

**The Forgotten Savannas of Western Victoria:  
Population Dynamics of Tree-form Silver Banksia (*Banksia  
marginata*) in a Severely Fragmented Landscape**

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An example of a *Banksia marginata* tree at Longpoint Reserve, western Victoria, Australia.

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## **STATEMENT OF AUTHORSHIP**

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis accepted for the award of any other degree or diploma.

No other person's work has been used without due acknowledgment in the main text of the thesis.

This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Chapters 2 and 3 are co-authored manuscripts intended for journal publication, the data collection, analysis and writing for these chapters was undertaken by me (SDH). The listed co-authors provided comments, edits and input of ideas behind these chapters.

Simon David Heyes

01 January 2020

## **PREFACE**

This thesis was written with an intention that Chapters 2 and 3 be submitted for publication in peer-reviewed journals. These were written as separate manuscripts and, consequently, there is some repetition, particularly in the Methods sections where the study system and study species have been described. Chapters 2 and 3 are co-authored manuscripts and therefore, I use the collective first person (we) while the rest of the thesis uses singular first person (I). Despite this, much of the work undertaken in this thesis was undertaken by me (SDH), including the design and implementation of field and laboratory experiments, the collection of data, statistical analyses and writing.

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## ABSTRACT

Land clearing for agriculture is a major cause of habitat fragmentation globally and this can have many deleterious effects on native ecosystems. Many fragmented habitats are at risk of changes to disturbance regimes (fire), inbreeding risk and changes to important plant-animal interactions. Many smaller populations that remain in fragments might be subject to reduced fitness (Allee effect), increased risk of stochastic extinction or a slow and inexorable decline towards extinction (extinction debt hypothesis).

*Banksia marginata* savanna in western Victoria are extremely fragmented because of land clearing for agriculture since European settlement. Many populations are recruiting well, however, recruitment becomes increasingly limited in smaller populations and represents an Allee effect. While natural plant-animal interactions, such as seed predation, is likely to be an important cause in small populations.

Two overarching questions were explored in this thesis, the first was to ask if fragmented populations of *B. marginata* (Proteaceae) were experiencing widespread recruitment bottlenecks across the study area. The second related question set out to determine if seed predation by the Yellow-tailed Black Cockatoo (*Calyptorhynchus funereus*) is a possible cause of recruitment limitation. I attempted to answer these questions by first evaluating stand dynamics to look for evidence of self-replacement (i.e. recruitment) and examine cone production to ascertain if seed set failure was an important contributor to recruitment-limitation. I then investigated the role of seed predation by *Calyptorhynchus funereus* on cone removal, seed losses and seed fitness.

Most populations (7 out of 15) were not recruitment limited as they contained substantial numbers of individuals across the smaller size classes. Five populations were found to be moderately recruitment limited with flatter size class distributions and smaller numbers of trees in the smaller size classes. Only three populations were

severely recruitment-limited, with little to no trees evident in the smaller size classes, suggesting these may be experiencing a recruitment bottleneck. Conforming to demographic Allee effects in smaller populations, recruitment declined sharply in populations below 100.

Cone set failure was widespread across all populations studied and this was extremely high in three populations, though two of the three populations experiencing recruitment bottlenecks were not included due to low sample size in these populations. My data suggests that an avian seed predator, likely *C. funereus*, was the most likely cause and I found high (> 50 – 100%) removal of cones between December and March. The timing of seed predation affected both seed release and seed fitness from discarded cones; seed predation in this study was a likely cause of the recruitment-limitation seen in some *B. marginata* stands from western Victorian.

Smaller populations below 100 individuals should be the focus of restoration efforts to raise populations above this critical number. For the species to persist in this landscape, every effort should be made to undertake largescale-scale restoration of grassy *Banksia* savanna across parts of western Victoria reduce impacts of seed predation and avoid demographic Allee effects.

# CHAPTER 1

## GENERAL INTRODUCTION

### *Fragmentation*

Globally, species loss is accelerating at an unprecedented rate with the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) estimating that around 1 million species of plants and animals are threatened with extinction; to date, 75% of terrestrial environments have been altered (IPBES, 2019). While the loss of species to land clearing is clearly evident, it is important to note that the fate of species that persist in habitat fragments can often be less clear.

The concept of fragmentation was first explored in the 1950s and 1960s (Moore, 1962; MacArthur and Wilson, 1967) and much has been done to understand how fragmentation, and the small population sizes that result, affect communities, populations and individuals (Allee, 1931; Gilpin and Soulé, 1986; Tilman *et al.*, 1994). The extinction debt hypothesis was first described by Tilman *et al.* (1994), who took a community level approach and developed a concept to explain the effects of fragmentation. Their mathematical model predicts the persistence of some species in fragmented habitat may be transient until a future point, at which they become extinct. Much of the work to test the extinction debt hypothesis comes from organisms with fast population turnover, such as the work by Gonzalez (2000) on arthropod communities in bryophyte fragmentation experiments. However, for longer-lived organisms, the long-time span between fragmentation and a population repaying its “debt” (extinction) means that the extinction debt hypothesis is difficult to experimentally test. Trees, for example, may persist for centuries, or even thousands of years (Schulman, 1954; Lynch *et al.*, 1998), while clonal and lignotuberous plants occupy the extreme end of the persistence niche (Bond and Midgley, 2001), perhaps persisting in fragments indefinitely such as the

naturally fragmented *Wollemia nobilis* stand in Wollemi National Park, NSW (Jones *et al.*, 1995; Burrows *et al.*, 2003). Determining whether extinctions are due to relaxation since fragmentation, or stochastic events along the way, is not always clear.

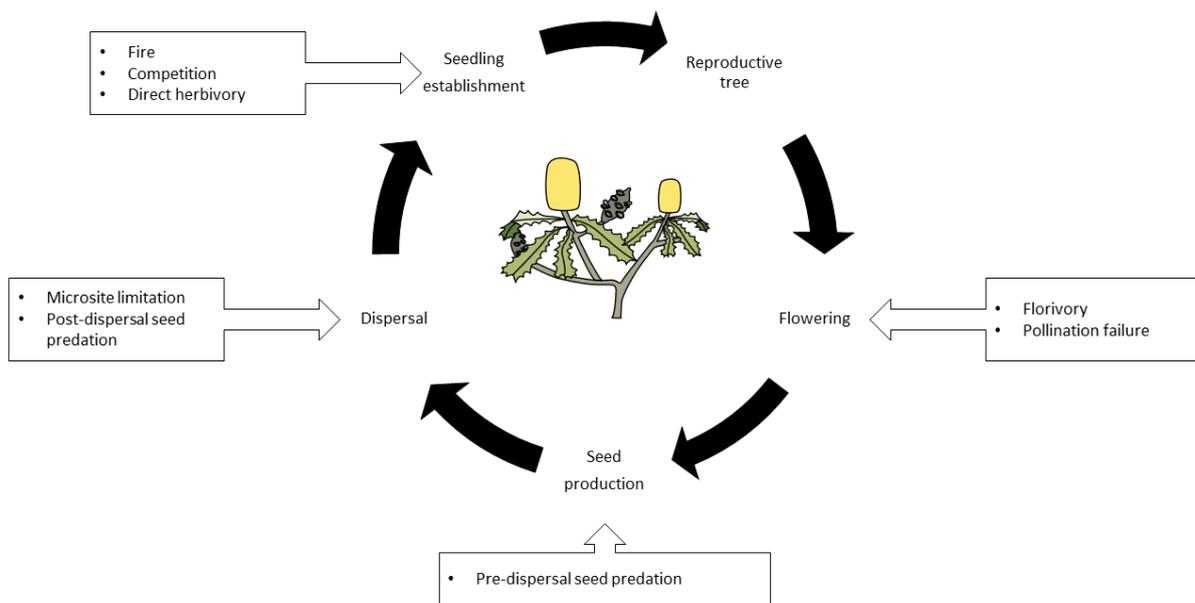
The process of fragmentation reduces populations to smaller sizes, and these are then susceptible to potentially catastrophic stochastic extinction events. As explained by Gilpin and Soulé (1986), this can lead to the immediate or deterministic extinction of a population, or further reduce the population, thereby leaving it vulnerable to future stochastic events (Potvin *et al.*, 2017). This positive feed-back, whereby a population is whittled away until its ultimate extinction, is known as the ‘extinction vortex’ (Gilpin and Soulé, 1986). These small populations may also be susceptible to Allee effects (Ghazoul *et al.*, 1998; Firestone and Jasieniuk, 2013) resulting in a loss of fitness, reducing a population’s ability to respond to environmental changes and disturbance, further pushing the population into the extinction vortex.

