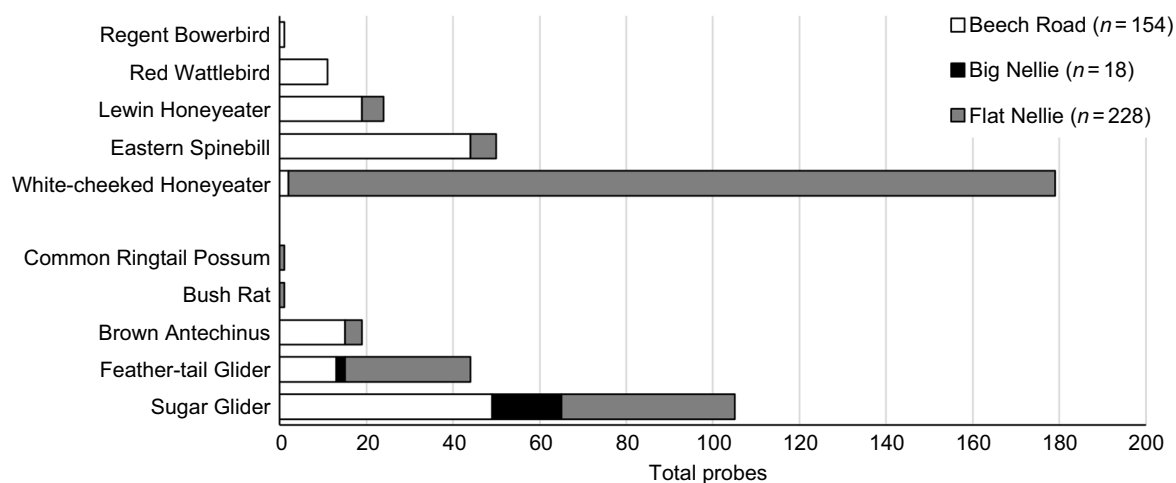
The three survey sites differed in the dominant fauna foragers (Fig. 2). White-cheeked Honeyeaters clearly dominated captures and probes at Flat Nellie (although predominantly at Camera 5, presumably because of a superior flowering effort here), whereas this species was virtually non-existent at both Beech Road (two probes) and Big Nellie (absent). At Beech Road, two species (Sugar Glider and Eastern Spinebill) comprised the bulk of all probes, and this site supported the greatest diversity of fauna foragers (nine species). Only two species were detected at Big Nellie, with the Sugar Glider comprising almost all interactions, but no birds were recorded.

### ***Banksia* size class**

Flat Nellie ( $n$  = 353; 7060 plants/ha) supported more than double the density of *Banksia* than did Beech Road ( $n$  = 73;

**Table 2.** Mammal and bird species interactions and probes with *Banksia conferta*.

Group	Species		Interactions	Probes
Mammals	Sugar Glider	<i>Petaurus breviceps</i>	179	70
	Feather-tail Glider	<i>Acrobates pygmaeus</i>	63	44
	Brown Antechinus	<i>Antechinus stuartii</i>	30	19
	Bush Rat	<i>Rattus fuscipes</i>	15	1
	Common Ringtail Possum	<i>Pseudocheirus peregrinus</i>	1	1
	Swamp Wallaby	<i>Wallabia bicolor</i>	10	–
Birds	White-cheeked Honeyeater	<i>Phylidonyris niger</i>	280	179
	Eastern Spinebill	<i>Acanthorhynchus tenuirostris</i>	60	50
	Lewin's Honeyeater	<i>Meliphaga lewinii</i>	32	24
	Red Wattlebird	<i>Anthochaera carunculata</i>	12	11
	Regent Bowerbird	<i>Sericulus chrysocephalus</i>	2	1
	White-browed Scrubwren	<i>Sericornis frontalis</i>	2	–
	Australian King Parrot	<i>Alisterus scapularis</i>	2	–
	Satin Bowerbird	<i>Ptilonorhynchus violaceus</i>	1	–
	Yellow-tailed Black Cockatoo	<i>Calyptrorhynchus funereus</i>	1	–
	Variegated Blue Wren	<i>Malurus lamberti</i>	1	–
Total			691	400

**Fig. 2.** Fauna captured probing *Banksia* across Beech Road, Flat Nellie and Big Nellie.

1460 plants/ha) and Big Nellie ( $n = 74$ ; 1480 plants/ha) combined. Four *Banksia* individuals at Flat Nellie attained a maximum height of 3 m (mean 1.56 m  $\pm$  s.e. 0.03), whereas at both Beech Road (mean 4.77 m  $\pm$  s.e. 0.16) and Big Nellie (mean 4.20 m  $\pm$  s.e. 0.20), the largest individuals reached 7 m (seven and six individuals respectively). There were differences in *Banksia* height and girth at all sites (Table 3), and linear regression identified significant relationships predicting girth from height within all three; strong relationships were evident at Beech Road ( $R^2 = 0.68$ ,  $F(1,71) = 147.94$ ,  $P < 0.001$ ;  $y = -1.4536 + 1.3537x$ ) and Big Nellie ( $R^2 = 0.79$ ,  $F(1,72) = 273.11$ ,  $P < 0.001$ ;

$y = -1.4766 + 1.4215x$ ), but a moderate relationship only occurred at Flat Nellie ( $R^2 = 0.33$ ,  $F(1,351) = 171.52$ ,  $P < 0.001$ ;  $y = -0.6843 + 0.9076x$ ). The latter result may be attributed to sampling issues relating to the smaller size of plants at this site, and/or differing habitat conditions (open heath/low woodland vs open forest). Collectively, linear regression on inflorescence presence (current and old) with *Banksia* size found a strong predictive relationship with girth ( $R^2 = 0.60$ ,  $F(1,498) = 735.04$ ,  $P < 0.001$ ;  $y = -3.8236 + 6.7845x$ ), but only a moderate predictive relationship with height ( $R^2 = 0.47$ ,  $F(1,498) = 447.57$ ,  $P < 0.001$ ;  $y = -12.1222 + 8.7893x$ ).



