

The ecology, evolution and management of mast reproduction in Australian plants

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ABSTRACT

Australia is home to a diverse assemblage of plant species that display marked population-level variation in inter-annual flower or seed output (i.e. masting). These include a semelparous bamboo with an estimated inter-crop period of 40–50 years, numerous iteroparous masting gymnosperms, angiosperms that include landscape-dominant eucalypts, arid-zone wattles and spinifex (*Triodia* spp.) grasses, and a rich selection of species that display disturbance-related forms of masting such as pyrogenic flowering and environmental prediction. Despite the prevalence of masting in the Australian flora, there has been a paucity of research on these plants. Nevertheless, from the literature available, it appears that, similar to other parts of the world, a continuum of inter-year reproductive variability exists, with a small number of species displaying extreme–high inter-annual seeding variability. From experimental studies and many anecdotal reports, most of the fitness benefits associated with masting evident overseas also operate in Australia (e.g. predator satiation, improved pollination efficiency, and environmental prediction). Additionally, some Australian masting species offer periodically important food resources for Aboriginal nations in the form of seed or fruit. These include the bunya pine (*Araucaria bidwillii*), members of the cycad genera *Cycas* and *Macrozamia*, spinifex (*Triodia*) grasses, and mulga shrubs (*Acacia aneura*). Key future research areas for effective conservation of Australian masting plants include (1) improved understanding of how management interventions such as burning and silvicultural thinning influence regeneration dynamics and higher-order trophic interactions, (2) further longitudinal monitoring across a range of habitats to identify other, as yet unknown, species that display reproductive intermittency, and (3) elucidation of how changes to temperature, precipitation and fire regimes under climate change will affect reproduction and regeneration dynamics of the Australian masting flora.

Keywords: iteroparous, mass flowering, masting, mast fruiting, predator satiation, pyrogenic flowering, semelparous, synchronised reproduction, wind pollination.

Introduction

Many perennial plants display marked variation in seed or fruit production from year to year. When such plant-level temporal seeding variation (CV_i) is coupled with high levels of synchrony among populations (S), then high population-level reproductive coefficient of variation (CV_p) occurs (abbreviation nomenclature from [Pearse *et al.* \(2020\)](#), and see [Koenig *et al.* 2003](#); [Pearse *et al.* 2016](#)). This phenomenon, referred to as ‘masting’, is an important driver of plant regeneration dynamics in many ecosystems ([Abrams and Johnson 2013](#); [Pearse *et al.* 2021](#)), and can have cascading ecological effects in communities where consumers depend on mast seed crops for food ([Koenig and Knops 2000](#); [Ostfeld and Keeling 2000](#)). Plant mast years can also have important implications for humans, by providing food resources [e.g. acorns (the nuts of *Quercus* spp.) and *Araucaria* nuts; [Bainbridge 1986](#); [Smith and Butler 2002](#); [Koenig 2021](#)] triggering population explosions of pest species that are destructive to crops ([Janzen 1976](#); [Jaksic and Lima 2003](#)), providing feed for domesticated animals [e.g. *Quercus* nuts and beech (*Fagus* spp.) seeds; [Rotherham 2013](#); [Koenig 2021](#)], and causing heightened risk of

zoonotic disease outbreaks by increasing population densities of wildlife reservoir hosts (Reil *et al.* 2017; Pearse *et al.* 2021).

More than four decades of research have uncovered that there is an interplay among adaptive, proximate, and genetic factors that cause masting. Adaptive drivers behind masting generally invoke 'economies of scale', whereby the reproductive output of individuals in concert with the scale of the population generates an evolutionary advantage for the individual. Such evolutionary advantages include satiation of seed predators (Janzen 1971; Tsvuura *et al.* 2011; Borchert and DeFalco 2016; Boggett *et al.* 2021; Zwolak *et al.* 2022), increased pollination efficiency in wind- and animal-pollinated species (Waller 1979; Kon *et al.* 2005; Crone and Lesica 2006; Schermer *et al.* 2019; Bogdziewicz *et al.* 2020a), increased seed dispersal by scatter-hoarding animals (Zwolak *et al.* 2016; Wang *et al.* 2021; Seget *et al.* 2022) and other proposed responses (Pearse *et al.* 2016; Pesendorfer *et al.* 2021). There may also be genetic controls behind high plant reproductive CVp (i.e. evolutionary conservatism), with species within phylogenetic clades often displaying similar phenological behaviour (Satake and Kelly 2021).

Proximate drivers behind masting can relate to factors that modulate plant internal resource budgets, with some studies demonstrating correlations between nutrient outlay (usually nitrogen and/or carbohydrate) and high reproductive CVp (Han and Kabeya 2017; Fernández-Martínez *et al.* 2019, 2020). In certain species, exhaustion of resources during high-output years also leads to an inability to reproduce for several years thereafter (Crone *et al.* 2011; Koenig *et al.* 2016). Presumably because of the link between resource availability and masting, there is also often a relationship between seed set and climate variables that control plant internal resources (e.g. temperature and precipitation; Hackett-Pain and Bogdziewicz 2021; Pesendorfer *et al.* 2021). Consequently, plants growing in more resource-poor environments often tend towards higher levels of CVp (Pearse *et al.* 2016; Fernández-Martínez *et al.* 2020). Climate may also exert a mechanistic control over plant reproduction, by acting as a synchronising cue for flowering and seed set (i.e. the Moran effect; Iwasa and Satake 2004; Bogdziewicz *et al.* 2017, 2021). Climatic cues that trigger masting are often associated with critical periods for pollination or fruit maturation, and include high spring temperatures, summer drought, spring frost, and high rainfall (Wright *et al.* 2014a; Bogdziewicz *et al.* 2020b).

The Australian continent is a particularly opportune environment to understand the interplay between adaptive factors and seasonal cues that control sporadic reproduction in plants. Australia is largely a semi-desert environment with extensive areas characterised by boom-and-bust rainfall conditions (Noy-Meir 1973; Fensham *et al.* 2009). In such variable environments, 'resource budget' models of masting are likely to be relevant and would predict that the amount of time needed to accumulate resources for a mast crop

should vary considerably among years. Additionally, there could be selective forces in inland Australia that exaggerate inter-year seeding variability (e.g. predator satiation and enhanced wind pollination efficiency), as has been found in arid systems on other continents (Crone and Lesica 2006; Meyer and Pendleton 2015a, 2015b; Auger *et al.* 2016; Borchert and DeFalco 2016).

Australia also contains vast tropical, subtropical, and temperate biomes, as well as some alpine ones, with much variation in potential mechanistic and adaptive drivers of masting among these systems. Although longitudinal plant reproductive data in most of these Australian biomes is scant, there are many Australian plant taxa that have close relatives that are known to mast in other parts of the world. Such plants include alpine grasses in the genus *Chionochloa* (Tanentzap *et al.* 2012; Monks *et al.* 2016), *Podocarpus* and *Araucaria* trees and shrubs in tropical forests (Sanguinetti and Kitzberger 2009; Souza *et al.* 2010), and *Nothofagus* and *Phyllocladus* trees from cool temperate forests (Barker 1995; Smaill *et al.* 2011; Allen *et al.* 2014).

Fire can also be an evolutionary stimulus behind masting and is a fundamental component of many Australian ecosystems. After fire, enhanced nutrient availability and reduced competition may be particularly favourable for seedling establishment. Woody plants can store seed in woody structures and release them *en masse* to exploit the advantages of the post-fire environment (Lamont *et al.* 2020). This adaptation, referred to as pyriscent serotiny, is prevalent in the Australian flora and has similar ecological consequences to masting (Fig. 1a). However, it is not considered masting in the true sense. In contrast, the production of flowers *en masse* following fire is considered a form of environmentally predictive masting (EPM) and is included in this review (Vacchiano *et al.* 2021; Fig. 1b, c). EPM occurs in plants that synchronise reproduction with environmental or climatic cues that portend future periods favourable for germination and/or recruitment (Ascoli *et al.* 2020; Vacchiano *et al.* 2021). There are several forms of fire-related EPM reported in Australian species, including pyrogenic flowering and climate-linked EPM, and these are included in this review.

In this paper, we review the literature on masting plants in Australia according to reproductive strategy (semelparous vs iteroparous) and biome [arid, tropical, and temperate (for iteroparous species only)]. Where relevant, we also include information relating to the ethnobotany of plants for which mast seed crops are known to have played an important role in the food economies of Australian Aboriginal nations. Finally, we summarise the literature concerning the poorly studied topics of the evolutionary ecology of Australian masting plants and the management and conservation of these species. By covering these various topics, it is hoped that this review will provide a useful resource for future research and conservation-related activities on masting plants in Australia.



Fig. 1. (a) Synchronised post-fire fruit opening in silver banksia (*Banksia marginata*), Tarkine, Tasmania (photo DCF). (b) Synchronised post-fire (pyrogenic) flowering in spikey grass tree (*Xanthorrhoea resinosa*), Cape Conran, Victoria (photo DCF). (c) Post-fire flowering in *Pyrorchis forrestii* (Orchidaceae), south-west Western Australia (photo Andrew Brown). (d) Mass flowering in inland white mahogany (*Eucalyptus acmenoides* sens. lat.), Herberton, North Queensland (photo DCF).