The Allee effect, named after Warder Allee’s work on animal aggregations (1931), is used to describe the relationship between population size or density and the fitness of individuals (Stephens *et al.*, 1999) and one may argue that the Allee effect and extinction vortex are intrinsically linked. Allee effects may manifest in reduced mate availability in smaller populations in animals (Hinton *et al.*, 2018; Pavlova *et al.*, 2016; Somers *et al.*, 2008) and plants (Byers and Meagher, 1992; Campbell and Husband, 2007; Morgan, 1995; Morgan, 1999; Yule and Bronstein, 2018). In plants, this is further compounded where plant self-incompatibility (SI) alleles are present, thus further reducing mate availability (Byers and Meagher, 1992; Levin *et al.*, 2009; Morgan *et al.*, 2013; Pickup and Young, 2008). Allee effects also manifest in other ways; for example, seed set may be much lower in smaller populations (Lamont *et al.*, 1993; Severns, 2003) and this may be a result of mate availability, limited pollinator visits (Agren, 1996;

Cheptou and Avendaño V, 2006) or predation of seed by granivores (Francisco *et al.*, 2002). This may limit recruitment by seed and lead to demographic bottlenecks, with few juveniles to replace an ageing population.

### ***Recruitment Limitation***

The ‘recruitment limitation’ hypothesis was first coined in the marine reef fish literature by Doherty (1981). Doherty suggested that recruitment of fish larvae to a reef determined population dynamics and that they were not necessarily regulated by density-dependent competition but by the supply of fish larvae to a given reef. However, Hixon



**Figure 1.** Schematic of the different reproductive stages of a tree and some causes of recruitment limitation affecting different stages. This study will investigate recruitment limitation occurring at the seed production phase, namely pre-dispersal seed predation.

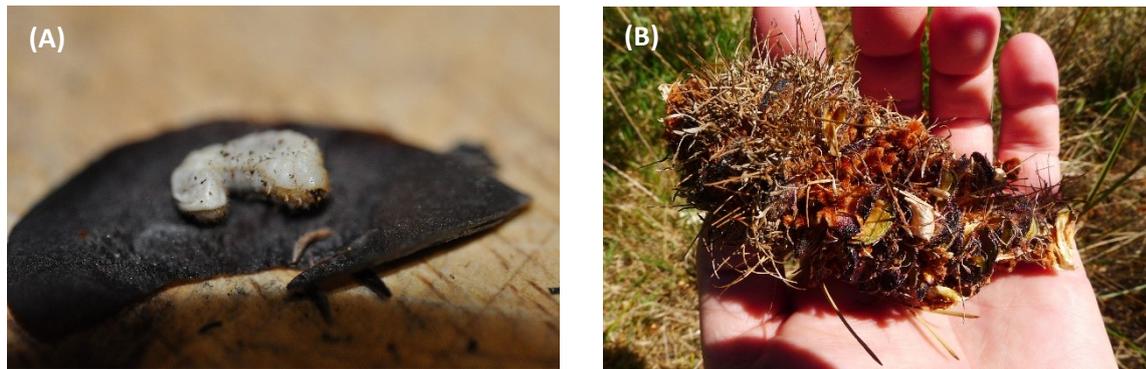
(1998) suggests recruitment limitation was likely to occur at multiple stages of an organism’s life cycle (Fig 1.). This may be habitat- or species-specific, particularly in plants where propagule dispersal strategies are varied. Demographic bottleneck studies

need to be able to identify at which stage recruitment limitation is occurring to provide effective management solutions to prevent population decline (e.g. Young *et al.* 2000).

In plants, recruitment limitation can be broken down into (i) pre- and (ii) post-dispersal recruitment limitation. Pre-dispersal recruitment limitation can occur in plants at the reproductive life stages and can include flowers, spores and seed. These can include biotic factors, such as plant pathogens (Powell *et al.*, 1992; Wilson *et al.*, 2017), or abiotic factors (Chang-Yang *et al.*, 2016; Fang *et al.*, 2009; Ogaya and Peñuelas, 2007). Post-dispersal recruitment limitation occurs once seed has been dispersed either by the parent plant or by a dispersal agent and can affect seed or young plants. Examples of these can be post-dispersal seed predation (Janzen, 1971), lack of suitable microsites (Morgan, 1997) or herbivory (MacDougall *et al.*, 2010; Tolera *et al.*, 2013)

Floral herbivory, or florivory, has been well documented in angiosperms (Carper *et al.*, 2016; Louda and Potvin, 1995; McCall and Barr, 2012; Soper Gordon and Adler, 2016), and this interaction has been shown to be important in the selection of floral traits such as colour (McCall *et al.*, 2013) and florivory defence (Lai *et al.*, 2015). Pollen, or the absence of pollination services, is also important factor in determining seed set (Pattimore and Anderson, 2013; Steffan-Dewenter and Tscharntke, 1999; Whelan and Goldingay, 1986) and flower exclusion studies show that some guilds of pollinators are more effective pollinators than others, with lower seed or fruit set an outcome of poor pollinator service (Botes *et al.*, 2009; Cunningham, 1991; Melidonis and Peter, 2015). In some cases, this can have catastrophic effects for seed set and plant recruitment (Anderson *et al.*, 2011) and pollinator loss might be particularly important if plant-pollinator mutualism is species-specific, such as in many orchids or figs (Wilcock and Neiland, 2002).

If flowers have avoided floral herbivores and have succeeded in the pollination lottery, the successful development of seeds is the next hurdle to overcome. Pre-dispersal seed loss has the potential to determine plant recruitment each year and excessive loss may represent an Allee effect in small populations of threatened plants (Kurkjian *et al.*,



**Figure 2.** (A) Unidentified beetle larvae extracted from the serotinous infructescence of *Banksia serrata*, south-eastern Australia (Photo by Susan Hoebee, 2012) and (B) evidence of vertebrate seed predation in *B. marginata* infructescence (Photo by Simon Heyes, 2018).

2017). Pre-dispersal seed losses can vary significantly between species, even among closely related co-occurring species (Espelta *et al.*, 2009). Habitat quality has been linked to rates of pre-dispersal seed loss (Francisco *et al.*, 2002), though this may not be the case in all systems (Brudvig *et al.*, 2015). Seeds are a relatively passive phase in a plant's life cycle; in some cases, they may persist on the plant for many years until they have dispersed (Barrett *et al.*, 2005; Bond, 1985; Su *et al.*, 2017). Seeds are also higher in nutrients compared to other plant parts (Janzen, 1971) providing larger nutritional reward for specialist herbivores that can access them. Seed predation by both invertebrates and vertebrates (Fig. 2) is a particularly important cause of pre-dispersal seed loss in gymnosperm and angiosperm taxa. A study in Argentina into pre-dispersal seed loss in two species of *Prosopis* (Fabaceae), for example, found that in one species seed loss was 32% and that 19% was attributable to invertebrate seed predators (Velez *et al.*, 2018). A study of the widespread daisy *Taraxacum officinale* found similarly large

proportions of seed damaged by pre-dispersal seed predators (Honek *et al.*, 2005). While seed predation by birds accounted for ~80% of pre-dispersal seed loss in *Pinus sylvestris* (Castro *et al.*, 1999) and seed predators have also been reported in cypress species (Battisti *et al.*, 2003).

In plants, recruitment can be constrained by low resource availability (resource limitation) (Iacona *et al.*, 2010) and, in some systems such as savannas, this can be facilitated by the interaction with other life forms such as grasses (Morrison *et al.*,



**Figure 3.** A roadside population near Ballarat, Victoria with older, senescing and dead *Banksia marginata* trees and no apparent evidence of recruitment to replace dying trees. recruitment limitation acts as a filter to prevent recruits from reaching reproductive age. The causes can occur at one or many stages of the plant's life cycle.

2019). recruitment limitation may also occur through consumers mediated limitation such as post-dispersal seed predation (Forget *et al.*, 2005), direct herbivory (MacDougall *et al.*, 2010; Salk *et al.*, 2011; Tolera *et al.*, 2013) or fire (Nguyen *et al.*, 2019; Prior *et al.*, 2010); however, fire-tolerant plants may merely be suppressed until fire or grazing has been eased (Knapp *et al.*, 2018; Laris, 2008).