**Table 3.** Variation in *Banksia* height and DBH across all sites.

Site	Years post-fire	n	Attribute	$\bar{x}$	Min.	Max.	s.e.
Beech Road	56	73	Height (m)	4.77	1.5	7	0.16
			DBH (cm)	5.00	0.32	11.78	0.26
Big Nellie	63	74	Height (m)	4.20	1	7	0.20
			DBH (cm)	4.50	0.32	10.51	0.32
Flat Nellie	11	353	Height (m)	1.56	0.3	3	0.03
			DBH (cm)	0.73	0.32	3.82	0.05

Structurally, the three *Banksia* populations displayed differing proportions of large and small individuals as determined through DBH data, reflecting fire history (Fig. 3). Beech Road supported a diverse profile of many individuals in the 2.1–8 cm DBH classes, but with limited numbers in smaller and larger classes. Flat Nellie supported no individuals >4 cm DBH, and presumably any larger standing individuals that may have remained after the wildfire in 1957–58 were consumed during the more recent fire in 2009–10. Big Nellie supported 89% of individuals within the 0–8 cm classes, suggesting that either a more recent recruitment event may have occurred well after the 1957–58 fire event, or, more likely, that resprouts from subsurface roots of larger individuals influenced size distribution in the data. Resprouting is previously unknown for *B. conferta* (discussed later) and was noted only at Big Nellie but may have also occurred at the other two populations, limiting interpretation of the structural profiles for each population.

**Follicle production and fire history**

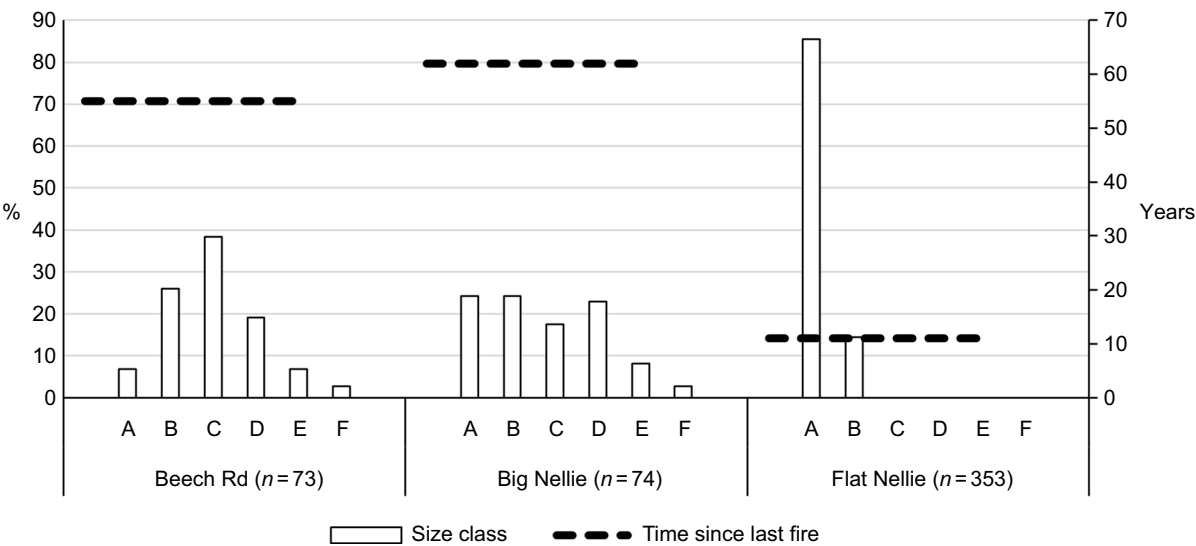
The collective number of infructescences with follicles compared with those without across 10 *Banksia* individuals

in each population at Beech Road (63 with, 154 without) and Big Nellie Road (78 with, 203 without) contrasted with those at Flat Nellie (110 with, 58 without). Relative follicle production differed among the three populations ( $F = 10.05$ ,  $P < 0.001$ ; Fig. 4), and Tukey’s HSD test identified significant differences between Flat Nellie with Beech Road ( $Q = 5.29$ ,  $P = 0.003$ ), and Flat Nellie and Big Nellie ( $Q = 5.67$ ,  $P = 0.001$ ). There was no significant difference in follicle presence between Beech Road and Big Nellie. The Flat Nellie *Banksia* population (last burnt 11 years ago) produced more fertile infructescences than did either of the other two populations (burnt 55 and 62 years previously), and although available data are scant, there is a trend suggestive of reduced reproductive output with time.