Australian masting plants

Quantifying masting

In this review, where data are available to illustrate inter-year reproductive variability, we use the CV_p, the population-level coefficient of variation of inter-year flower or seed production. The CV_p is calculated by dividing the standard deviation of population-level annual seed production by the mean of the annual seed production dataset. The CV_p is the most-commonly used metric for estimating plant reproductive variability, with 0 = no inter-annual variation, values >1 sometimes being interpreted as masting, and, in more extreme forms, values approaching or exceeding 3 (Pearse *et al.* 2017, 2020; and see Fig. 2 for an illustration of how inter-year reproductive variability compares between *Quercus laevis* Walter, a northern hemisphere species with well-documented high CV_p, and three Australian plant species with differing CV_p).

The use of CV_p in measuring inter-year reproductive variability does have some inherent limitations. These include the dependence of the CV_p on the mean and duration of the dataset, and problems when non-normally distributed data

are encountered (Fernández-Martínez and Peñuelas 2021). Other indices, such as ‘proportional variability’ and the ‘consecutive disparity index’ may provide more robust estimates than does the CV_p when comparing datasets that have different sample sizes and/or that are non-normally distributed (Fernández-Martínez and Peñuelas 2021). However, these other metrics have not been widely employed to describe masting and also have their own inherent flaws. Therefore, we refer only to the CV_p in this review.

Among-year variability in plant reproduction follows a continuous gradient, so using dichotomous classifications such as ‘masting’ and ‘non-masting’ can be problematic (Herrera *et al.* 1998; Koenig and Knops 2000; Fernández-Martínez and Peñuelas 2021). This was recently demonstrated by Pearse *et al.*'s (2020) global analysis of mean CV_ps of 311 species, where the dataset showed a unimodal continuous distribution of CV_ps ranging from 0.5 to 3.3 (Fig. 3a; and see Fig. 3b for a comparison histogram derived from Australian plant reproductive CV_ps). Pearse *et al.*'s (2020) unimodal CV_p distribution is consistent with the findings of other similar studies (Herrera *et al.* 1998), with the absence of a multimodal CV_p distribution suggesting that

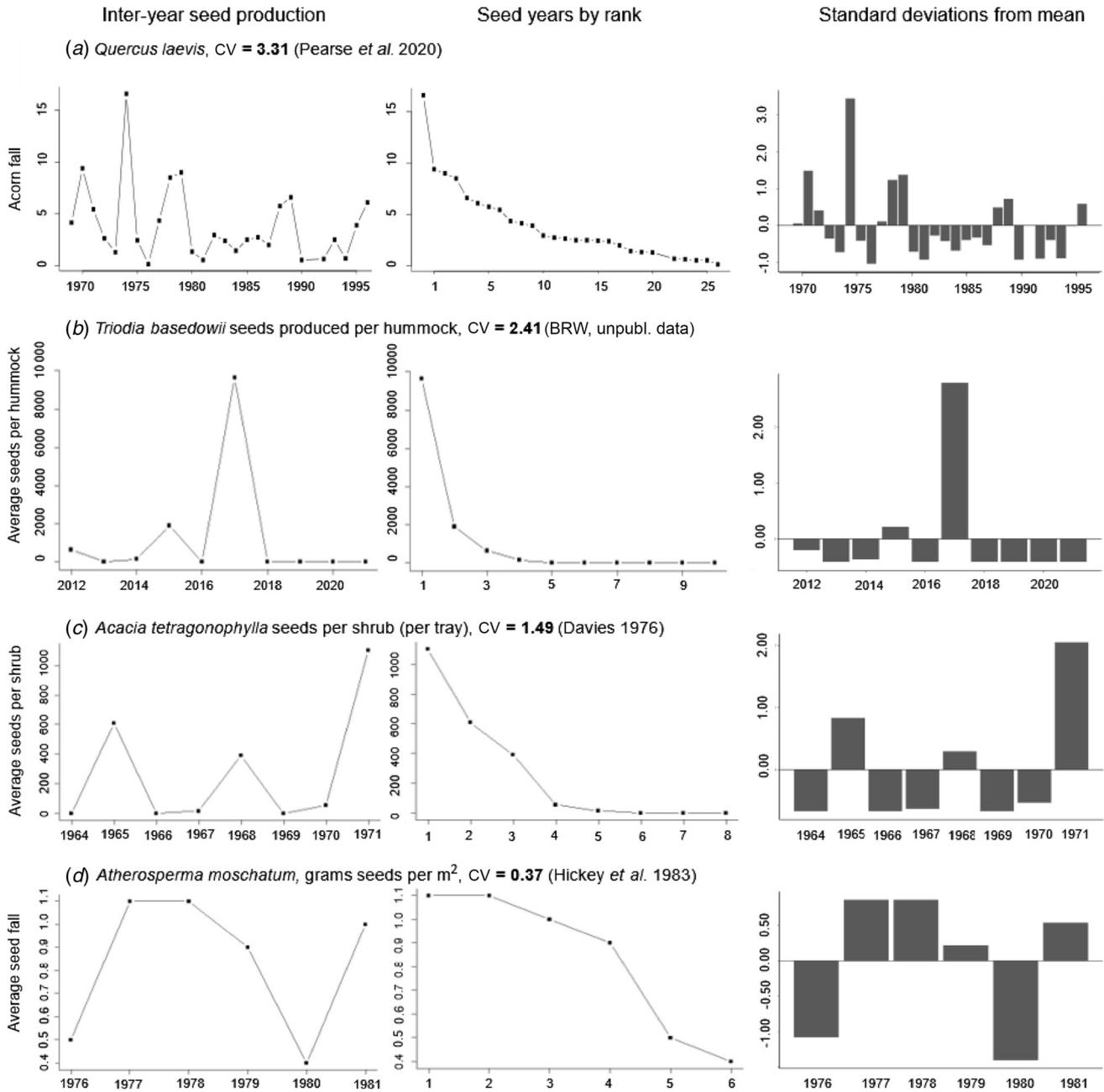


Fig. 2. Four long-term phenological datasets with varying degrees of population-level reproductive synchrony (as measured by the CVp): (a) *Quercus laevis*; (b) *Triodia basedowii*; (c) *Acacia tetragonophylla*; and (d) *Atherosperma moschatum*. The left panel of each species shows the inter-year seeding variability, the middle panel shows ranked inter-year seed production, the right panel shows inter-year seeding output (represented as standard deviations from the long-term mean). Species are arranged from top to bottom in descending order of CVp, with *Q. laevis* being the most variable (CVp = 3.31) and *A. moschatum* the least (CVp = 0.37). Data for *Q. laevis* were obtained from a global species CVp dataset compiled by Pearse et al. (2020).

masting is not a distinct reproductive strategy among plants. For this reason, some researchers prefer simply to indicate whether plants have comparatively high or low inter-year reproductive CVp. However, in this review we elect to retain use of the term masting as we agree with Koenig (2021), that despite problems in definition, ‘retaining the term ‘masting’ offers a clear way to emphasise the focus of

a study and identifies a life history of biological, evolutionary and management significance’.

Semelparous plants

Semelparous plants and animals reproduce only once in a lifetime, dying after reproduction. Among plants, semelparity

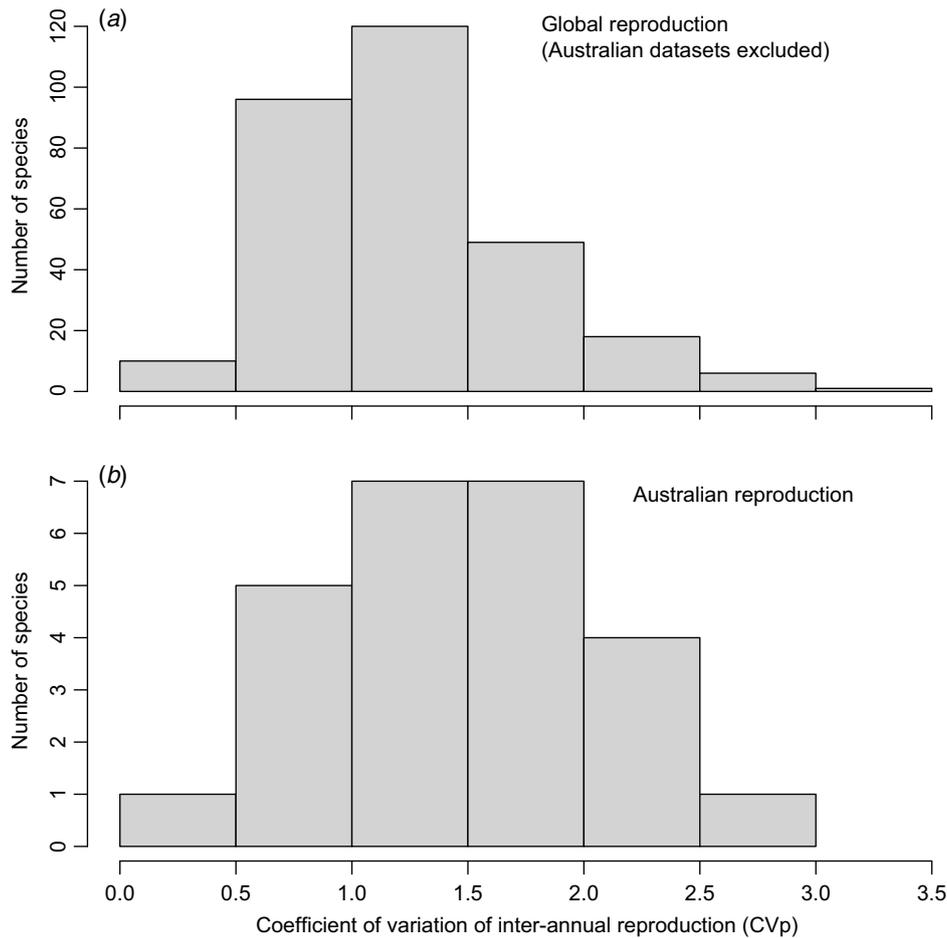


Fig. 3. Histograms comparing inter-year reproductive CVps from (a) Pearse *et al.*'s (2020) global dataset with (b) Australian inter-year reproductive CVp dataset (data from Table 1). Species CVps from Australia were removed from the global dataset prior to production of histogram a.

is also known as monocarp. Simmonds (1980) regarded monocarp as occurring in three discrete forms, monocarp by definition (annuals and biennials), monocarp by morphology (unbranched perennials such as certain palms), and monocarp by adaptation in branched perennials (e.g. many bamboos, some shrubs and trees). In perennials, including long-lived woody plants, when flowering and subsequent mortality are synchronised within populations, the phenomenon is variously referred to as the plietesial life history, semelparous masting or gregarious semelparity. Hereafter, we refer to it as semelparous masting.