### ***Fragmentation and the Loss of a Keystone Tree***

The decline and loss of keystone species can be felt across an entire community, affecting the abundance or presence of other species, thereby affecting community assembly (Morgan and Brown, 2001; Paine, 1966; Paine, 1969). Understanding whether keystone species are in decline, and why, is a critically important task that allows for timely conservation management of the organism and other species that might rely on it.

*Banksia marginata* (Proteaceae) is an important (but largely unrecognised) keystone species in savannas and woodlands of the basalt plains in western Victoria. It provides nectar resources for vertebrate and invertebrate species, a seed source for granivorous birds and insects, and acts as a host for the *B. marginata* specialist gall wasp *Mesostoa kerri* (Austin and Dangerfield, 1998; Wilson *et al.*, 2017). While this species is widespread across south-east Australia (Collins, 2009; Taylor, 1988), its role as a keystone species is situational and probably more important in grassy ecosystems where forest species like *Eucalyptus* are largely absent. Flowering in grasslands occurs mostly in cooler months (Groves, 1965), with peaks in flowering between September to December. Flowering of *B. marginata* have been observed to occur from March onwards (S. Heyes, pers. obs), thereby providing an important resource outside of the grassland peak flowering time. This species, however, has suffered widespread land clearing since European settlement (Hateley, 2010; Sinclair and Atchison, 2012) and while much of the cascading effects of their loss will have already been felt, but the remaining fragments are likely important for many organisms. Because many *B. marginata* populations are now small and exist in a fragmented landscape, they are subject to both determinate extinction events and the further erosion of the population through stochastic events as they slip inexorably into an extinction vortex. These smaller populations may also suffer from Allee effects such as lower seed set and recruitment, leaving only older individuals

in stands. Eventually older trees will senesce, further reducing population size and the pool of reproductive trees (Fig 3).



**Figure 4.** Lone veteran *Banksia marginata* at Dundonnell, Victoria was reported to have died in 2015 with no obvious recruitment to replace the individual (Photo by Susan Hoebee, 2011)

## THESIS RATIONALE AND AIMS

Concern amongst land managers and community groups has been growing that fragmented populations of *Banksia marginata* are continuing to decline, and that this decline is even accelerating amid anecdotal reports of dead and dying veteran trees (Fig 4), a failure to produce seed (Liber, 2004) and widespread absence of recruitment. This spurred the establishment of community groups and projects such as the Bring Back the *Banksia* project by the Australian Network for Plant Conservation (Driver, 2016) and the Friends of the Forgotten Woodlands in 2015 (FoFW, 2016) to mobilise on-ground action to protect and restore *B. marginata* populations. Based on some of this concern, it makes

sense to test some of the hypotheses around widespread recruitment failure in the species, low seed set, and associated contributing factors.

Chapter 2 is titled How widespread are recruitment bottlenecks in fragmented populations of the savanna tree *Banksia marginata* (Proteaceae)? This chapter tested the assumption that *B. marginata* is experiencing widespread seed set and recruitment failure across western Victoria. This was done by investigating stand dynamics across multiple populations spanning different population sizes, and quantifying seed set across each stand.

Chapter 3, titled Effects of pre-dispersal seed predation on fruit crop and seed fitness in a highly fragmented savanna tree, further examined the determinants of seed limitation by investigating the causes behind the absence of cones observed in Chapter 2, specifically how an avian seed predator affects *B. marginata* reproductive output.

Chapter 4 brings together the findings of these two studies and makes general recommendations for both future research and ongoing conservation management.

Each experimental chapter was written as a manuscript for publication. Chapter 2 has been submitted to Plant Ecology and Chapter 3 has been submitted to Austral Ecology. As such, there is some unavoidable duplication of introduction of concepts, species and system descriptions in the thesis presented here.

## CHAPTER 2

# How widespread are recruitment bottlenecks in fragmented populations of the savanna tree *Banksia marginata* (Proteaceae)?

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### **Abstract**

Land clearing of habitat into smaller isolated remnants is a major driver of plant and animal extinctions globally. In south-eastern Australia once widespread temperate savannas have been subjected to extensive land clearing since European settlement. However, some small fragments have persisted but declines in the dominant trees have been reported, with anecdotal observations of widespread recruitment bottlenecks and seed set failure. To test the hypothesis that populations of *Banksia marginata* in the study area are experiencing widespread recruitment bottlenecks, we examined tree size class distribution and production of infructescences (cones) of 15 populations on the western plains of Victoria, Australia. We found no evidence of widespread recruitment bottlenecks or a failure to set seeds: most populations were recruiting, though we did find evidence of declining recruitment with

population size, suggesting evidence of a potential Allee effect. The proportion of trees without cones varied between populations with three populations having large numbers of trees (>40%) lacking mature fertile cones. Managers should focus on minimizing threats to seedling survival and augment populations below 100 individuals to improve recruitment and maintain stand persistence in the landscape.

**Keywords:** Allee effect, Demography, seedling regeneration, senescence, size-class distribution.

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## INTRODUCTION

Fragmentation is a global problem with around 1.5 billion hectares of habitat converted to farmland (IPBES, 2019). In temperate South-East Australia, extensive land clearing since European settlement (Bennett, 1993; Bradshaw, 2012; Chesterfield, 1986; Gordon *et al.*, 2003) has resulted in highly fragmented ecosystems, particularly temperate grasslands (Kirkpatrick *et al.*, 1995) and woodlands (Fisher & Harris, 1999; Yates & Hobbs, 1997). Fragmentation can have many detrimental effects on species in the remnant ecosystems. The slow decline of remnant tree populations in fragments represents an extinction debt (Tilman *et al.*, 1994), and has been reported elsewhere in woodlands and savannas (Abrams, 2003; Mogoutnov & Venning, 2014; Tolera *et al.*, 2013). For instance, smaller population sizes inhabiting uncleared fragments may be vulnerable to the effects of inbreeding or stochastic events that further reduce population sizes (Morgan *et al.*, 2013; Westemeier *et al.*, 1998). However, in the short term, indirect effects of fragmentation on animal-plant interactions also have the potential to drive changes to plant populations (Kolb, 2008). The loss of insectivorous birds in forest fragments

has, for example, been linked to increased insect herbivory (Elzinga *et al.*, 2005; Levey *et al.*, 2016; Peter *et al.*, 2015). Habitat fragmentation can also lead to changes in foraging behaviour of pollinators (Elliott *et al.*, 2012; Goverde *et al.*, 2002; Montgomery *et al.*, 2003) or changes in the composition of the pollinator community (Brosi *et al.*, 2007; Elliott *et al.*, 2012; Hatfield & LeBuhn, 2007). With such changes in animal-plant interactions, there is potential for small populations to be subject to Allee effects (Allee, 1931; Lamont *et al.*, 1993) that impact plant fitness or recruitment.

Size and age class distributions can provide insights about plant populations that can be used to make inferences about the demographic trajectory (Hazard & Parsons, 1977; Tolera *et al.*, 2013) or reproductive biology of a species (Ashton, 1976; Zammit & Westoby, 1987). This makes age and size class data particularly useful when investigating long-term declines in recruitment, particularly for species that recruit continually and should exhibit the reverse j-curve type distribution (Glenn-Lewin *et al.*, 1992; Lykke, 1998). A demographic bottleneck can be defined as the decline in populations size in one or more size or age classes (Beck, 1995; Holdo *et al.*, 2014). Demographic bottlenecks may be caused by disturbance such as a fire that removes the reproductively mature plants from a population (Enright & Lamont, 1989) or herbivores that may browse the smaller, younger recruits (Di Stefano, 2003). A demographic bottleneck may not be a problem in the short-term if the cause is fleeting, however long-term demographic bottlenecks may lead to population decline (population bottleneck). For example, short fire intervals may reduce population sizes in resprouters (Fairman *et al.*, 2017), while long-term herbivory has led to population declines in many species (MacDougall *et al.*, 2010; Salk *et al.*, 2011; Tolera *et al.*, 2013).