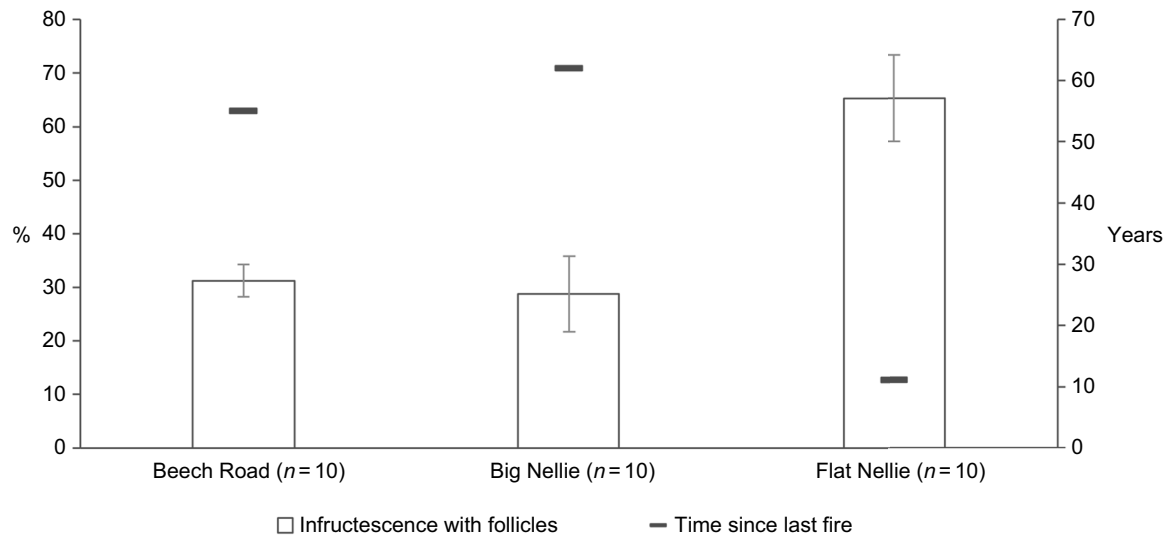
**Discussion**

**Potential pollinators**

The hypothesis that an absence or low density of arboreal mammals within flowering *Banksia* stands at Coorabakh was limiting pollination opportunities was not supported in



**Fig. 3.** Population size distribution of *Banksia conferta* relative to last fire event: A = 0.0–2.0 cm; B = 2.1–4.0 cm; C = 4.1–6.0 cm; D = 6.1–8.0 cm; E = 8.1–10.0 cm; F = 10.1–12.0 cm. Size classes relate to diameter at breast height.



**Fig. 4.** Mean percentage infructescences with follicles on 10 *Banksia* individuals at each site, showing standard errors and time since last fire.

this study. Two of four postulated pollinating mammals (Feather-tail Glider and Sugar Glider) were detected at all three sites investigated. Sugar Gliders were dominant at Big Nellie, and this species (and Eastern Spinebill) was equally dominant at Beech Road. Additionally, Bush Rats and Common Ringtail Possums (both Flat Nellie), and Brown Antechinus (Beech Road) were (rarely) captured visiting inflorescences. Five bird species (White-cheeked Honeyeater, Eastern Spinebill, Lewin's Honeyeater, Red Wattlebird and Regent Bowerbird) were observed probing inflorescences, with White-cheeked Honeyeaters predominating in the only stand consistently producing infructescences (Flat Nellie). Very few instances of invertebrates foraging on flowers were captured by cameras, with ants and moths noted on <10 occasions; however, cameras were not set to target this fauna group. Given the range of faunal visitors, *B. conferta* is likely to be a pollinator-generalist (see Saffer 2004), with birds (and particularly White-cheeked Honeyeater) operating as the key species during the day and small mammals (particularly Sugar Glider) at night. Morphological features of pollen presenters and styles in *B. conferta* (George 1981) are also indicative of a species likely to be pollinated by vertebrates; rigid styles are a trait adapted to vertebrate pollination, particularly in the role this rigidity plays in forcing pollen entry into the pollination chamber via the stigmatic groove (Sedgley *et al.* 1993; Ladd *et al.* 1996).

White-cheeked Honeyeaters have been implicated in the pollination of other *Banksia* species elsewhere (Collins and Spice 1986; Dalgleish 1999); however, in some areas pollen transfer via this species appears limited. For example, Hackett and Goldingay (2001) found only low pollen loads of *Banksia ericifolia* and *B. integrifolia* on White-cheeked Honeyeaters in comparison to Silvereyes (*Zosterops lateralis*), suggesting that on the NSW northern coast this honeyeater

was not an important pollinator for those species. A similar trend was found by Paton and Turner (1985) for *Banksia ericifolia* near Sydney. In Western Australia, Hopper (1980) observed that New Holland Honeyeaters (*Phylidonyris novaehollandiae*) carried considerably more pollen from *Banksia occidentalis* than did White-cheeked Honeyeaters, but concluded that this was perhaps related to territorial and aggressive interactions between these two species.

At Coorabakh, Eastern Spinebill foraged predominantly at the Beech Road site where White-cheeked Honeyeaters were rare. At this location, this species dominated diurnal visitation to *B. conferta*, but nocturnal visitation by Sugar Gliders was equally important. Eastern Spinebill is low in the hierarchy of foraging guilds (Ford 1979; Ford and Paton 1982), and other studies have inferred that spinebills (Eastern and Western) avoid feeding in *Banksia* stands dominated by larger honeyeaters (Hopper 1980; Newland and Wooller 1985; Paton and Turner 1985; Armstrong 1991). The presence of a resident population of White-cheeked Honeyeaters at Flat Nellie is, therefore, likely to competitively exclude extensive foraging of *B. conferta* by Eastern Spinebill at that location. The dominance of White-cheeked Honeyeaters at Flat Nellie, and its absence or low abundance at both Big Nellie and Beech Road, may reflect resource availability. At Flat Nellie, *Banksia* densities of 7060 plants per hectare are substantially greater than the 1460–1480 plants per hectare at Beech Road and Big Nellie respectively. This represents a considerable contrast in nectar resource availability, and it is possible that insufficient nectar at Beech Road and Big Nellie may preclude a resident population of White-cheeked Honeyeaters persisting in these areas. Such a situation was reported by Ford and Pursey (1982), who found Eastern Spinebills to be the most abundant honeyeater at their site in north-eastern NSW and

suggested that perhaps the available nectar supply was inadequate to maintain larger species there.