Most, but not all, long-lived semelparous plants exhibit masting (e.g. see Poorter *et al.* 2005 for one that is not). In long-lived plants, the risk of reproductive failure in a single event is argued to favour a strong association of semelparity with masting via the mechanisms of creating communal space for offspring (Keeley and Bond 1999; Read *et al.* 2021), satiation of seed predators (Janzen 1976; Tsuura *et al.* 2011), and ensuring cross-pollination (Mizuki *et al.* 2014) - arguments of which only the first is unique to

semelparous species. Parental death in semelparous masting plants is associated with a flush of seedlings, this cohort repeating the life-cycle. Semelparous masting is best documented in bamboos (Poaceae) (reviewed in Janzen 1976), is particularly prevalent in the Acanthaceae (Daniel 2006; Tsuura *et al.* 2011), and is known among other Poaceae and also Areaceae, Scrophulariaceae, Fabaceae and Apocynaceae (Daniel 2006; Stevenson 2008; Read *et al.* 2021). These plants include bamboos, other grasses, palms, trees, shrubs, and long-lived herbs.

Many semelparous masting species exhibit more-or-less fixed lifespans, with population periodicities ranging from as few as 5 years (Stevenson 2008) up to 120 years (Kawamura 1927; Janzen 1976). This is believed to be the product of an endogenous clock (Janzen 1976; Wright *et al.* 2014b), although its structure and function remain unknown. Some semelparous masting plants exhibit variable lifespans (Burd *et al.* 2006), for example 4–7 years in a sub-tropical forest herb (*Isoglossa woodii* C.B. Clarke (Acanthaceae)) (Tsuura *et al.* 2011), and 45–>100 yrs in a tropical

rainforest tree [*Cerberiopsis candelabra* Vieill. ex Pancher & Sebert (Apocynaceae)] (Read et al. 2021).

Gregarious semelparity in Australia

The only known semelparous masting plant in Australia is the pachymorphic (clump-forming) bamboo, *Bambusa arnhemica* F.Muell. (Fig. 4a, b). This species is endemic to the tropical north-west of the Northern Territory where it occurs in riparian forests and a few non-riparian vine-thickets (Franklin 2004; Franklin and Bowman 2004). Mature clumps consist of dozens to 100s of culms each up to ~10 cm in diameter and 20 m tall on favourable sites (Franklin et al. 2010). *Bambusa arnhemica* has an inter-mast interval of ~40–50 years and flowers in a spatio-temporal wave over a number of consecutive years (Franklin 2004). In a given year, >95% of clumps in a patch flower then die, with most of the remainder initiating flowering in the year before or after (this is known as the seeding distribution; Janzen 1976). In Franklin's (2004) study, patches varied in area from 0.2 ha to 3200 km² and were arranged in a haphazard geographical pattern. Flowering commenced in the tropical dry season and seed germinated with the first heavy rains of the following wet season, as the previous generation was dying (Franklin and Bowman 2003). Seedlings were generally abundant, although only under old clumps

(few to 1000s per m²), and grew rapidly, being mostly up to 50 cm tall by the end of the first wet season.

The flowering wave observed in *B. arnhemica* was similar to that noted among semelparous masting bamboos in Asia and the Americas (e.g. Janzen 1976); the significance of which is not understood. Franklin (2004) proposed that strong natural selection acts to ensure high levels of synchrony within stands via an endogenous clock. However, a clock would likely count something external to the plant such as seasonal fluctuations in day length or temperature. Miscounts might be induced by extreme events (wildfire, flood, drought, extreme temperature), accounting both for the small percentage of plants within a stand that flower in the year prior to or after the main event, and temporal offsets affecting entire stands. Temporal offsets would generate, over many generations, a flowering wave. Vigorous regeneration only under old clumps provides strong support for the hypothesis that semelparous masting serves to create space for offspring.

Reproductive data are scant for Australia's two other native bamboos, the climbing *Mullerochloa moreheadiana* (F.M.Bailey) K.M.Wong of northern Queensland Wet Tropics and the Iron Range bamboo (*Neololeba atra* (Lindl.) Widjadjaja) of Cape York Peninsula and the northern Wet Tropics. Both species might be iteroparous, although evidently



Fig. 4. (a) Gregarious flowering in Top End bamboo (*Bambusa arnhemica*), Tortilla Flats, Adelaide River, NT (photo DCF); (b) mass regeneration of *B. arnhemica* seedlings subsequent to die-off of adults, Tortilla Flats (photo DCF); (c) high-intensity wildfire in mulga (*Acacia aneura*) woodland in 2011, Mount Everard, central Australia (photo J. Williams); (d) dense post-fire mulga seedling recruitment in 2012 in mulga community, Central Mount Wedge station, central Australia (photo BRW).

flowering infrequently (D. C. Franklin, pers. obs.), so they may mast.

Kennedy palm, *Corypha utan* Lam., occurs on floodplains on Cape York Peninsula and the Northern Territory, and ranges into Southeast Asia as far north as Assam in India (Dowe 2010). The species is slow-growing, long-lived and semelparous (Jones 1984). Whether it is masting is unknown, although it is certainly not a strong masting species because populations commonly comprise a mix of live and dead individuals, with live plants being at various stages of development (Jones 1984; D. C. Franklin, pers. obs.).

Iteroparous gymnosperms

In contrast to semelparous plants, iteroparous (polycarpic) plants reproduce multiple times during their life-cycle. Iteroparity is the far more common reproductive strategy among long-lived plants, and, in Australia, some of the most commonly reported iteroparous masting species are gymnosperms. Masting Australian gymnosperms occur mainly in temperate and subtropical ecosystems, and include bunya pine (*Araucaria bidwillii* Hook., Araucariaceae), huon pine (*Lagarostrobos franklinii* (Hook.f.) Quinn, Podocarpaceae), pencil pine (*Athrotaxis cupressoides* D.Don, Cupressaceae), members of cycad genera such as *Macrozamia* and *Cycas* (Zamiaceae, Cycadaceae, resp.), and certain species of cypress pine [Cupressaceae: e.g. *Callitris glaucophylla* F.Muell., (white cypress pine), and *C. intratropica* Baker, R.T. & Smith, H.G., (northern or blue cypress pine)].

Bunya pine (*Araucaria bidwillii*)

The bunya pine is a large evergreen conifer that occurs in south-eastern Queensland and in two small disjunct populations in tropical far-northern Queensland. It produces heavy and general seed crops on a 3- to 4-yearly basis, although low-level cone production also occurs during inter-mast years (Smith and Butler 2002; Haines *et al.* 2018). Mast seed crops of the bunya pine provide episodic but important food resources for Aboriginal peoples in south-eastern Queensland. The approximately triannual crops allowed different tribal groups to gather for purposes such as ceremonies, trading, the arrangement of marriages, and the sharing of dances and songs (Mathew 1910; Jones 1997; Huth 2002; Parsons 2020).

Like most other gymnosperms, the bunya pine is a wind-pollinated species, with pollination occurring in early spring months (September and October) and cone maturation taking approximately 17–18 months (Smith and Butler 2002). Cone fall occurs in January to early March in south-eastern Queensland populations, although to our knowledge, there is no documentation of when cone fall occurs in the far-northern Queensland populations. It has been suggested that, like the closely related South American *A. araucana* (Molina) K.Koch (monkey puzzle tree), the mast cycles of bunya pines are influenced by the El Niño–Southern

Oscillation (ENSO) meteorological phenomena (Smith and Butler 2002). For *A. araucana*, increased rainfall in spring during the pollination period interferes with pollination efficiency and impedes subsequent cone production (Sanguinetti *et al.* 2002; Sanguinetti and Kitzberger 2008, 2009). It is possible that this occurs also for *A. bidwillii*, although further research is required to evaluate whether this is the case.

Callitris pines

Callitris glaucophylla and *C. intratropica* are widespread small–medium-sized trees that form woodlands over large areas of eastern and tropical Australia respectively. These species of *Callitris* are non-serotinous and release seeds more or less immediately following fruit maturation. They also both play important roles in the Australian timber industry, and both are highly susceptible to fire damage during uncontrolled wildfires (Farjon 2005; Thompson and Eldridge 2005; Trauernicht *et al.* 2012). Like bunya pine, *C. glaucophylla* and *C. intratropica* produce heavy and general seed crops on an approximately 3-yearly basis, and large crops always follow a year of heavy pollen flow (Hawkins 1966; Stocker 1966). Crops of moderate size sometimes occur during inter-mast periods. However, the seed viability of such crops is invariably low, presumably because they are produced from low-intensity flowerings with low rates of cross-pollination (Hawkins 1966). On the basis of data collected over 5 years from populations near Dalby in south-eastern Queensland, the CVp of interannual seed output for *C. glaucophylla* was 1.72 (Hawkins 1966). Disruption to the seeding cycles of *C. glaucophylla* may occur when crops are subjected to heavy and prolonged infestations by the cypress pine aphid, *Cinara tujafilina* (Hemiptera, Aphidae) (Hawkins 1966).