The savannas of western Victoria were once dominated by tree species such as *Banksia marginata* (Proteaceae), *Allocasuarina verticillata* (Casuarinaceae), *Acacia melanoxylon* (Fabaceae) and *Bursaria spinosa* (Pittosporaceae) (Sinclair & Atchison, 2012). Early reports

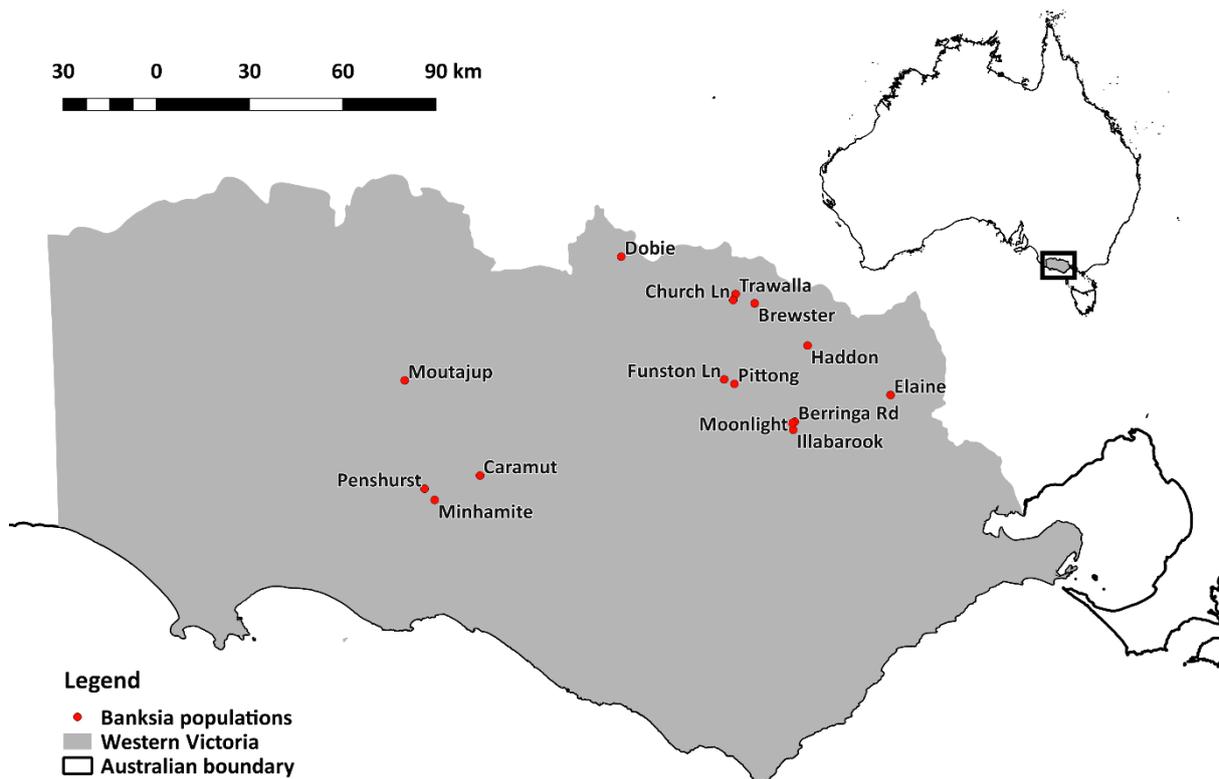
and surveyors' maps show that these trees were once widespread, but scattered in these savanna-like ecosystems (Nicholson, 1855; Webster, 1858); more recent interpretations of vegetation change confirm that these landscapes were once common across western Victoria (Hateley, 2010; Sinclair & Atchison, 2012). However, they are now either locally extinct or verging on extinction due to extensive land clearing and habitat fragmentation (Sinclair & Atchison, 2012). As such, trees like *B. marginata* may be vulnerable to the effects of small population size, altered biotic interactions and disturbance regimes. There are concerns among land managers that trees are experiencing widespread decline, demographic bottlenecks and low fecundity. In non-serotinous species, such as *B. marginata*, where seed release is not cued by fire (Lamont & Enright, 2000), ongoing recruitment might be expected if viable seeds are produced continually and 'safe sites' (Harper *et al.*, 1965) are maintained.

Fragmented stands of *B. marginata* are reported to be in decline by land managers, with reports of widespread failure to set seed and a lack of recruitment, although empirical data are lacking to support these assertions. There have been several attempts to grow savanna trees in isolated stands and expand the remnant populations, create additional insurance populations, and create seed orchards. Such efforts have been led by community groups across western Victoria, reflecting widespread community concern (Liber, 2004; Swan, 2017). In this study, we test the hypotheses that *B. marginata* are suffering widespread failure to produce seed and that there are widespread demographic recruitment bottlenecks across western Victoria. However, studies in other *Banksia* species suggest some are self-incompatible (Ramsey & Vaughton, 1991) and an alternative hypothesis is that small populations are vulnerable to small population Allee effects (Lamont *et al.*, 1993).

## METHODS

### *Study area*

The study aimed to sample remnant *Banksia marginata* populations across western Victoria and encompassed an area between the towns of Hamilton (37° 44' 31.6" S, 142° 01' 43.8" E) in the West to Ballarat (37° 36' 46.0" S, 144° 14' 11.7" E) in the East (Figure 1). The climate is Mediterranean, with winter-dominant rainfall and summer drought. Mean annual rainfall ranges between 558–702 mm, and mean temperatures range 7.1–19.2 °C (Australian Bureau of Meteorology, 2018). The study area covers a range of geologies, including the Volcanic Plains with basalt flows from the late Tertiary to late Quaternary, and adjoining sediments of the Dundas Tablelands and Central Victorian Uplands.



**Figure 5.** Map of the study area of western Victoria, Australia. Red points represent populations of *Banksia marginata* sampled in this study.

### ***Study species***

*Banksia marginata* is a shrub or small tree endemic to south-eastern Australia (Collins *et al.*, 2008; Taylor, 1988). The species is highly variable, but to date it has defied attempts for any subspecific or variant recognition (George, 1998), though Christopoulos (1988) found extensive clonality in the shrub while the tree-form was not clonal. Our study system is dominated by native C4 and C3 grasses (Stuwe & Parsons, 1977) and *B. marginata* grows as the non-serotinous tree-form. It is possible that there has been selection for arborescence and the loss of serotiny in favour of frequent seed release, which may have occurred in response to the emergence of grassy biomes in South East Australia. This is analogous to the emergence of savanna during the Miocene with taller forms and the loss of serotiny in *Protea* (Lamont *et al.*, 2013).

Small individual trees can be reproductive, and in our study, flowers and infructescences were observed on young trees (> 58 mm DBH). It is capable of resprouting after fire and we observed post-fire resprouting of saplings and young trees from lignotubers and epicormic buds after fires in some populations.

### ***Demographic surveys***

Fifteen populations, representing 30% of populations distributed across the western plains' savanna, were selected to encompass populations of varying sizes and assessed for stand structure. Most populations are relatively small (< 500 trees); hence entire populations were censused (except the largest stand at Minhamite where a subset of the stand was censused). Diameter at breast height (DBH, at 1.3 m) was measured for each tree. For multi-stemmed trees, all main stems over 20 mm diameter were measured and combined by calculating the square root from the sum of all the squared DBH measurements to obtain an equivalent DBH

(MacDicken *et al.*, 1991; Stewart & Salazar, 1992). If a fork occurred at 1.3 m, then the stem was measured below the fork. All living trees under 20 mm DBH, were classed as saplings and assigned as the smallest size-class.

The presence of cones, which support few to many fruits (follicles) in *Banksia*, was noted by inspection of the entire crown. Anecdotal observations by land managers suggested that a failure to produce infructescences was happening over multiple years. Therefore, the assessment of cones included both new (developed from previous year's flowers) and old (older than previous year's crop) cones. We aimed to determine if an absence of cone set occurred at the population level over multiple years

### ***Statistical analyses***

While many studies use histograms to make inferences about recruitment and stand dynamics (Condit *et al.*, 2013; Erdos *et al.*, 2015; Hulme, 1996), there is some emerging evidence that histograms can be misinterpreted (Boels *et al.*, 2019; Lem *et al.*, 2013). To overcome this we regressed the number of individuals in each of 15 size classes (y-axis) against the size class mid-point (x-axis) and used the slope of the regression line as a measure of recruitment success (Condit *et al.*, 1998).