The Eastern Pygmy Possum is thought to be an important pollinator of *B. conferta* in Queensland (Harris *et al.* 2007), and *Banksia* pollen forms a major dietary component in this species (van Tets and Whelan 1997). The lack of captures of Eastern Pygmy Possums at any site in the Coorabakh stands of *B. conferta* (even in the recently burnt Flat Nellie site) suggests this species to be of low importance here, pollination being effected primarily by other species. However, low rates of capture of Eastern Pygmy Possums in surveys and seasonal variations in abundance mean that population densities are often under-estimated (Harris and Goldingay 2005; Goldingay and Keohan 2017), and there remains the possibility that this species may still frequent the area. Other arboreal mammals captured in the present study are also known feeders and potential pollinators of *Banksia* species (see Goldingay *et al.* 1991; Carthew 1993b; Hackett and Goldingay 2001; O'Rourke *et al.* 2020), although none has been reported feeding on *B. conferta*. Brown Antechinus and Bush Rat have occasionally been recorded frequenting *Banksia* flowers (Goldingay *et al.* 1987; van Tets and Whelan 1997; Goldingay 2000); however, this does not seem to be widespread (see Watts and Braithwaite 1978; Hall 1980; Fox and Archer 1984; Carron *et al.* 1990; Gray *et al.* 2016). Although primarily a ground-dwelling mammal, Bush Rats have been observed foraging for food and nectar at heights of up to 4 m (Carpenter 1978; O'Rourke *et al.* 2020); so, the single record of this species probing *B. conferta* flowers at Coorabakh is not unusual.

### Stand structure and follicle production

The three stands of *B. conferta* at Coorabakh display different size classes consistent with older (Beech Road, Big Nellie) and younger (Flat Nellie) populations, although during data collection it was discovered that *B. conferta* is capable of resprouting from lateral subsurface roots when older individuals are dying or are under severe stress (discussed later). This may have affected categorisation of a small component of the younger cohort of individuals, particularly when assessing older dead individuals at Big Nellie; however, we have no way to retrospectively ascertain the extent of this. Despite this, the strong correlation between plant height and DBH evident in the older stands was not replicated at the younger stand. Significantly more individuals were present at Flat Nellie than at Beech Road or Big Nellie, with this site supporting nearly five times the number of plants of the other two. As noted earlier, such high densities of *Banksia* may well determine the pollinator composition present at a site, in this case allowing White-cheeked Honeyeaters to dominate the area.

Follicle production was significantly greater at Flat Nellie than at Beech Road and Big Nellie and could be aligned with

fire history. Incidental observations of follicles on older plants at Beech Road and Big Nellie showed many to have been in a decayed state, implying that any seed contained therein may be inviable. This has implications on future recruitment, particularly in long-unburnt stands that are poorly serviced by pollinators and where new seed production is consequently limited. These plants may ultimately reach a point where low attention by pollinators restricts input into the canopy seed bank, and the species is lost from that area on the death of standing individuals.

### Inter-fire recruitment and asexual reproduction

Very few true seedlings (<20 cm high) have been observed within stands of *B. conferta* at Coorabakh, and those that are present rarely seem to persist for long. This trait has been reported in other *Banksia* species and is representative of serotinous species that release seed predominantly after fire. Enright *et al.* (1996) found that no seedlings of *Banksia hookeriana* establishing between fire events survived for more than 1 year, likely being due to competition with other plants. For *B. conferta*, no seedlings were recorded within study transects, but scattered individuals elsewhere in the populations suggest that sporadic establishment does occur. Assuming that some of these seedlings do persist, distinguishing them from resprouts emanating via subsurface roots is difficult without careful excavation. During data collection, it was noted at Big Nellie that resprouts from roots were associated predominantly with older trees. These suckering resprouts (~1 m high) may be a response to water stress or non-fire-related tree damage, given that fire has been absent from this site for 62 years; however, this is unclear.

The suckering habit from lateral roots is rare in the *Banksia* genus, with *B. elegans*, *B. paludosa* and certain forms of *B. marginata* and *B. integrifolia* being examples of the few known (George 1981). He *et al.* (2011) suggested that such clonality via suckering is an advanced growth trait in *Banksia* and allows individuals to persist through drought and fire for up to 1000 years. For the functionally sterile *Banksia elegans*, Lamont (1988) found the suckering habit to be significant in persistence and spread after fire, although subsequent post-fire flowering relied on epicormic recovery of larger plants and medium-sized individuals resprouting from lignotubers, with limited flowering in suckers. In the context of the present study, it is plausible that, like in *Banksia elegans*, recovery from fire in *B. conferta* is aided by both a lignotuber and suckering resprouts from subsurface lateral roots; however, it is yet to be determined how important seedling recruitment post-fire is in this species. Both flowering and fruiting were more abundant at the most recently burnt Flat Nellie site than at Beech Road or Big Nellie, suggesting that seed-bank development is more likely to occur here than at the two other sites, which are currently persisting primarily through asexual reproduction.



## Lack of fire and implications

A substantially variable at the sites examined during this study is fire history and how it influences stand structure, floristic composition, and habitat. Flat Nellie, the only site where abundant follicles have been produced in recent years, has burnt twice in recorded history, namely, 63 and 11 years ago. In contrast, Beech Road and Big Nellie last burnt 56 and 63 years ago respectively, and the current individuals at those two sites are now of considerable age. The more recent fire at Flat Nellie explains the prevalence of *Banksia* individuals of shorter stature (presumably all new germinants, but possibly also older resprouted individuals from lignotubers and/or lateral root suckers), and it is likely that better flowering and fruiting has occurred here because plants (or ramets) are younger. Elapsed time since fire and its influence on flowering and fruiting can differ in resprouting versus fire-sensitive *Banksia* species (e.g. most seed production in the resprouting *Banksia oblongifolia* occurred <10 years versus mostly >16 years in the fire-sensitive *Banksia ericifolia*; Zammit and Westoby 1987; and see Gill and McMahon 1986; Enright *et al.* 1996; McCaw 2008). For *B. conferta*, time to first flowering at Flat Nellie was observed to be 8 years, possibly shorter, and such a timeframe fits the model of other resprouting species.