Cycads

Cycads are slow-growing dioecious plants that form a prominent part of the understorey in many Australian tropical and subtropical ecosystems (Halliday and Pate 1976; Ornduff 1990) and some arid-zone ecosystems (Preece *et al.* 2007). There are three families of cycad in Australia, namely Cycadaceae, Stangeriaceae and Zamiaceae, and the propensity to mast has been documented in the genera *Cycas* (Cycadaceae) and *Macrozamia* (Zamiaceae) (Beaton 1982; Burbidge and Whelan 1982; Ballardie and Whelan 1986; Ornduff 1990; Hall and Walter 2013). Among masting cycads, localised variation in shading and soil nutrients has been shown to affect cone output in *M. communis* L.A.S.Johnson (Ornduff 1990), whereas favourable precipitation conditions have been reported to lead to more profuse coning, shorter inter-mast periods, and more rapid growth of plants of *M. riedlei* (Fisch. ex Gaudich.) C.A.Gardner and *M. communis* (Halliday and Pate 1976; Ornduff 1990, 1991).

Fire is commonly reported to stimulate flowering and coning of cycads, although the effects are complex and

variable among species (Beaton 1977, 1982; Harris 1977; Ornduff 1991; Lamont and Downes 2011). For certain species, fire increases the yield of individual plants [e.g. *M. dyeri* (F.Muell.) C.A.Gardner, *M. communis*; Beaton 1977, 1982; Hill and Baird 2003; Lullfitz *et al.* 2020], increases the fraction of female cones (e.g. *C. media* R.Br. and *M. communis*; Beaton 1982; Lamont and Downes 2011; Fig. 5a), and promotes the synchronisation of seeding among populations (e.g. *M. riedlei*; Harris 1977; Ornduff 1991; Nield *et al.* 2019). However, for other species [e.g. *M. macdonnellii* (F.Muell. ex Miq.) F.Muell. ex A.DC. and *M. platyrhachis* F.M.Bailey], uncontrolled high-intensity fires during summer can damage populations because of fire-induced damage to cones and negative impacts on seedlings and pollinators (Preece *et al.* 2007; Terry *et al.* 2008). Fire is less likely to be important in the ecology of the many cycads of low-flammability Australian systems such as rainforests.

Seeds of masting cycads of the genera *Cycas* and *Macrozamia* were traditional foods of Aboriginal peoples in many regions (Hann 1873; Le Souef 1897; Roth 1901; Hill and Baird 2003). To utilise cycad seeds as food, Aboriginal people had to master various processing techniques to enable detoxification of the nuts. The toxins involved, including cycasin and macrozamin, β -glycosides of methyl-azoxymethanol (MAM), lead to rapid vomiting

and death, depending on the quantity of seeds consumed (Beaton 1982). Aboriginal peoples remove/denature these toxins via various combinations of leaching, fermenting, aging, grinding and/or roasting of the seeds depending on the species and locality of the plants involved (Beck 1992; Marika *et al.* 2009; W. Beck, pers. comm. 2022; Fig. 5b).

Iteroparous angiosperms – arid zone

Mulga (*Acacia aneura*)

Members of the mulga complex are shrubs or small trees that dominate arid and semi-arid woodlands across ~20% of Australia (Johnson and Burrows 1994). A recent revision of the mulga complex by Maslin and Reid (2012) recognised 12 species of mulga, which, in addition to *A. aneura* F.Muell. ex Benth, includes various widespread and ecologically important species such as *A. aptaneura* Maslin & J.E.Reid (slender mulga), *A. ayersiana* Maconochie (Uluru mulga), *A. minyura* Randell (bastard mulga) and *A. paraneura* Randell (weeping mulga). Mast seed crops of many mulga species were used as food resources by Aboriginal peoples across much of arid and semi-arid Australia (see Maslin *et al.* (1999) for a summary of ethnographic information on the consumption of mulga seed by central and southern Australian Aboriginal tribal groups).

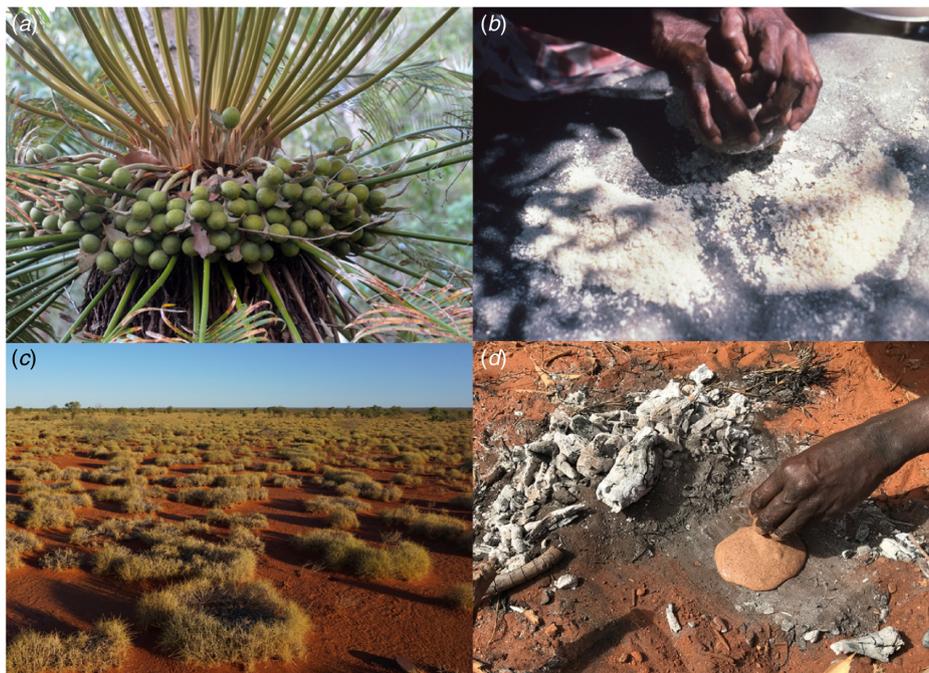


Fig. 5. (a) Heavy seed crop of *Cycas media*, Northern Territory (photo DCF); (b) traditional preparation of cycad seeds using grinding stone and top stone to produce edible flour (photo with permission, Wendy Beck); (c) hard spinifex (*Triodia basedowii*) grassland during low-rainfall inter-mast period in the Gibson Desert, Western Australia (photo BRW); (d) traditional cooking of *Triodia* seed cake, Kiwirrkurra community, Western Australia (photo BRW).

Mulga (*A. aneura*) is a good example of an Australian plant with a very high reproductive CVp, with no seed being produced in most years and large crops being produced in some. Seeding intermittency in *A. aneura* was first quantified by Davies (1976) in a phenological study on arid-zone trees and shrubs at Mileura station in Western Australia. His observations showed a mean CVp across four populations of 1.76. Similar observations of exaggerated seeding intermittency in mulga were made by Hodgkinson (Hodgkinson *et al.* 1980; Hodgkinson 1991) in western New South Wales (NSW), where *A. aneura* populations were observed flowering only once over a 10-year study period at 'Oakvale' station. In arid central Australia, T. Guest (pers. comm. 2021) observed no fruiting in *A. aneura* populations during 10 years of observing *A. aneura* populations at Uluru-Kata Tjuta National Park. However, she was absent from the Park during the latter part of 2010 when other populations in central Australia were fruiting. Rainfall requirements for masting in the mulga complex are quite specific, with heavy rain in summer being required to initiate flowering and good rain in winter needed to set the fruit (Everist 1949; Preece 1971; Davies 1976).

An important point raised by Davies' (1976) research was that even in an environment with precipitation as variable as arid Australia, some species maintain extremely consistent inter-year crop production. Throughout the duration of the Mileura study of Davies (1976), *Eremophila fraseri* F.Muell. (Myoporaceae) displayed high levels of crop production, fruiting heavily even during the exceptionally dry years of the early-mid-1960s. Black gidgee (*Acacia pruinoarpa* Tindale), an inland wattle that fruits in autumn rather than spring (as almost all other arid-zone *Acacia* do), was also very consistent at Mileura, showing greatly reduced crop production in only 3 of the 10 study years. The importance of such consistently fecund species for the diets of native fauna was emphasised by Davies (1978), with the fruits of *E. fraseri* often being a major component of emu (*Dromaius novaehollandiae*) diets. The observation that certain species reproduce consistently in variable environments where others are masting is interesting and qualifies further research.

Spinifex (*Triodia* spp.) grasses

Spinifex grasses (*Triodia* spp., Poaceae) are long-lived grasses that form compact or straggly hummocks, or, in certain species, rings, up to 3 m or more in diameter (Fig. 5c). They dominate grasslands across ~25% of the Australian continent and most arid species have the peculiar habit of flowering profusely in most years but then aborting most flowers in all except occasional extreme-high-rainfall years (Jacobs 1973; Rice *et al.* 1994). Recent studies in central Australia monitored crop production at two *T. pungens* R.Br. populations from 2012 to 2021 (Wright 2021). Although flowering occurred in all years of the study, in most years little or no viable seed was produced and only two

high-output years were observed. Both these mast years were triggered by exceptionally high rainfall and the estimated mean seeding CVp for the two populations over the 10-year study period was 1.71. At the same sites, the hard or lobed spinifex, *T. basedowii*, showed more variable reproduction among years than *T. pungens*, with a mean 10-year CVp averaged across both sites of 2.42.