We used ten DBH size classes (after Condit *et al.*, 1998): 10 – 19, 20 – 29, 30 – 39, 40 – 49, 50 – 99, 100 – 199, 200 – 299, 300 – 399, 400 – 499, 500 – 999 mm. The number of stems ( $n_i$ ) within each class was calculated by dividing the number of stems by the width of the size class (see Condit *et al.* 1998) to obtain an adjusted total number of stems for each class while the mid-point of the size class ( $d_i$ ) was used. Both  $n_i$  and  $d_i$  were then  $\text{Log}_{10}$  transformed. We then calculated a regression  $\text{Log}_{10}(d_i)$  as the independent variable and  $\text{Log}_{10}(n_{i+1})$  as the dependent variable. As per Lykke (1998), where a size class had  $n_i = 0$ , we chose to retain the 0 values. The removal of 0 values at the smaller size classes produces

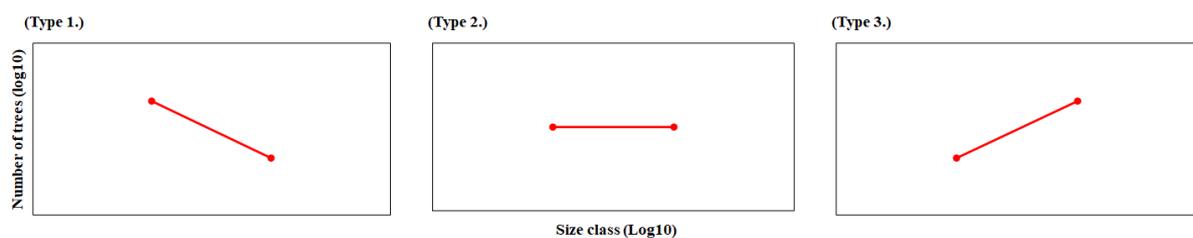
regressions with slopes that have a smaller negative value, while the removal of 0 values at larger size classes produces a smaller positive values and therefore creates an impression that a population is experiencing more or less recruitment than it is. The slopes of these regressions were then used to define stand type; all slopes are henceforth referred to as ‘Condit slopes’. Figure 2 is a simple schematic of these outcomes, which can broadly be described as:

Type 1 - Recruitment not limited: large numbers of juveniles, saplings and young trees relative to older trees; slopes are steeper with large negative values ( $< -1.0$ )

Type 2 - Recruitment moderately limited: fewer sapling and juvenile trees relative to older trees; slopes are flatter, with values falling between 0 and  $-1.0$ .

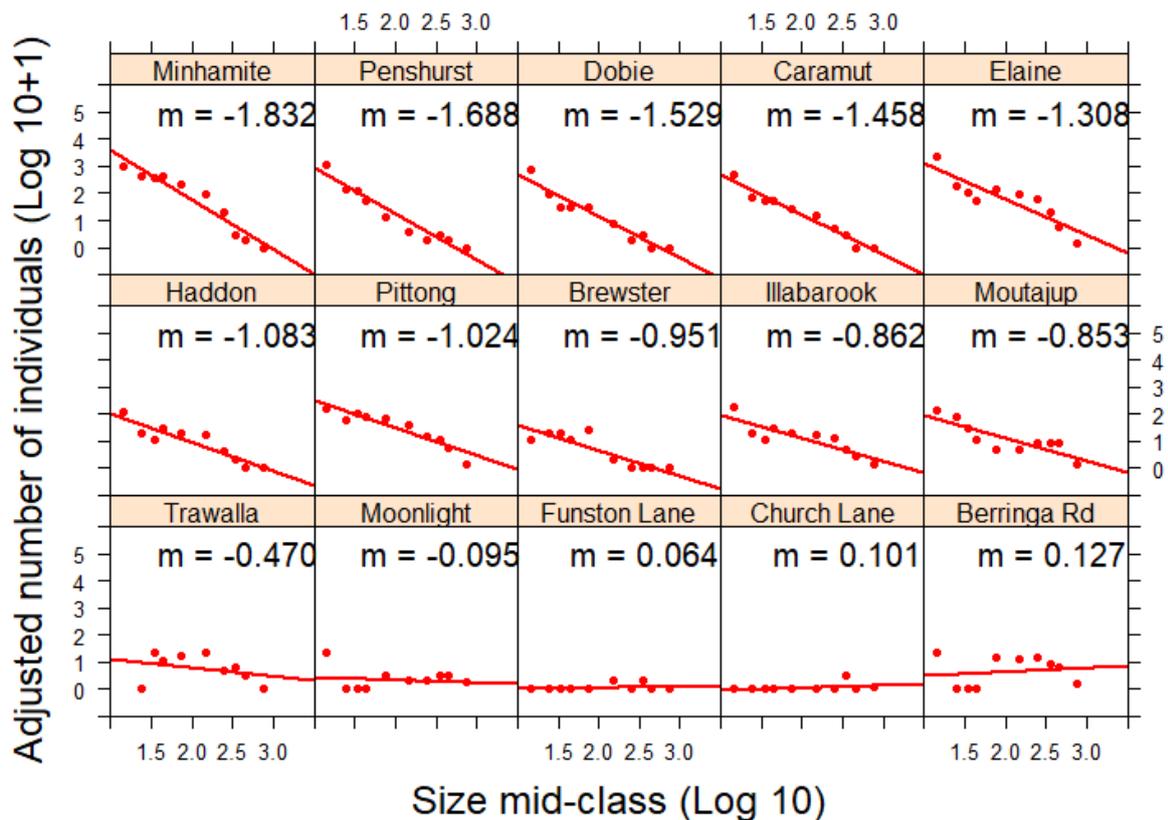
Type 3 - Recruitment severely limited: few to no observable trees in the smaller size classes relative to older trees; the slopes are flat with positive values ( $>0$ ).

It was assumed that all stems represent individual trees, however, in some shrub-forms of *B. marginata*, some plants may have arisen from root suckers (Specht & Rayson, 1957) rather than be genetically distinct individual trees. However, Christopoulos (1988) found no clonality in one population of tree-form *B. marginata* while in the same study area, recent work by Miller *et al.* (2020) found clones were in low frequency (between 0 and 6 clones) and in this system we believe root suckers contribute few stems in a populations., Where clonal species are involved, care needs to be taken when interpreting population dynamics using this method.



**Figure 6.** Conceptual model of three predicted stand types using Condit analysis. **Type 1:** Recruitment not limited. **Type 2:** Recruitment moderately limited. **Type 3:** Recruitment severely limited

To determine if an absence of fertile cones was widespread, we tested the differences in the proportion of trees with and without cones across 10 of the 15 sampled populations. Given juvenile plants are not likely to produce cones and we were able to determine that plants < 58 mm DBH were not reproductive, these were removed from the analyses. The proportion of trees (with >58 mm DBH) with and without cones was analysed using  $\chi^2$  test for homogeneity and pairwise comparisons were undertaken using Fisher's exact test. Regressions were then computed to determine if there was a relationship between population size and proportion of trees without cones. A non-linear regression was also computed to determine if there was a relationship between population size and the value of the Condit slopes for each population.