Fire plays a major role in the ecology of seed release in many *Banksia* species (Lamont *et al.* 2007; Huss *et al.* 2019). Queensland populations of *B. conferta* are reportedly serotinous (George 1981), releasing seeds from the canopy only after a fire event. The very few seedlings and numerous closed follicles observed at Coorabakh in recent years suggest that these populations also display this trait. Serotiny can be variable within a species and reflect environmental conditions (Cowling and Lamont 1985; Whelan *et al.* 1998; Lamont *et al.* 2020), but, nevertheless, it compromises persistence in some species when fire is excluded from a population for extended periods of time (Lamont *et al.* 2007). For example, Gill and McMahon (1986) estimated the viable canopy seed store of *Banksia ornata* to increase with stand age up to 38 years post-fire, but declined by 50 years owing to dieback and senescence. There is currently no data on the collective number of infructescences and viable seed store within the canopy of *B. conferta* populations, but it is plausible that many hundreds or thousands of seeds may be present. Data from this study found a total of 665 old and current inflorescences on 30 plants across all three populations; however, only 251 of these had follicles developed (no counts of viable seeds per infructescence were undertaken). Despite this, the absence of fire from both Beech Road and Big Nellie populations for over 55 years remains a concern, and with observations reported here of low follicle production (despite the presence of pollinators) and decaying older follicles, it seems likely that little new recruitment will occur without intervention. Fortunately, the ability of this species to resprout from lignotubers and subsurface roots

should ensure persistence through drought and other stressors while awaiting fire.

Deriving appropriate fire prescriptions is difficult for many ecosystems and target species (Gosper *et al.* 2013), and these can vary across different landscapes. The results from this study suggest that a fire (prescribed or wildfire) in one or both of Beech Road and Big Nellie will be beneficial to rejuvenate habitat and promote germination of those viable seeds that remain in the canopy before further follicle decay occurs. Importantly, this should be followed by a fire-free interval of perhaps 10 years to allow maturation and restoration of the canopy seed store. Smith *et al.* (2021) highlighted how short intervals between fires threaten the ability of this species to mature and produce seed in Queensland. However, at the Coorabakh populations, lack of fire, at least initially, appears to be constraining replenishment of the population, but fires in quick succession, which restricts seed development, will remain a threat to this species.

Ongoing studies into the ecology and viability of pollination and seed development in *B. conferta* are also needed to further inform management of this species. Pollination in *Banksia* is typically low across the genus (Collins and Rebelo 1987; Goldingay and Carthew 1998), and in part this is due to the inactivity and inconsistency of pollinators (Copland and Whelan 1989). Controlled pollination studies (e.g. Collins and Spice 1986; Ramsey 1988) aimed at identifying limitations to pollination would be informative in this regard. Seed production is highly variable over most species, and poor follicle development can follow copious flowering events across individuals and populations, with few clear reasons (Vaughton 1988; Carthew 1993a). Successful fruit set as low as 0.92–1.77% has been reported for *Banksia spinulosa* (Carthew 1993a), but up to 9.5% for *B. neoanglica* (Vaughton 1988), and the average fruit set across 15 species was found to be just 2.5% by Collins and Rebelo (1987). Gaining an understanding of seed production and expected rates of fruit set in *B. conferta* will assist future management of this species after fire events.

## References

- Armstrong DP (1991) Aggressiveness of breeding territorial honeyeaters corresponds to seasonal changes in nectar availability. *Behavioral Ecology and Sociobiology* **29**, 103–111. doi:10.1007/BF00166484
- Bell S (2017) New insights into the ecology of the critically endangered '*Banksia conferta*' (Proteaceae) from the mid-north coast of NSW. *Australasian Plant Conservation* **26**, 15–18. Available at <https://search.informit.org/doi/10.3316/informit.178254394062662>
- Bladon RV, Dickman CR, Hume ID (2002) Effects of habitat fragmentation on the demography, movements and social organisation of the eastern pygmy-possum (*Cercartetus nanus*) in northern New South Wales. *Wildlife Research* **29**, 105–116. doi:10.1071/WR01024
- Brown J, York A, Christie F, McCarthy M (2017) Effects of fire on pollinators and pollination. *Journal of Applied Ecology* **54**, 313–322. doi:10.1111/1365-2664.12670
- Carbone LM, Tavella J, Pausas JG, Aguilar R (2019) A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography* **28**, 1487–1498. doi:10.1111/geb.12939