Seed cakes of masting desert spinifex grasses were occasional food resources for certain Aboriginal tribal groups, although first-hand observations of the consumption of spinifex seed cakes are scarce (Fig. 5d). Observations of the use of spinifex seeds as food include those of Long (1971), who documented their use by Pintupi people in the Gibson Desert, and Cane (1987), who documented their use by Mardutjarra people in the Great Sandy Desert. It is likely that the use of spinifex seed as food by desert Aboriginal peoples is rare because (1) mast seed production in these plants is uncommon, (2) processing techniques required to produce *Triodia* seed cakes are complex, and (3) other more easily processed plant and animal foods are abundant during the high-rainfall years when spinifex masts occur.

Cattle bush (*Alectryon oleifolius*)

Cattle bush [*Alectryon oleifolius* (Desf.) S.T.Reynolds] is a medium-sized tree up to 9 m tall that occurs across drier inland regions of all mainland Australian states. Fruiting of cattle bush is reported to be irregular, with occasional abundant production followed by numerous years of none across the entire species' range (Duretto 1999). 2021 was a mast year for cattle bush, with the exceptionally high rainfall of the La Nina years of 2020 and 2021 being the likely trigger (Fiona Murdoch, Mallee Conservation, pers. comm. 2021). The seed is subject to high levels of pre-dispersal predation by instars of soapberry bugs (*Leptocoris mitellatus*), which are specialist seed predators of plants in the family Sapindaceae (Carroll *et al.* 2005). Owing to this seed predation, and also presumably the short-term viability of seeds, soil-borne seedbanks of this species are typically extremely sparse (Callister *et al.* 2018).

Crinkle leaf cassia (*Senna artemisioides* subsp. *helmsii*)

The crinkle leaf cassia [*Senna artemisioides* subsp. *helmsii* (Symon) Randell] is a rounded or flat-topped shrub that occurs as isolated individuals or small stands on red earths, sandplains and skeletal soils on rocky hill slopes. It is widespread across the arid and semi-arid regions of all mainland states except Victoria. The crinkle leaf cassia population at Davies' (1976) Ejah site had the highest CVp of inter-annual seeding variability (2.33) of any of the 144 species examined in Herrera *et al.*'s (1998) study on annual seed crop variability in woody plants.

Iteroparous angiosperms – tropical, temperate, and alpine regions

It has been suggested that most canopy trees in Australian tropical and subtropical rainforests are mast seeders (Floyd 1999; Nadolny 1999; S. Shaw, pers. comm. 2022, and see Table S1 for Shaw's list of species with propensity to mast in northern Queensland rainforests). Nevertheless, at present, lack of longitudinal data prevents empiric calculation of how synchronous or erratic the reproduction of any of these species is. A longitudinal study of rainforest flowering and fruiting is currently underway in the rainforests of the Gold Coast hinterland in south-eastern Queensland. However, the results of this research are not yet published, and further monitoring is required before publication occurs (B. McDonald, Queensland Herbarium, pers. comm. 2021).

Myrtle beech (*Nothofagus cunninghamii*)

Myrtle beech [*Nothofagus cunninghamii* (Hook.f.) Heenan & Smissen (Nothofagaceae)] is a tall evergreen tree of the cool, temperate rainforests of Tasmania and Victoria, where it is often the dominant species. Quantitative phenological studies of myrtle beech were conducted over 22 years in Tasmania by Hickey *et al.* (1983) and CVps of inter-year reproduction ranged across sites from 1.05 to 2.12. The climatic drivers behind masting years in myrtle beech appear to be complex and no distinctive rainfall pattern was observed prior to any of the four major seed-fall years of Hickey *et al.*'s (1983) study.

Brigalow (*Acacia harpophylla*) and Gidgee (*A. cambagei*)

Brigalow (*Acacia harpophylla* F.Muell. ex Benth.) is a tree up to 20 m tall that forms dense woodlands on fertile clay and clay-loam soils in subtropical eastern Australia. It occurs primarily in the 300–700 mm mean annual rainfall zone and is generally a habitat dominant or co-dominant. Brigalow once covered ~8.7 million ha in Queensland and NSW but was subject to extensive clearing throughout much of the 19th and 20th centuries (Accad 2001). It is estimated that only 7% of the brigalow scrub present at the time of European settlement now remains (Thornton and Shrestha 2021).

Although no quantitative longitudinal data on brigalow seed production exist, it is commonly reported in the literature to be a masting species. Dwyer (2017) mentioned regional masting in brigalow as occurring at intervals of 10–30 years and noted that high rates of floral abscission are common in non-mast years. The intermittency of brigalow seeding can be inferred from Mueller's initial description of the species, where he commented that pods (legumes) of brigalow were unknown (see Johnson 1964). The flowering period for brigalow is April to October, with peak flowering occurring between July and August (Johnson 1964; Pedley 1978). Good rainfall during winter and early spring is important for ensuring fruit set during mast years, and it is

common for isolated trees/populations to flower well even in non-mast years if soil-moisture relationships are favourable (Johnson 1964).

Gidgee (*Acacia cambagei* R.T.Baker) is another widespread species, related to brigalow, that reproduce intermittently (Fensham and Fairfax 2005). Both brigalow and gidgee are in the *Microneuræ* series of *Acacia* and both of these species disperse soft 'green' seeds with no capacity for soil storage. This factor determines that waves of generation coincide with high-output seeding events. Single-aged cohorts are especially the case with gidgee, which, unlike brigalow, has a limited capacity to root sucker (Fensham and Fairfax 2005).

Chionochloa grasses

Grasses of the genus *Chionochloa* are robust perennials that usually occur in alpine or upland areas and grow in clumps up to 1.5 m tall. The genus is one of the best studied masting genera in the world, and the flowering, seeding and regeneration dynamics of nearly all of the 22 New Zealand species have received at least some research attention. Most *Chionochloa* species are highly intermittent seeders (Mark 1965; Connor 1966, 1991), and some, including *C. crassiuscula* (Kirk) Zotov (CVp = 3.02) and *C. teretifolia* (Petrie) Zotov (CVp = 2.57), are recognised as having among the most extreme forms of masting in the world (Kelly *et al.* 2000). Australia has two *Chionochloa* species, namely *C. frigida* (Vickery) Conert (robust wallaby grass) from the alpine Mount Kosciuszko region of NSW, and *C. howensis* S.W.L.Jacobs, known only from the cliffs of Mounts Lidgbird and Gower on Lord Howe island. The Australian *Chionochloa* species lack quantitative long-term phenological study, although *C. frigida* has been reported to flower only rarely (Linder 2005).

For most of the New Zealand *Chionochloa*, satiation of pre-dispersal seed predators belonging to the gall midge family, Cecidomyiidae, is the primary evolutionary benefit of mast seeding (Kolesik *et al.* 2007). It is unclear whether low flowering frequency in *C. frigida* is an anti-predator adaptation, because no cecidomyiid predators of *C. frigida* have been reported or described (P. Kolesik, pers. comm. 2021). However, members of this seed predator guild have been observed parasitising the seeds of species of arid spinifex grass (Wright *et al.* 2014a; Wright 2021; P. Kolesik, pers. comm. 2014) and various crop species in Australia (Congdon *et al.* 2002; Lloyd *et al.* 2007; Kolesik and Gagné 2016). It is therefore possible that parasitism by gall midges could be driving seeding intermittency in *C. frigida*, although further research is required to test this.

Eucalypts: *Eucalyptus*, *Corymbia* and *Angophora*

Collectively, the closely related genera *Eucalyptus*, *Corymbia* and *Angophora* (Myrtaceae) comprise about 800 species of trees, shrubs, and mallees. They are structurally and numerically dominant over vast areas of temperate,

subtropical and tropical open forest and woodland, semi-arid mallee scrub and tropical savanna in Australia. Given this abundance, there are surprisingly few long-term, quantitative phenological studies from which the propensity for masting might be evaluated. The most notable studies (10 years or greater) are those of Loneragan (1979), Pook *et al.* (1997) and Law *et al.* (2000). However, there are numerous reports of among-year variability in reproductive effort based on shorter-term quantitative studies, short- or long-term qualitative studies, and anecdotal reports. The 128 species-specific reports that we have identified as relating to eucalypt reproduction are detailed in Supplementary Table S2.

From our literature search, data sufficient to calculate CVp is available for 31 eucalypt species, but only 12 datasets (for 10 species) are for four or more years and all of these are for species of temperate forests in south-eastern or south-western Australia. CVp for these ranges from 0.34 to 2.52 (Table 1), with 8 of 10 species having a CVp close to or exceeding 1.0, the highest recorded being 2.52, for *Corymbia maculata* (Hook.) K.D. Hill & L.A.S. Johnson. Convincing reports of high among-year variability in flowering effort also exist for eucalypts in subtropical open forest (Law *et al.* 2000), dry temperate woodlands (Yates *et al.* 1994; Mac Nally *et al.* 2009), upland tropical dry sclerophyll forest (Franklin *et al.* 2016), and tropical savanna (Brady 2009; Table S2). However, lack of suitable data preclude calculation of CVp for these species.