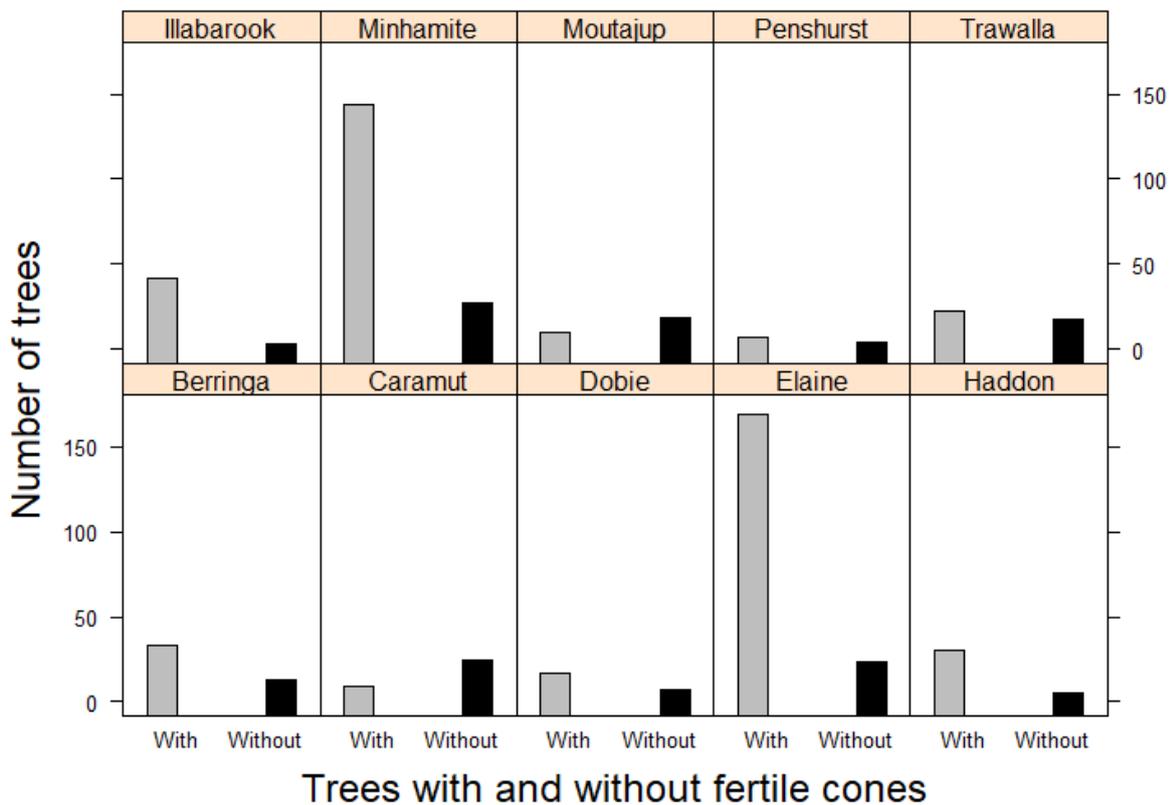


**Figure 7.** Condit slope outputs for 15 analysed populations. Regressions are arranged from highest negative value (recruitment not limited) through to the highest positive value (substantial recruitment limitation). The x-axis represents the mid-point of the size class and has been Log10 transformed. The y-axis is the number of individuals and has been adjusted using the method outlined in Condit (1998). This was then Log10 + 1 transformed to ensure 0 values were retained

With the exception of the calculations outlined in Condit *et al.* (1998), all analyses and plotting were performed using R version 3.5. (R Core Team, 2018) and RStudio version 1.1.453 (RStudio Team, 2016). Plots were produced using Lattice (Sarkar, 2008) and ggplot2 (Wickham, 2016).

## RESULTS

Stand dynamics encompassed all Condit slope types (Figure 3). Seven populations had a stand Type 1, with high negative Condit slopes (-1.024 to -1.8158), indicating recruitment was evident. Five populations exhibited Type 2 dynamics, with Condit slopes between -0.1776 and -0.7998. Three populations had Type 3 stand dynamics (Condit slopes

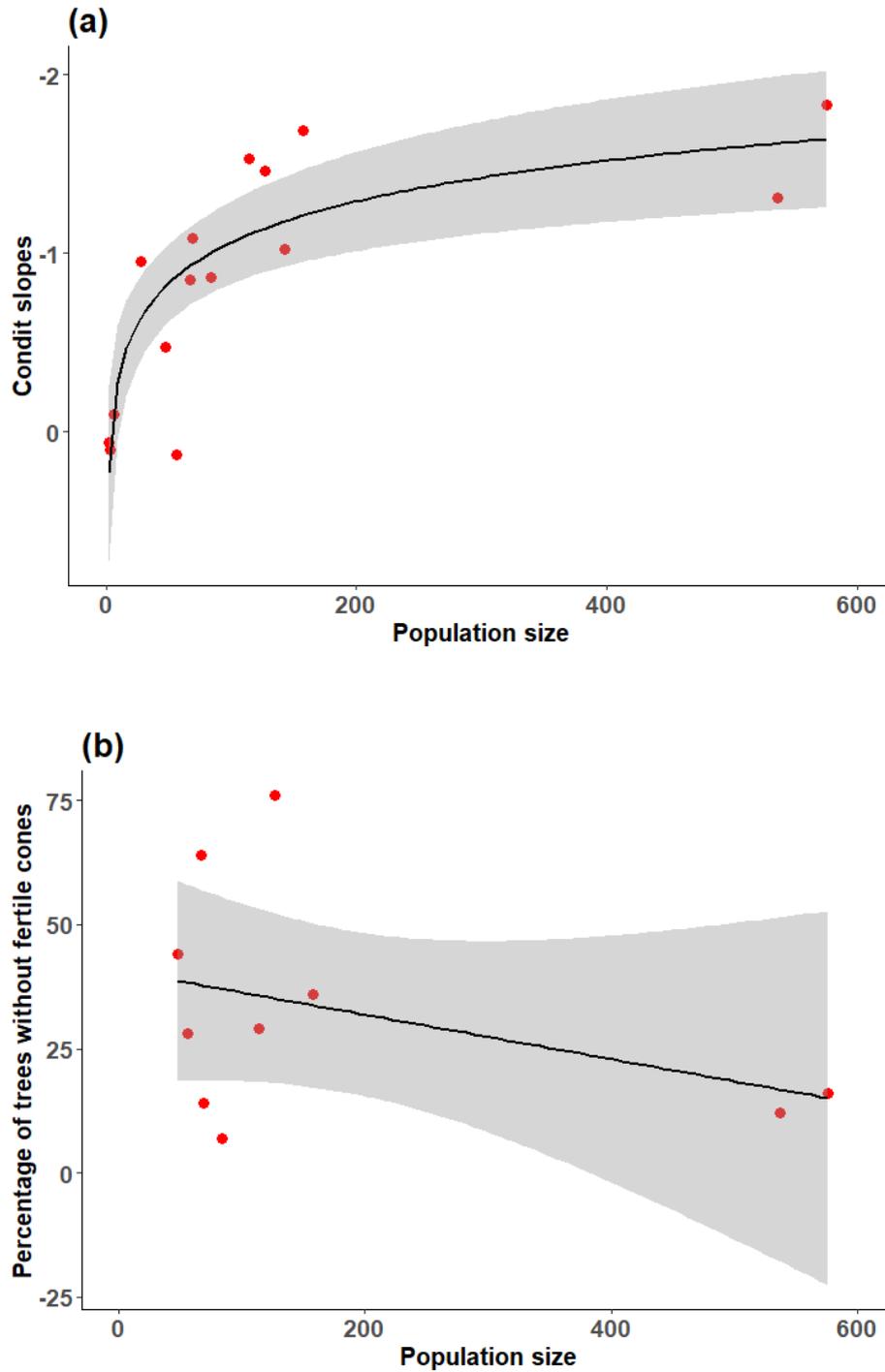


**Figure 8.** Proportion of *Banksia marginata* trees with and without fruit at ten populations distributed across the western plains, Victoria.

between 0.0649 and 0.1276), indicating recruitment bottlenecks. While this might not suggest evidence of widespread demographic bottlenecks, we did find evidence of a non-linear

relationship (Figure 5a;  $F(1,13) = 28.38$ ,  $p < 0.001$ ,  $r^2 = 0.6858$ ) between recruitment and population size, which suggest an Allee effect in smaller populations.

The failure of mature trees to produce fertile cones was widespread across the populations and proportion varied between populations, nonetheless three populations did



**Figure 9.** The relationship between *Banksia marginata* population size and (a) Condit slope values (with a fitted log curve) and (b) percent of trees (>58 mm DBH) without fruit (with a linear line of best fit).

have substantial cone set failure (> 40% of cones were barren). The results from the pairwise comparison using Fisher's exact test to compare the proportion of trees with and without fertile cones, showed that 20 pairs of *Banksia* populations out of a total of 36 comparisons were significant ( $p < 0.05$ ), however, 3 populations (Moutajup, Trawalla and Caramut) stood out, with the most comparisons that were significant. While these populations were also found to have high proportions of mature trees without cones (Figure 4). The results of the linear regression suggest no significant relationship between population size and the percentage of trees without fertile cones (Figure 5b;  $F(1,8) = 1.42$ ,  $p = 0.27$ ,  $r^2 = 0.1508$ ) and a Pearson test only found a moderate negative correlation between *B. marginata* population size and the percentage of trees that were not producing fertile cones.

## DISCUSSION

Despite their fragmented nature, rural trees still provide many important ecosystem services (Manning *et al.*, 2006) but their persistence may be transient (Tilman *et al.*, 1994). Understanding if rural tree populations are in decline is an important task that informs policy makers and allows land managers to effectively manage small rural tree populations. *Banksia marginata*, has been subjected to extensive habitat modification and land clearing since European settlement and we could expect to see evidence of decline, while reports from land managers suggest this species is failing to recruit and set seed. While we did find that many populations had proportions of mature trees failing to produce fertile cones, only three populations had a substantially large proportion that failed to produce cones. Despite this, we did not observe widespread demographic bottlenecks in *Banksia* savannas in western Victorian, with only 3 of 15 populations found to have a demographic (recruitment)

bottleneck. Most stands exhibited a Type 1 Condit slopes, signifying a recruiting stand, although Type 2 and Type 3 stands were also observed, the latter consistent with an absence of recruitment. Thus, despite the highly fragmented and isolated nature of some populations, recruitment is still occurring.