- Carpenter FL (1978) Hooks for mammal pollination? *Oecologia* **35**, 123–132. doi:10.1007/BF00344725
- Carron PL, Happold DCD, Bubela TM (1990) Diet of two sympatric Australian subalpine rodents, *Mastacomys fuscus* and *Rattus fuscipes*. *Australian Wildlife Research* **17**, 479–489. doi:10.1071/WR9900479
- Carthew SM (1993a) Patterns of flowering and fruit production in a natural-population of *Banksia spinulosa*. *Australian Journal of Botany* **41**, 465–480. doi:10.1071/BT9930465
- Carthew SM (1993b) An assessment of pollinator visitation to *Banksia spinulosa*. *Australian Journal of Ecology* **18**, 257–268. doi:10.1111/j.1442-9993.1993.tb00453.x
- Collins BG, Rebelo T (1987) Pollination biology of the Proteaceae in Australia and southern Africa. *Australian Journal of Ecology* **12**, 387–421. doi:10.1111/j.1442-9993.1987.tb00958.x
- Collins BG, Spice J (1986) Honeyeaters and the pollination biology of *Banksia prionotes* (Proteaceae). *Australian Journal of Botany* **34**, 175–185. doi:10.1071/BT9860175
- Copland BJ, Whelan RJ (1989) Seasonal variation in flowering intensity and pollination limitation of fruit set in four co-occurring *Banksia* species. *Journal of Ecology* **77**, 509–523. doi:10.2307/2260766
- Cowling RM, Lamont BB (1985) Variation in serotiny of three *Banksia* species along a climatic gradient. *Australian Journal of Ecology* **10**, 345–350. doi:10.1111/j.1442-9993.1985.tb00895.x
- Dalgleish E (1999) Effectiveness of invertebrate and vertebrate pollinators and the influence of pollen limitation and inflorescence position on follicle production of *Banksia aemula* (family Proteaceae). *Australian Journal of Botany* **47**, 553–562. doi:10.1071/BT97070
- Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N, Fensham R, Friend G, Gill M, James S, Kay G, Keith DA, MacGregor C, Russell-Smith J, Salt D, Watson JEM, Williams RJ, York A (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928–1939. doi:10.1016/j.biocon.2010.05.026
- Enright NJ, Lamont BB, Marsula R (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *Journal of Ecology* **84**, 9–17. doi:10.2307/2261695
- Evans KM, Bunce A (2000) A comparison of the foraging behaviour of the eastern pygmy-possum (*Cercartetus nanus*) and nectarivorous birds in a *Banksia integrifolia* woodland. *Australian Mammalogy* **22**, 81–86. doi:10.1071/AM00081
- Ford HA (1979) Interspecific competition in Australian honeyeaters: depletion of common resources. *Australian Journal of Ecology* **4**, 145–164. doi:10.1111/j.1442-9993.1979.tb01205.x
- Ford HA, Paton DC (1982) Partitioning of nectar sources in an Australian honeyeater community. *Australian Journal of Ecology* **7**, 149–159. doi:10.1111/j.1442-9993.1982.tb01588.x
- Ford HA, Pursey JF (1982) Status and feeding of the Eastern Spinebill *Acanthorhynchus tenuirostris* at New England National Park, north-eastern NSW. *Emu - Austral Ornithology* **82**, 203–211. doi:10.1071/MU9820203
- Fox BJ, Archer E (1984) The diets of *Sminthopsis murina* and *Antechinus stuartii* (Marsupialia: Dasyuridae) in sympatry. *Australian Wildlife Research* **11**, 235–248. doi:10.1071/WR9840235
- Gallagher RV, Allen S, Mackenzie BDE, et al. (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
- García Y, Castellanos MC, Pausas JG (2018) Differential pollinator response underlies plant reproductive resilience after fires. *Annals of Botany* **122**(6), 961–971. doi:10.1093/aob/mcy122
- George AS (1981) The genus *Banksia* L.f. (Proteaceae). *Nuytsia* **3**, 239–473. Available at <https://biostor.org/reference/217708>
- George AS (1999) *Banksia* (Proteaceae). In 'Flora of Australia. Vol. 17B'. (Ed. A Wilson) pp. 175–251 (ABRS/CSIRO Australia: Melbourne, Vic., Australia) Available at <https://www.dcceew.gov.au/sites/default/files/env/pages/6d8c5c3b-8545-437e-b9b3-944ac95ee07a/files/flora-australia-17b-proteaceae-3-hakea-dryandra.pdf>
- Gill AM, Bradstock R (1995) Extinction of biota by fires. In 'Conserving biodiversity: threats and solutions'. (Eds R Bradstock, T Auld, D Keith, R Kingsford, D Lunney, D Sivertsen) pp. 309–322. (Surrey Beatty and Sons: Sydney, NSW, Australia) Available at <http://hdl.handle.net/102.100.100/233144?index=1>