The nature of among-year seeding and flowering variability in eucalypts is itself highly variable. Some eucalypt species do not flower at all in a majority of years (e.g. *C. maculata*; Pook *et al.* 1997), whereas others flower in most or all years, with >10-fold variation among years (e.g. *E. grandis* W.Hill), and some with >100-fold variation (e.g. *E. saligna* Sm., *C. maculata*; Table S2). Some species flower at irregular intervals (e.g. some of the species in Law *et al.* 2000) whereas others exhibit temporal periodicities, with quantitative evidence of 2-year cycles in *E. tricarpa* (L.A.S. Johnson) L.A.S. Johnson & K.D. Hill, *E. leucoxylon* F. Muell., *E. macrocarpa* Hook. and *E. polyanthemos* Schauer (Hudson *et al.* 2011) and 4- and 5-year cycles respectively, in *E. regnans* F. Muell. and *E. delegatensis* R.T. Baker (Fig. 6; Ferguson 2011). Whereas masting primarily implies among-year synchrony among neighbours (i.e. within a site), among-site synchrony ranged from low to high across species in two longer-term studies by Law *et al.* (2000) but was mostly concordant across several 100 km in studies of *E. tricarpa* by Mac Nally *et al.* (2009). In a mass-flowering year for inland white mahogany (*E. mediocris* L.A.S. Johnson & K.D. Hill), 97% of trees flowered over a c.100 km² study area, but there was spatial structure in timing within the 3.5-month flowering season (Franklin *et al.* 2016).

The processes driving flowering (or lack thereof) in eucalypt populations in a given year are complex and poorly resolved, and co-existing species may respond quite

differently to the same environmental conditions. Severe drought may inhibit flowering (Law and Chidel 2009; Mac Nally *et al.* 2009) by suppressing development of flowers from existing buds (Ashton 1975; Pook *et al.* 1997; Law *et al.* 2000), whereas abnormally heavy rain may promote flowering (Law *et al.* 2000; D. C. Franklin, pers. obs.). Cool temperatures may encourage bud formation in the following year (Law *et al.* 2000), whereas antecedent flowering may depress subsequent flowering for one or more years (Keatley *et al.* 2021), as also suggested by the periodicities previously mentioned for *E. regnans* and *E. delegatensis*. Other factors driving variation in flowering rhythms may include heat stress, insect attack, variation among sites in resource availability such as soil nutrients, and among-species differences in the time required to recover resources before the next flowering (Law *et al.* 2000). Staggered eucalypt flowering among species across years could also relate to minimising competition for shared pollinators (Ashton *et al.* 1988; Newstrom *et al.* 1994).

Very few studies have addressed the evolutionary drivers of masting in eucalypts, though some studies have demonstrated satiation of seed predators, namely ants, by mass-flowering (Ashton 1975; O'Dowd and Gill 1984; Wellington and Noble 1985). Given the likely major role of gregarious and highly mobile fauna, such as flying-foxes (*Pteropus* spp.) and lorikeets (Psittacidae), as pollinators, the evolutionary role of masting in successful pollination seems worthy of further investigation. Slow development of reproductive structures in some eucalypts, for example 27–29 months from bud emergence to flowering in *E. regnans* (Ashton 1975), might have predisposed eucalypts to masting behaviour, although at the other extreme two tropical eucalypts (*E. miniata* A. Cunn. ex Schauer and *E. tetradonta* F. Muell.) completed their reproductive cycle from bud emergence to capsule fall in 8 months (Setterfield and Williams 1996).

Fire-related forms of masting

Pyrogenic flowering

Species with pyrogenic flowering can be either herbaceous or woody, and typically display increased or peak flowering during the first 1–3 years after burning. This is then followed by little or no flowering until the next fire occurs (Gill and Ingwersen 1976; Denham and Auld 2002). Pyrogenic flowering is very well represented in the Australian flora, with a review paper by Lamont and Downes (2011) reporting 212 Australian species that are known to display it. The majority of these occur in Mediterranean (70.3%) and maritime (25.5%) climates, and a small fraction in arid (1%), alpine (1.4%), and savanna (1.9%) environments. In a case study of post-fire plant regeneration in dry sclerophyll bushland to the north of Sydney, the post-fire behaviour of 537 native and 250 exotic vascular plant species was recorded (Kubiak 2009). Post-fire flowering was more common in the Australian vascular plant flora

Table 1. Reproductive CVps of Australian plants with information on life-history traits, population-level coefficient of flowering or seeding variability (CVp), biome, and relevant references.

Species	Family	Biome	CV (plus number of years of study)	Seed dispersal	Pollination	References
<i>Acacia adsurgens</i>	Fabaceae	Arid, semi-arid	1.47 (9)	Endozoochorous	Animal	Davies (1976)
<i>Acacia aneura</i>	Fabaceae	Arid, semi-arid	1.66 (9), 1.80 (9), 1.87 (8), 1.72 (7)	Endozoochorous	Animal	Davies (1976)
<i>Acacia craspedocarpa</i>	Fabaceae	Arid, semi-arid	2.07 (8)	Endozoochorous	Animal	Davies (1976)
<i>Acacia cuthbertsonii</i>	Fabaceae	Arid, semi-arid	1.50 (9)	Endozoochorous	Animal	Davies (1976)
<i>Acacia sclerosperma</i>	Fabaceae	Arid, semi-arid	0.95 (9), 1.36 (9)	Endozoochorous	Animal	Davies (1976)
<i>Acacia</i> sp.	Fabaceae	Arid, semi-arid	2.24 (9)	Endozoochorous	Animal	Davies (1976)
<i>Acacia tetragonophylla</i>	Fabaceae	Arid, semi-arid	1.48 (9), 1.87 (9)	Endozoochorous	Animal	Davies (1976)
<i>Acacia victoriae</i>	Fabaceae	Arid, semi-arid	2.00 (9), 1.11 (9)	Endozoochorous	Animal	Davies (1976)
<i>Atherosperma moschatum</i>	Atherospermataceae	Temperate	0.37 (6), 0.67 (6)	Wind	Animal	Hickey et al. (1983)
<i>Callitris glaucophylla</i>	Cupressaceae	Arid, semi-arid, temperate	1.72 (5)	Wind	Wind	Hawkins (1966)
<i>Corymbia maculata</i>	Myrtaceae	Warm temperate	2.52* (15)	Nonzoochorous	Animal	Pook et al. (1997)
<i>Eucalyptus camphora</i>	Myrtaceae	Temperate	0.96* (5)	Nonzoochorous	Animal	J. Greet (unpubl. data)
<i>Eucalyptus denticulata</i>	Myrtaceae	Temperate	0.34* (4)	Nonzoochorous	Animal	Murray et al. (2004)
<i>Eucalyptus diversicolor</i>	Myrtaceae	Temperate	1.49* (11)	Nonzoochorous	Animal	Loneragan (1979)
<i>Eucalyptus fastigata</i>	Myrtaceae	Temperate	1.78* (5)	Nonzoochorous	Animal	Murray et al. (2004)
<i>Eucalyptus globoidea</i>	Myrtaceae	Temperate	1.16* (4)	Nonzoochorous	Animal	Bassett (2002)
<i>Eucalyptus obliqua</i>	Myrtaceae	Temperate	0.96* (4)	Nonzoochorous	Animal	Murray and Lutze (2004)
<i>Eucalyptus regnans</i>	Myrtaceae	Montane temperate	1.23 * (5)	Nonzoochorous	Animal	Ashton (1975)
<i>Eucalyptus sieberi</i>	Myrtaceae	Temperate	0.65* (4)	Nonzoochorous	Animal	Bassett (2002)
<i>Eucalyptus viminalis</i>	Myrtaceae	Temperate	0.96* (6)	Nonzoochorous	Animal	Dooley et al. (2010)
<i>Eucryphia lucida</i>	Cunoniaceae	Temperate	0.67 (6), 0.77 (6)	Ectozoochorous	Animal	Hickey et al. (1983)
<i>Nothofagus cunninghamii</i>	Nothofagaceae	Temperate	1.05 (7), 1.30 (7), 2.12 (22)	Nonzoochorous	Wind	Hickey et al. (1983), Hickey and Wilkinson (1999)
<i>Senna artemisioides</i> subsp. <i>sturtii</i>	Fabaceae	Arid, semi-arid	201.9 (9), 172.2 (9), 174.6 (8)	Endozoochorous	Animal	Davies (1976)
<i>Senna artemisioides</i> subsp. <i>helmsii</i>	Fabaceae	Arid, semi-arid	2.33 (9), 1.49 (9), 1.99 (9), 2.25 (8)	Endozoochorous	Animal	Davies (1976)
<i>Triodia basedowii</i>	Poaceae	Arid, semi-arid	2.42 (10)	Endozoochorous	Wind	Wright (unpubl. data)
<i>Triodia pungens</i>	Poaceae	Arid, semi-arid	1.71 (10)	Endozoochorous	Wind	Wright (2021)

CVps for species with an asterisk after the CVp are our calculations based on data available in the source literature. Only those CVps for which four or more years of data are available are included (see Table S2 for cases of *Eucalyptus* with 2 or 3 years of data). For the *Eucalyptus* and *Corymbia* species, the parameter quantified was the fall of (outer) opercula into litterfall traps as a measure of variation in flowering effort. Species author citations and other details for the *Corymbia* and *Eucalyptus* datasets are provided in Table S2.

(21.1% probable; 5.0% possible) compared to the exotic flora (0.0% probable; 2.0% possible). Of the large families (i.e. families with more than 10 species), pyrogenic flowering was most prevalent in the Rutaceae (43.8% of 16 species); Fabaceae (34.3% of 35 species); Mimosaceae (31.6% of 19 species) and Goodeniaceae (30.0% of 10 species).