Nevertheless, long-term persistence of some of these populations is not assured, given their isolated nature (Tilman *et al.*, 1994) and the prospect of climate change accelerating declines as demonstrated in other *Banksia* species (Challis *et al.*, 2016; Steel *et al.*, 2019). We did observe that as populations increase in size, their Condit slope shift from positive (Type 3) to highly negative slopes (Type 1), suggesting that recruitment in this species declines rapidly when the population become small (<100 individuals). This is suggestive of a demographic Allee effect, whereby potential recruitment declines as the population becomes much smaller and fewer reproductive trees are present in a population. Alternatively, herbivory both direct and indirect (granivory or florivory) may be driving this. However, the mechanisms that underpin this relationship needs to be resolved if (very) small populations are to be maintained into the coming decades.

The proportion of trees without cones was not consistent across populations. Three populations (Trawalla, Moutajup and Caramut), in particular, had few cones, but there was no relationship between population size and the proportion of trees producing cones. Other factors, such as landscape context (isolation, distance to nearest native vegetation) or habitat quality, may affect seed set through their effects on pollinator movements (Llorens *et al.*, 2012; Thavornkanlapachai *et al.*, 2018). *Banksias* are often vertebrate (mammals and birds) pollinated (Cunningham, 1991; Hackett & Goldingay, 2001; Hooper, 1980; Krauss *et al.*, 2009) and factors that affect pollinator movements in fragmented landscapes will inevitably affect cone set. This has been demonstrated for many fragmented plants (Berry & Calvo,

1991; Nayak & Davidar, 2010; Pellegrino, 2014), including other members of the Proteaceae (Holmes *et al.*, 2008; Lamont *et al.*, 1993).

All populations are likely to be experiencing recruitment limitations to differing degrees and factors limiting successful recruitment of individuals into populations are likely to include biotic (e.g. competition, herbivory) and abiotic (e.g. soil moisture availability) drivers. In savannas, recruitment limitation may be driven by seasonally limited resources, such as competition for moisture with native (and increasingly) non-native grasses (D'Onofrio *et al.*, 2015; Holdo & Brocato, 2015; Sankaran *et al.*, 2005; Vadigi & Ward, 2013). Grasses both suppress tree growth (February *et al.*, 2013; Riginos, 2009) and limit the survival of trees (Morrison *et al.*, 2018; Scholes & Archer, 1997), particularly the more vulnerable smaller size classes, where the root zones of trees and grasses are more likely to interact (Holdo & Brocato, 2015). Grasses also have the capacity to impact fire regimes, with concomitant effects on tree sapling survival (Haverkamp *et al.*, 2018; Peterson & Reich, 2001). However, we observed recruitment at sites where grasses, like *Themeda triandra*, were present and dominant in the understorey and given this, it seems unlikely that grass competition alone is the main cause of the recruitment limitation observed in some *Banksia* stands.

Another powerful biotic agent that affects recruitment is consumer-driven limitation (Bird *et al.*, 2012; MacDougall *et al.*, 2010; Price & Morgan, 2003). The effects of herbivores may affect plants at multiple life stages, either through the direct consumption of seedlings and saplings or by more indirect effects (florivory, seed predation) that affects the pool of plant propagules in a population (Ferreira *et al.*, 2011; Kurkjian *et al.*, 2017). The preferential browsing of some palatable species by herbivores can lead to recruitment failure, a demographic bottleneck and ultimately leading to changes in vegetation composition over time (Bradshaw & Waller, 2016; Dexter *et al.*, 2013; Neave & Tanton, 1989; Salk *et al.*,

2011). Exotic herbivores, such as the European rabbits, as well as ungulates, may also be involved. Bird *et al.* (2012) suggests that, even at low densities, rabbits may inhibit recruitment of *Allocasuarina verticillata* in an Australian coastal shrubland community. In North America, introduced European rabbits led to increased mortality of *Quercus garryana* (MacDougall *et al.*, 2010). If *B. marginata* is palatable to herbivores, then this could explain recruitment limitation, yet a further study on the role of herbivory was inconclusive and found that summer drought may be a more immediate cause of seedling mortality (unpublished data) .

Initially we thought that the absence of cones may have been a result of pollination failure, particularly in smaller or isolated fragments where some pollinators might be missing. However, while many trees had no cones, we did observe discarded and damaged *B. marginata* cones under the crowns of many reproductive trees across many of the populations. This is consistent with observations by landholders and land managers of *Calyptorhynchus funereus* (Yellow-tailed Black cockatoos) visiting populations to consume seeds; damage to the cones appeared to be consistent with damage by cockatoo foraging described elsewhere (Scott & Black, 1981). Pre-dispersal granivory by cockatoos in *Banksia* species has previously been documented in Western Australia (Johnston *et al.*, 2016; Lamont *et al.*, 2007; Scott & Black, 1981; Valentine *et al.*, 2014; Witkowski *et al.*, 1991) and studies in South and Central America have also found parrots to be important pre-dispersal seed predators, contributing to significant loss of seed (Coates-estrada *et al.*, 1993; Francisco *et al.*, 2008; Villaseñor-Sánchez *et al.*, 2010). In contrast, there has been little work to investigate the role of seed predation by parrots on recruitment limitation in eastern states of Australia but recent work found that cone removal by *C. funereus* was exceptionally high, with between 50-100% of cones removed (Heyes *et al.*, in review)

This study has demonstrated that there are limits to recruitment under current conditions in several populations. The reasons for these limits remains unclear and are yet to be explored, but probable causes could relate to fragmentation and small population size (Lamont *et al.*, 1993; Morgan, 1995), exotic plants (Hoffmann & Haridasan, 2008), herbivory (MacDougall *et al.*, 2010) or too much/little fire (Gent & Morgan, 2007; Henzler *et al.*, 2018). As the climate continues to warm and dry this may lead to changes in microsite suitability that further limits tree recruitment. Under these conditions, recruitment in some populations may decline from higher rates of recruitment (Type 1 slopes), becoming increasingly recruitment limited (Type 2 or Type 3 slopes) and this may be tested with revisitation studies (Gent & Morgan, 2007; Naccarella *et al.*, 2019).

## CONCLUSIONS

We quantified recruitment in fifteen populations using the Condit method (Condit *et al.*, 1998; Lykke, 1998) and showed that most stands are recruiting. Only three stands were found to be experiencing recruitment failure and indicates that anecdotal observations of widespread recruitment bottlenecks in highly fragmented *Banksia* savanna populations are exaggerated. Severe recruitment limitations in these savannas are most likely governed by several local factors rather than a single widespread phenomenon. While there still is some recruitment at these sites, the question remains: is this type of recruitment enough to replace mortality of larger size classes in small fragments or will these fragments experience further declines in recruitment?

Condit values approaching zero or positive are indicative of little to no recruitment and the relationship between population size and the Condit slopes seems to indicate that once populations fall below 100, their Condit scores also change to positive values. Therefore, as well as managing causes of recruitment limitations, conservation efforts should

also focus on maintaining larger population sizes, above 100 individuals, to prevent further population decline and extinction. Further research is needed to understand the causes of recruitment limitation in populations of *B. marginata*, particularly in fragmented populations such as those in our study area. Understanding the causes of limited seed availability might be of particular importance with focus on seed predation. Given the role of grasses in tree recruitment in other grassy ecosystems, further understanding of grass competition in these savannas is likely to be a valuable contribution.

## CHAPTER 3

# Effects of pre-dispersal seed predation on fruit crop and seed fitness in a highly fragmented savanna tree

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### Abstract

Seed predation is an important cause of seed loss in plants and has the potential to limit plant recruitment. Recent work has shown that some stands of the tree-form of *Banksia marginata* in western Victoria, Australia, suffer from a recruitment bottleneck. We hypothesise that this may, in part, be due to excessive seed predation by Yellow-tailed Black Cockatoos (*Calyptorhynchus funereus*). To investigate pre-dispersal seed predation in this species, we quantified the amount of infructescence (hereafter ‘cone’) removal at four populations across western Victoria. *C. funereus* foraging also results in discarded cones that may still contribute seed for recruitment; therefore, we also examined the impact of pre-dispersal seed predation timing on seed fitness by removing cones at different times in their development to quantify seed mass and germinability. We found that all sites experienced significant seed predation; some sites had 100% removal of cones within a season. The early removal of cones resulted in only 18% of follicles opening to release seed and had a significant negative impact on seed mass. Percent germination of seed from cones removed early from trees was significantly lower in three of the four populations. Coupled with existing limits on tree recruitment in savannas, such as grass competition, fire and herbivory, we argue that pre-dispersal seed predation by cockatoos is likely to be a significant

contributor to recruitment-limitation in small savanna fragments by reducing the pool of seed available for dispersal.