- Gill AM, McMahon A (1986) A postfire chronosequence of cone, follicle and seed production in *Banksia ornata*. *Australian Journal of Botany* **34**, 425–433. doi:10.1071/BT9860425
- Goldingay RL (2000) Small dasyurid marsupials: are they effective pollinators? *Australian Journal of Zoology* **48**, 597–606. doi:10.1071/ZO00015
- Goldingay RL, Carthew SM (1998) Breeding and mating systems of Australian Proteaceae. *Australian Journal of Botany* **46**, 421–437. doi:10.1071/BT97037
- Goldingay RL, Keohan J (2017) Population density of the eastern pygmy-possum in a heath-woodland habitat. *Australian Journal of Zoology* **65**, 391–397. doi:10.1071/ZO18026
- Goldingay RL, Carthew SM, Whelan RJ (1987) Transfer of *Banksia spinulosa* pollen by mammals: implications for pollination. *Australian Journal of Zoology* **35**, 319–325. doi:10.1071/ZO9870319
- Goldingay RL, Carthew SM, Whelan RJ (1991) The importance of non-flying mammals in pollination. *Oikos* **61**, 79–87. doi:10.2307/3545409
- Gosper CR, Prober SM, Yates CJ (2013) Estimating fire interval bounds using vital attributes: implications of uncertainty and among-population variability. *Ecological Applications* **23**, 924–935. doi:10.1890/12-0621.1
- Gray EL, Burwell CJ, Baker AM (2016) Benefits of being a generalist carnivore when threatened by climate change: the comparative dietary ecology of two sympatric semelparous marsupials, including a new endangered species (*Antechinus arktos*). *Australian Journal of Zoology* **64**, 249–261. doi:10.1071/ZO16044
- Griffith SJ (2005) *Banksia conferta* subsp. *conferta* in Coorabakh National Park: Preliminary observations and guidelines for fire management. Unpublished Report to Manning Area of the Parks and Wildlife Division, Department of Environment and Conservation.
- Hackett DJ, Goldingay RL (2001) Pollination of *Banksia* spp. by non-flying mammals in north-eastern New South Wales. *Australian Journal of Botany* **49**, 637–644. doi:10.1071/BT00004
- Hall S (1980) The diets of two coexisting species of *Antechinus* (Marsupialia: Dasyuridae). *Australian Wildlife Research* **7**, 365–378. doi:10.1071/WR9800365
- Harris JM (2008) *Cercartetus nanus* (Diprotodontia: Burramyidae). *Mammalian Species* **815**, 1–10. doi:10.1644/815.1
- Harris JM (2015) *Acrobates pygmaeus* (Diprotodontia: Acrobatidae). *Mammalian Species* **47**, 32–44. doi:10.1093/mspecies/sev003
- Harris JM, Goldingay RL (2005) Detection of the eastern pygmy-possum *Cercartetus nanus* (Marsupialia: Burramyidae) at Barren Grounds Nature Reserve, New South Wales. *Australian Mammalogy* **27**, 85–88. doi:10.1071/AM05085
- Harris JM, Gynther IC, Eyre TJ, Goldingay RL, Mathieson MT (2007) Distribution, habitat and conservation status of the eastern pygmy-possum *Cercartetus nanus* in Queensland. *Australian Zoologist* **34**, 209–221. doi:10.7882/AZ.2007.020
- Harris JM, Goldingay RL, Brooks LO (2014) Population ecology of the eastern pygmy-possum (*Cercartetus nanus*) in a montane woodland in southern New South Wales. *Australian Mammalogy* **36**, 212–218. doi:10.1071/AM13044
- He T, Lamont BB, Downes KS (2011) *Banksia* born to burn. *New Phytologist* **191**, 184–196. doi:10.1111/j.1469-8137.2011.03663.x
- Hopper SD (1980) Bird and mammal pollen vectors in *Banksia* communities at Cheyne Beach, Western Australia. *Australian Journal of Botany* **28**, 61–75. doi:10.1071/BT9800061
- Huss JC, Fratzl P, Dunlop JWC, Merritt DJ, Miller BP, Eder M (2019) Protecting offspring against fire: lessons from *Banksia* seed pods. *Frontiers in Plant Science* **10**, 283. doi:10.3389/fpls.2019.00283
- Keith D (1996) Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. *Proceedings of the Linnean Society of NSW* **116**, 37–78. Available at <https://biostor.org/reference/68152>
- Krauss SL, He T, Barrett LG, Lamont BB, Enright NJ, Miller BP, Hanley ME (2009) Contrasting impacts of pollen and seed dispersal on spatial genetic structure in the bird-pollinated *Banksia hookeriana*. *Heredity* **102**, 274–285. doi:10.1038/hdy.2008.118
- Krauss SL, Roberts DG, Phillips RD, Edwards C (2018) Effectiveness of camera traps for quantifying daytime and nighttime visitation by vertebrate pollinators. *Ecology and Evolution* **8**, 9304–9314. doi:10.1002/ece3.4438