Australian monocots known to flower *en masse* after fire include various species of *Xanthorrhoea* (Baird 1977; Crisp et al. 2014; Fig. 1b), the Gynea lily [*Doryanthes excelsa*

Correa (Doryanthaceae); Paroissien and Ooi 2021], the sheath rush [*Cyathochaeta diandra* (R.Br.) Nees (Cyperaceae); Ingwerson 1977], the red ink sundew [*Drosera erythrorhiza* Lindl. (Droseraceae); Dixon and Pate 1978] and some members of the bloodwort family Haemodoraceae (Baird 1977). There is also clear evidence that the flowering of many ground orchids, which are very diverse in temperate Australia (Silcock et al. 2021), is either obligately associated with fire or strongly stimulated by fire (Coates and Duncan 2009). The species

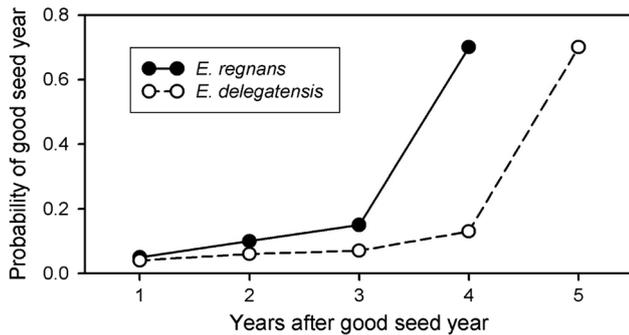


Fig. 6. Probability of repeat heavy seeding events in stands of two montane Victorian *Eucalyptus* species. The data are from Ferguson (2011; see Table 3 therein) and are based on long-term forestry records.

that are obligately dependent on fire include certain species in the genera *Burnettia*, *Leptoceras*, *Prasophyllum* and *Pyrorchis* in south-eastern Australia (Duncan 2012; Copeland and Backhouse 2022), and certain species in the genera *Caladenia*, *Cyanicula*, *Diuris*, *Eriochilus*, *Leptoceras*, *Microtis*, *Prasophyllum* and *Pyrorchis* in south-western Australia (Brown 2022). Woody podocarps and eudicotyledon species reported to flower almost exclusively in the first couple of years following fire include *Podocarpus drouynianus* F.Muell. and *P. spinulosus* (Sm.) R.Br. ex. Mirb. (Podocarpaceae; Ladd and Enright 2011), the dwarf apple [*Angophora hispida* Sm. Blaxell. (Myrtaceae); Auld 1986], *Stirlingia latifolia* (R.Br.) Steud. (Proteaceae; Bowen and Pate 2008), the wild parsley [*Lomatia silaifolia* (Sm.) R.Br. (Proteaceae); Denham and Whelan 2000], *Telopea speciosissima* (Smith) R.Br. (Proteaceae; Denham and Auld 2002), and *Nuytsia floribunda* (Labil.) R.Br. (Loranthaceae; Gardener 1957).

Proximate mechanisms that trigger post-fire flowering are reported to include heating, leaf damage, improved light or warmth around plants owing to foliage loss, and/or smoke inoculation during fire (in particular the ethylene content of smoke;) (Gill and Ingwersen 1976; Gill 1981; Lamont and Downes 2011). Evolutionary mechanisms behind synchronised post-fire flowering have been reported to relate to post-fire seedbed conditions that are optimal for seedling establishment (Bond 1985; Lamont and Downes 2011; Clarke *et al.* 2013), improved pollination efficiency for wind-pollinated species, predator satiation (O'Dowd and Gill 1984; Wellington and Noble 1985; Hanley and Lamont 2001), and increased disperser attraction for animal-dispersed species [e.g. *Podocarpus drouynianus* (Podocarpaceae); Chalwell and Ladd 2005].

Environmentally predictive masting

Ecological disturbances often result in more favourable seedling-growth environments and there can be strong fitness advantages for plants to time reproductive episodes with such events. Because weather patterns often drive spatiotemporal disturbance regimes, plants may cue into

weather signals over evolutionary time to 'pre-empt' future post-disturbance periods where seedling-survival chances are high (i.e. the environmental prediction hypothesis of masting; Williamson and Ickes 2002; Peters *et al.* 2005; Piovesan and Adams 2005). For such environmentally predictive syndromes to emerge in plant populations, there must be exposure to recurrent disturbance regimes with linkages to weather signals over evolutionary time scales. There are many examples that meet such criteria, with Vacchiano *et al.* (2021) finding that most such disturbance-linked masting syndromes were fire-related (e.g. plants that cue into weather conditions such as drought that dry out fuels and lead to widespread fires), with others relating variously to hurricane, frost, drought.

In Australia, mulga and spinifex exist in arid and semi-arid environments where extreme-high-rainfall years promote grassy fuel accumulations and lead to large-scale wildfires. Both plants respond to such rainfall periods by seeding heavily and the seed germination of both is enhanced by environmental stimuli associated with the passage of fire (high temperatures for mulga seeds, and the butanolide karrikinolide (KAR1) present in smoke for spinifex seeds; Davidson and Adkins 1997; Wright and Fensham 2016). As seedbank persistence is constrained in arid Australia by dense granivore populations, mulga and spinifex masting during flammable periods has multiple, potentially selective, benefits: satiation of pre- and post-dispersal seed predators, the triggering of germination of fire-cued dormant seeds, and enhanced survival of seedlings in favourable post-fire environments (Wright and Fensham 2017, 2018).

For mulga and spinifex, fire timing in relation to masting is a key driver of seedling recruitment after fire (Wright and Fensham 2017, 2018). Because seedbanks are depleted rapidly by granivores after masting, fires during the early post-mast period typically trigger profuse post-fire seedling recruitment because the abundant granivore fauna are temporarily overwhelmed and seedbank densities are high (Fig. 7). Conversely, fires that occur during inter-mast periods are usually associated with much lower rates of regeneration, as seedbanks during such periods have generally been depleted by high rates of seed depredation by granivores (Wright 2007; Wright and Zuur 2014; Wright and Fensham 2018).

Evolutionary ecology

The evolutionary ecology of masting has not been extensively studied in Australia. For wind-pollinated masting plants, synchronised reproduction can relate to enhanced availability of outcross pollen during mast years (pollen coupling; Iwasa and Satake 2004), or to fluctuating environmental conditions such as drought or excessive rainfall driving pollination failure over large spatial areas (the Moran effect; Bogdziewicz *et al.* 2017). In Australia, although experimental studies are lacking,

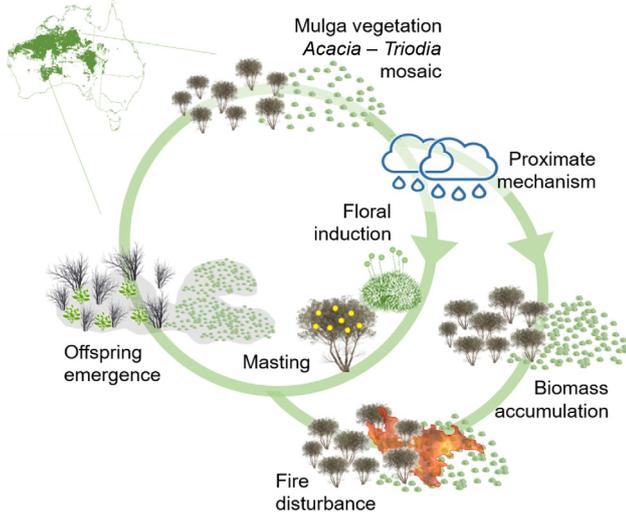


Fig. 7. Mechanistic drivers of post-fire seedling recruitment of fire-sensitive *Acacia aneura* shrubs and *Triodia* spp. grasses in arid Australia. High-rainfall periods provide a proximate mechanism that synchronises masting and leads to fuel accumulations and increased fire likelihood. Map shows occurrence of *Triodia* grasslands in Australia (northern regions where *Triodia* is a common subdominant species not included). Figure previously published by Vacchiano *et al.* (2021) reproduced with permission.

enhanced wind-pollination efficiency as a possible selective benefit behind masting has been suggested for the bunya pine (Burrows and Stockey 1994; Smith and Butler 2002), river oak (*Casuarina cunninghamiana* Miq.; Woolfrey and Ladd 2001), white and blue cypress pines (*Callitris glaucophylla* and *C. intratropica*; Hawkins 1966; Stocker 1966; Thompson and Johnson 1986), Top End bamboo (*Bambusa arnhemica*; Franklin 2004), and Wollemi pine (*Wollemia nobilis* W.G.Jones, K.D.Hill & J.M.Allen; Zimmer *et al.* 2015).

The predator satiation (PS) hypothesis of masting holds that mast reproduction is an anti-predator strategy that overwhelms seed consumers during mast years and starves them during intervening low-output years (Janzen 1971; Silvertown 1980). The PS hypothesis has been supported by experimental evidence from two Australian studies [O’Dowd and Gill 1984 (*Eucalyptus delagatensis*) and Wright 2021 (*Triodia pungens*)] but not from two others [Ballardie and Whelan 1986 (*Macrozamia communis*); Denham and Auld 2002 (*Doryanthes excelsa* and *Telopea speciosissima*)]. Aside from these experimental studies, predator satiation has been suggested as being a possible evolutionary driver behind high reproductive CVP in the bunya pine (Smith and Butler 2002), slender mulga (Wright and Zuur 2014; Wright *et al.* 2016; Wright and Fensham 2017), the black booyong (Nadolny 1999), *Chrysophyllum* sp. nov. (Connell and Green 2000), the emu berry (*Podocarpus drouynianus*; Chalwell and Ladd 2005; Ladd and Enright 2011), various species of *Eucalyptus* (Franklin *et al.* 2016), and the celery

top pine (*Phyllocladus aspleniifolius* (Labill.) Hook.f., Podocarpaceae; Barker 1995).