- Ladd PG, Alkema AJ, Thomson GJ (1996) Pollen presenter morphology and anatomy in *Banksia* and *Dryandra*. *Australian Journal of Botany* **44**, 447–471. doi:10.1071/BT960447
- Lamont BB (1988) Sexual versus vegetative reproduction in *Banksia elegans*. *Botanical Gazette* **149**, 370–375. doi:10.1086/337728
- Lamont BB, Enright NJ, Witkowski ETF, Groeneveld J (2007) Conservation biology of banksias: insights from natural history to simulation modelling. *Australian Journal of Botany* **55**, 280–292. doi:10.1071/BT06024
- Lamont BB, Pausas JG, He T, Witkowski ETF, Hanley ME (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
- Llorens TM, Byrne M, Yates CJ, Nistelberger HM, Coates DJ (2012) Evaluating the influence of different aspects of habitat fragmentation on mating patterns and pollen dispersal in the bird-pollinated *Banksia sphaerocarpa* var. *caesia*. *Molecular Ecology* **21**, 314–328. doi:10.1111/j.1365-294X.2011.05396.x
- McCaw L (2008) Variation in age to first flowering and fruiting of *Banksia baxteri* and *Banksia coccinea* at the Stirling Range, south-western Australia. *Journal of the Royal Society of Western Australia* **91**, 269–273. Available at [https://www.rswa.org.au/publications/Journal/91\(4\)/VOL%2091%20PT%204%20269-273.pdf](https://www.rswa.org.au/publications/Journal/91(4)/VOL%2091%20PT%204%20269-273.pdf)
- McLauchlan KK, Higuera PE, Miesel J, et al. (2020) Fire as a fundamental ecological process: research advances and frontiers. *Journal of Ecology* **108**, 2047–2069. doi:10.1111/1365-2745.13403
- Newland CE, Wooller RD (1985) Seasonal changes in a honeyeater assemblage in *Banksia* woodland near Perth, Western Australia. *New Zealand Journal of Zoology* **12**, 631–636. doi:10.1080/03014223.1985.10428312
- NSW National Parks and Wildlife Service (2007) Coorabakh National Park plan of management. NSW National Parks and Wildlife Service, Department of Environment and Climate Change NSW, Australia.
- NSW Scientific Committee (2007) *Banksia conferta* A.S. George subsp. *conferta*: critically endangered species listing. Final Determination. Available at <https://www.environment.nsw.gov.au/Topics/Animals-and-plants/Threatened-species/NSW-Threatened-Species-Scientific-Committee/Determinations/Final-determinations/2004-2007/Banksia-conferta-A-S-George-subsp-conferta-critically-endangered-species-listing>
- O'Rourke RL, Anson JR, Saul AM, Banks PB (2020) Limits to alien black rats (*Rattus rattus*) acting as equivalent pollinators to extinct native small mammals: the influence of stem width on mammal activity at native *Banksia ericifolia* inflorescences. *Biological Invasions* **22**, 329–338. doi:10.1007/s10530-019-02090-x
- Paton DC, Turner V (1985) Pollination of *Banksia ericifolia* Smith: birds, mammals and insects as pollen vectors. *Australian Journal of Botany* **33**, 271–286. doi:10.1071/BT9850271
- Potts SG, Vulliamy B, Dafni A, Ne'eman G, O'Toole C, Roberts S, Willmer P (2003) Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* **101**, 103–112. doi:10.1034/j.1600-0706.2003.12186.x
- Ramsey MW (1988) Differences in pollinator effectiveness of birds and insects visiting *Banksia menziesii* (Proteaceae). *Oecologia* **76**, 119–124. doi:10.1007/BF00379609
- Redpath P, Steed A, Kendall P, Snelson B (2008) *Banksia conferta* A. S. George subspecies *conferta*: a critically endangered species, its habitat, condition, extent and management. Scientific Services Division and Conservation Protection and Regulation Division, DECC, North Coast Region.
- Saffer VM (2004) Are diel patterns of nectar production and anthesis associated with other floral traits in plants visited by potential bird and mammal pollinators? *Australian Journal of Botany* **52**, 87–92. doi:10.1071/BT02056
- Scheele BC, Legge S, Armstrong DP, Copley P, Robinson N, Southwell D, Westgate MJ, Lindenmayer DB (2018) How to improve threatened species management: an Australian perspective. *Journal of Environmental Management* **223**, 668–675. doi:10.1016/j.jenvman.2018.06.084
- Sedgley M, Sierp M, Wallwork MA, Fuss AM, Thiele K (1993) Pollen presenter and pollen morphology of *Banksia* L.f. (Proteaceae). *Australian Journal of Botany* **41**, 439–464. doi:10.1071/BT9930439
- Smith MJ (1973) *Petaurus breviceps*. *Mammalian Species* **30**, 1–5. doi:10.2307/3503785
- Smith I, Velasquez E, Pickering C (2021) Quantifying potential effect of 2019 fires on national parks and vegetation in South-East Queensland. *Ecological Management & Restoration* **22**, 160–170. doi:10.1111/emr.12479
- Thavornkanlapachai R, Byrne M, Yates CJ, Ladd PG (2019) Degree of fragmentation and population size do not adversely affect reproductive success of a rare shrub species, *Banksia nivea* (Proteaceae), in a naturally fragmented community. *Botanical Journal of the Linnean Society* **191**, 261–273. doi:10.1093/botlinnean/boz041
- Tulloch AI, Dickman CR (2006) Floristic and structural components of habitat use by the eastern pygmy-possum (*Cercartetus nanus*) in burnt and unburnt habitats. *Wildlife Research* **33**, 627–637. doi:10.1071/WR06057
- Turner V (1984) *Banksia* pollen as a source of protein in the diet of two Australian marsupials *Cercartetus nanus* and *Tarsipes rostratus*. *Oikos* **43**, 53–61. doi:10.2307/3544245
- Turner V (1985) The ecology of the eastern pygmy possum *Cercartetus nanus* and its association with *Banksia*. PhD Thesis, Monash University, Melbourne, Vic., Australia.
- van Tets IG, Whelan RJ (1997) *Banksia* pollen in the diet of Australian mammals. *Ecography* **20**, 499–505. doi:10.1111/j.1600-0587.1997.tb00418.x
- Vaughton G (1988) Pollination and seed set of *Banksia spinulosa*: evidence for autogamy. *Australian Journal of Botany* **36**, 633–642. doi:10.1071/BT9880633
- Watts CHS, Braithwaite RW (1978) The diet of *Rattus lutreolus* and five other rodents in southern Victoria. *Australian Wildlife Research* **5**, 47–57. doi:10.1071/WR9780047
- Whelan RJ, Burbidge AH (1980) Flowering phenology, seed set and bird pollination of five Western Australian *Banksia* species. *Australian Journal of Ecology* **5**, 1–7. doi:10.1111/j.1442-9993.1980.tb01225.x
- Whelan RJ, de Jong NH, von der Burg S (1998) Variation in bradyspory and seedling recruitment without fire among populations of *Banksia serrata* (Proteaceae). *Australian Journal of Ecology* **23**, 121–128. doi:10.1111/j.1442-9993.1998.tb00710.x
- Wooller SJ, Wooller RD (2001) Seed set in two sympatric banksias, *Banksia attenuata* and *B. baxteri*. *Australian Journal of Botany* **49**, 597–602. doi:10.1071/BT00084
- Wooller SJ, Wooller RD (2002) Mixed mating in *Banksia media*. *Australian Journal of Botany* **50**, 627–631. doi:10.1071/BT01075
- Wooller RD, Wooller SJ (2003) The role of non-flying animals in the pollination of *Banksia nutans*. *Australian Journal of Botany* **51**, 503–507. doi:10.1071/BT02063
- Zammit C, Westoby M (1987) Population structure and reproductive status of two *Banksia* shrubs at various times after fire. *Vegetatio* **70**(1), 11–20. <http://www.jstor.org/stable/20038124>

**Data availability.** The data that support this study will be shared upon reasonable request to the corresponding author.

**Conflicts of interest.** The authors declare no conflicts of interest.

**Declaration of funding.** Data collected and analysed for this project were completed under contract to the first author, funded via the NSW Government Saving our Species initiative and supported in-kind by remaining authors.

**Acknowledgements.** Thanks go to Luke Foster and Michael Murray for assistance in camera placement/retrieval and fauna identifications, and the anonymous reviewers and the editors for constructive comments on an earlier draft. Funding for parts of this work was made available through the NSW Governments Saving Our Species program.

**Author affiliations**

<sup>A</sup>Conservation Science Research Group, School of Environmental and Life Sciences, University of Newcastle, Callaghan, NSW 2308, Australia.

<sup>B</sup>Department of Planning, Industry and Environment, PO Box 488G, Newcastle, NSW 2300, Australia.