A masting hypothesis with few examples of empiric testing and validation, either in Australia or overseas, is the animal-dispersal hypothesis (Kon *et al.* 2005; Zwolakl *et al.* 2016). This hypothesis holds that masting improves animal seed-disperser attraction and/or results in increased dispersal distances of animal-dispersed seeds. In Australia, the animal-dispersal hypothesis was not supported by experimental studies on *Macrozamia communis* (Ballardie and Whelan 1986) and Connell and Ladd (1993) noted that 45% of seeds remained undispersed and within 0.5 m of parent plants during a mast year. Similarly, in a study of seed dispersal and masting in *Macrozamia miquelii* (F.Muell.) A.D.C., Hall and Walter (2013) found low levels of seed dispersal in masting populations in central Queensland. These authors hypothesised that the seeds of this species were not adapted to dispersal by contemporary fauna, but to dispersal by Australia’s vast extinct megafauna, which would have transported large numbers of seeds in their guts and facilitated grove formation by passing them collectively at new locations.

In parts of the world affected by the El Niño–Southern Oscillation (ENSO) climatic pattern, inter-annual fluxes in the El Niño and La Niña warm and cool phases are believed to drive masting in forest trees (Schauber *et al.* 2002; Wion *et al.* 2021). In Southeast Asia, ENSO-linked droughts synchronise flowering in the Dipterocarpaceae. It has been hypothesised that drought-triggered masting in these species represents a form of environmental prediction, because it improves the likelihood of seedling establishment as droughts reduce root competition and increase light resources after canopy death (Williamson and Ickes 2002). In Australia, Fletcher (2015) drew on data from contemporary and palaeo-ecological/paleoclimatic (~130 000 years) studies to analyse pollen production cycles of the Tasmanian Huon pine (*Lagarostrobos franklinii*). He found that over the study period, pollen production was in step with the frequency and amplitude of El Niño events. In accord with the conclusions of Piovesan and Adams (2005) and Williamson and Ickes (2002), it was suggested that forest-floor vacancies and enhanced light conditions created in closed Tasmanian forests during strong El Niño events may have provided a selective stimulus that has accentuated reproductive synchrony in huon pine and driven selection for masting.

Management

Management interventions that affect the intensity (i.e. output), timing and/or synchrony of flowering and seed-crop production are likely to have important implications for the conservation of Australian masting species and the wildlife that depends on them. Fire management is one of

the most widespread and frequently used management tools in Australia. It is used in many systems by pastoralists to increase productivity and improve the palatability of grasses for grazing animals (Craig 1999). It is also used by Aboriginal peoples to promote the growth of fire-promoted food plants (e.g. *Solanum centrale* J.M.Black, *S. chippendalei* Symon; Latz 2018), and by conservation managers to promote biological diversity and to reduce fuel loads (Allan and Southgate 2002; Gamage *et al.* 2012).

As previously discussed, fire timing in relation to masting can have strong implications for population regeneration of arid mulga and spinifex species. Fire timing in relation to masting is also likely to have strong implications for regeneration of many resprouting eucalypt species. Fire may adversely affect flowering of eucalypts either by burning immature reproductive structures and, particularly in the event of canopy loss, by causing trees to redirect resources to canopy regrowth (Setterfield and Williams 1996; Law *et al.* 2000). In Tasmania, marked adverse effects of fire on flower production were observed for two eucalypts, *E. globulis* Labill. (southern blue gum) and *E. ovata* Labill. (swamp or black gum), whose flowering intensity varies among years and whose nectar is important food for a threatened bird species, the swift parrot, *Lathamus discolor* (Hingston and Piech 2011). In sub-tropical areas, relationships with time-since-fire can be complex and management implications can be unclear because widespread crown fires may impede, or synchronise, subsequent flowering depending on the species (Law *et al.* 2000).

In addition to fire management, silvicultural practices such as stand thinning and logging are likely to have impacts on many Australian masting species by influencing pollen loads of wind-pollinated species and by affecting the density of seed trees available for regeneration after logging. Hickey *et al.* (1983) cautioned that logging operations in forests dominated by *Nothofagus cunninghamii* should wait until after major seed-fall events occur, because the seeds of this species are short-lived (~2 years) and sufficient seed for regeneration may be available only for short periods after high-output seeding years. In eucalypt forests, clear-fell logging eliminates nectar production for a number of years until trees reach reproductive age (Birchnell and Gibson 2006). This effect is then extended because younger reproductive-age trees flower less often and are substantially less productive than are older trees when flowering (Law *et al.* 2000; Law and Chidel 2009). The effects of selective logging on eucalypts are less definitive than clear-fell logging, but may vary from strongly negative (Law and Chidel 2009), to variable and species-dependent (Law *et al.* 2000; Birchnell and Gibson 2006).

Masting also has management applications for conservation of threatened species dependent on mast crops as food, as reviewed in a global context by Pearse *et al.* (2021). In Australia, several animal species have been bred for reintroduction and/or translocation and are known to feed

on the flowers or seeds of masting plants. As such, the timing of reintroductions of these animals relative to masting may be critical. Such animals include the bilby (mast crop: seeds of *Triodia* grasses; Southgate and Carthew 2007), the mala or rufous hare wallaby (mast crop: seeds of *Triodia* grasses; Bolton and Latz 1978), and the emu (*Dromaius novaehollandiae*; mast crop: seeds of *Acacia aneura*; Davies 1978). Additionally, the critically endangered regent honeyeater (*Anthochaera phrygia*) and the endangered swift parrot are being reintroduced and depend heavily on the mass-flowering of eucalypts for nectar (Franklin *et al.* 1989; Crate *et al.* 2017).

Masting events may also be linked to the spread of zoonotic diseases (Pearse *et al.* 2021). Overseas, human incidences of Lyme disease, spotted fever, African swine fever, haemorrhagic fever, and hantavirus have been associated with population explosions of animal hosts that feed on mast crops (Jaksic and Lima 2003; Reil *et al.* 2017). Consequently, knowledge of the weather conditions that trigger masting, and prescribing management activities during population peaks of host species, may result in more successful control of outbreaks of these diseases. In Australia, flying foxes (genus *Pteropus*) that feed on the nectar and/or pollen from flowers of various masting species are carriers of the potentially fatal Hendra virus and bat lyssavirus (Plowright *et al.* 2008; Moore *et al.* 2010). Ominously, hantavirus antibody-positive rodents have been found across the continent, although as yet there have been no confirmed human cases (Bi *et al.* 2005). Awareness of mast-linked outbreaks of host species and close sero-epidemiological monitoring of humans (and hosts) in regions where host outbreaks occur is therefore warranted for public health management.

For masting species with seeds that are harvested for human consumption, optimising the timing and quantity of harvests of mast crops can be important to ensure that adequate seed remains in a system for animal consumers and for regeneration of masting populations. There are many examples from other parts of the world where markets exist for wild-harvested mast crops. Some of these are small-scale and local, such as the markets for bilberry and wild durian (Salafsky 1995). Others are large-scale and global, such as the markets for pine nuts (Awan and Pettenella 2017) and acorns (Overstreet *et al.* 2015). In Australia, the crops of masting species such as the bunya pine and mulga are used in the burgeoning bush foods industry (Smith and Butler 2002; Walsh and Douglas 2011). Although neither are as yet globally traded, both produce gluten-free flours, and hence could increase in popularity as the demand for alternative flours increases. Over-exploitation of the crops of these species, with carry-over effects on regeneration and wildlife, could occur if demand increases continue and unregulated commercially-oriented wild harvest occurs at large scales.

Conclusions and recommendations for research

There has been only limited formal recognition of masting as a reproductive phenomenon in long-lived Australian plants. However, we have shown that synchronised supra-annual reproduction is a feature of numerous species, including many that are dominant across a wide range of Australian ecosystems. These species include many eucalypts in forests, woodlands and savannas; dominant *Acacia* species through much of arid and semi-arid Australia; spinifex (*Triodia* spp.) grasses in arid grasslands; trees of temperate, subtropical and tropical rainforest (although documentation of these is limited); and many pyrogenic flowering monocots in heathland and temperate open forests.

A major contributor to the failure to recognise the prevalence of masting in Australia has been the scarcity of phenological data gathered over multiple years. To increase understanding of the diversity of the phenological syndromes in the Australian flora, existing but unpublished natural history data relating to Australian masting species should be published or made publicly available. Also, where possible, long-term flowering and seed-fall studies in plant communities should be initiated across a range of habitats.

It follows from the prevalence and frequent dominance of masting species in so many Australian vegetation communities that a strong grasp of masting processes is essential to understanding and successfully managing Australian ecosystems. Potential areas for future research include further understanding the role of specific weather events and climate as drivers of reproduction and reproductive failure; the impact of management interventions including fire management, logging, and harvesting on reproductive success and ecosystem stability; and understanding the evolutionary drivers behind high plant reproductive CVps in Australia. Finally, because masting in most species is cued by weather or fire (bamboo notably excepted), masting plants and the ecosystems in which they feature may be particularly susceptible to the impacts of anthropogenic climate change. This is now being recognised in masting species outside of Australia (Czeszczewik *et al.* 2020; Hackett-Pain and Bogdziewicz 2021; Karniski 2021). However, there has been little consideration given to this topic in Australia and research in this key area is urgently required.

Supplementary material

Supplementary material is available [online](#).

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