**Keywords:** *Banksia marginata*; parrots; granivory; germination; recruitment limitation; seed.

## **ACKNOWLEDGEMENTS**

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## **INTRODUCTION**

Seed limitation affects the ability of plants to recruit new individuals into a population (Eriksson and Ehrlén, 1992), with consequent impacts on population viability and plant community assembly (Bryndís, 2014; Foster and Tilman, 2003; Grubb, 1977). Plant population size is an important determinant of seed set (Broadhurst *et al.*, 2008; Morgan, 1995; Severns, 2003) and fragmented populations may produce fewer seeds (per individual) than larger unfragmented populations due to Allee effects (Forsyth, 2003; Xia *et al.*, 2013). This may reflect low pollinator visitation (Dauber *et al.*, 2010), loss of compatible mates (Pickup and Young, 2007; Young *et al.*, 2000a) or inbreeding outcomes. Therefore, to understand causes of recruitment-limitation, it is important to understand the processes that limit seed production.

The loss of seed through predation by animals has long-fascinated scientists (Brannon, 1927; Janzen, 1971) and is of particular interest in agricultural systems (Brannon, 1927; Brown *et al.*, 2007; Tschumi *et al.*, 2018) but is rarely included in fragmentation studies. Some species of plants have evolved strategies to avoid or minimise seed loss to seed predators, such as hiding fruit and seed by use of a decoy (Groom *et al.*, 1994), protective mechanisms (spines and thorns) (Coffey *et al.*, 1999), production of toxins (Veldman *et al.*, 2007) or seed masting events (Wright *et al.*, 2014). Even serotiny, the ability of some plants to store seed in woody fruit to be released after disturbance, is often considered to be a fire-adapted trait. However, some authors also hypothesise that it may have evolved as a response to granivorous animals (Lamont *et al.*, 2016; Meehan *et al.*, 2015). Given that some plant species have evolved deterrents to prevent both pre-dispersal and post-dispersal seed loss (Filardi and Tewksbury, 2005; Groom *et al.*, 1994; Lamont *et al.*, 2016; Meehan *et al.*, 2015), one would expect a clear reproductive cost to the removal of fruit and destruction of seed by seed predators. However, defences against seed predators need to be balanced by the need to attract seed dispersers and therefore, the evolution of directed deterrence traits might lessen seed predation while also remaining attractive to seed dispersers (Filardi and Tewksbury, 2005; Samuni-Blank *et al.*, 2012).

Seed predators can be particularly important where plant populations are small and fragmented. Kurkjian *et al.* (2017) found that the rate of seed predation by small mammals on the threatened legume *Lupinus constancei* would likely lead to its extinction. In neotropical Brazilian savannas, seed predation has been recorded to be as high as 60% in woody species (Salazar *et al.*, 2012). The exclusion of seed predators has also been shown to increase seedling establishment (Ferreira *et al.*, 2011), a clear

demonstration that seed predators can be important drivers of recruitment-limitation and community assembly in plant populations.

Much of the work documenting pre-dispersal seed predation has focused on impacts of invertebrates (Andersen, 1989; Burgos *et al.*, 2008; Cummings *et al.*, 1999; Espelta *et al.*, 2009; Fenner *et al.*, 2002; Hosaka *et al.*, 2009; Leimu *et al.*, 2002; Minchinton, 2006; Ostergard *et al.*, 2007) but vertebrates are also important pre-dispersal seed predators (Gautier-Hion *et al.*, 1993; Van Blerk *et al.*, 2017). Many mammals are scatter-hoarders of seed and incidental seed dispersers (Blackham and Corlett, 2015; Forget, 1993; Hulme and Hunt, 1999; Razafindratsima, 2017) and play a role as pre-dispersal seed predators (Kurkjian *et al.*, 2017; Pender *et al.*, 2013). Birds are significant pre-dispersal seed predators (Boyes and Perrin, 2010; Coates-Estrada *et al.*, 1993; Francisco *et al.*, 2008; Francisco *et al.*, 2002; Seburanga, 2014; Villaseñor-Sánchez *et al.*, 2010) and their role in seed limitation may be of particular importance where forest and woodland patches have become fragmented (Francisco *et al.*, 2002; Pizo and Vieira, 2004).

In Australia, parrots consume the seeds of a range of plant species (Lee *et al.*, 2013; McNab and Sanders, 2014; Stock *et al.*, 2013). Forest Red-tailed Black Cockatoos (*Calyptorhynchus banksii*) from Western Australia are known to feed on a number of native plants in the Myrtaceae, Casuarinaceae and Proteaceae families (Johnston *et al.*, 2016), as well as some exotic species (Roper, 2016). Carnaby's Black Cockatoo (*C. latirostris*) is another generalist, consuming the seeds of many species in the Myrtaceae and Proteaceae (Johnston *et al.*, 2016), as well as more novel food sources such as seeds from introduced plantation pine species (Stock *et al.*, 2013). Others, such as the Glossy Black Cockatoo (*C. lathami*), are specialists on a single species of plant, namely *Allocasuarina verticillata* (Drooping She-Oak) (Chapman and Paton, 2006). The diet of

the Yellow-tailed Black Cockatoo, *C. funereus*, appears to consist of both invertebrate larvae and seeds of native and exotic plants (McInnes and Carne, 1978; Possingham, 1986). Most work has looked at plants solely as food sources for cockatoos, while the impact of foraging for seeds by birds on plant populations has been largely overlooked in the seed predation literature, particularly as a driver of decline in fragmented ecosystems.

Woodlands and savannas in south-eastern Australia have experienced extensive land clearing and modification since European settlement. As a result, what remains is now highly fragmented (Yates and Hobbs, 1997). Trees such as *Banksia marginata* Cav. (Proteaceae), once thought to be common in some of these areas (Lunt, 1997; Sinclair and Atchison, 2012), are now limited to small, linear remnants along road and rail reserves (Heyes *et al.*, 2020; Sinclair and Atchison, 2012). These populations show evidence of seed predation, with cone destruction consistent with damage recorded for other *Banksia* species by cockatoos (Scott and Black, 1981; Witkowski *et al.*, 1991). Many populations, as reported anecdotally by seed collectors, appear to have lost entire seed crops over multiple years (D. Frost, pers. comm). The loss of seed in such quantities in highly fragmented stands could mean that cockatoos are an important cause of recruitment-limitation. Based on these observations, we hypothesize that *C. funereus* seed predation is removing entire crops of *B. marginata* cones in these fragmented stands. The removal and discarding of uneaten seeds (intact within cones) during the foraging process may allow some seeds to be dispersed by cockatoos, particularly if the cones are dropped at some distance from the parent tree. However, depending on the timing of seed predation, this is likely to incur a cost to seed fitness (i.e. seed is likely removed before it has fully developed) and we predict a loss of fitness in seed from

cones that have been removed early in the fruiting season. Therefore, we also ask, does the different timing of foraging activity affect seed fitness in discarded fruit?

## METHODS

### *Study area*

The study occurred in woodland/savanna remnants dominated by tree-form *Banksia marginata* in western Victoria (Table 1). The four study sites include *B. marginata* population sizes ranging from 56 to >500 individuals, occupy linear roadsides and are surrounded by agricultural landscapes comprising mostly dryland grazing. Populations occur on a range of Quaternary, basalt-derived soils, granitic soils, and sedimentary soils, as summarised in Table 1. Mean annual rainfall ranges between 558-702 mm and mean maximum annual temperature is 17.4-19.2°C (Bureau of Meteorology, 2013).

**Table 1.** Location and site descriptions of *Banksia marginata* populations.

Site name	Abbreviation	Location	Bioregion	Geology	Annual Rainfall (mm)	Population size
Illabarook	ILA	37° 48' S, 143° 40' E	Central Victorian Uplands	Ordovician sandstones (Taylor, 1996)	558	56
Caramut	CAR	37°56' S, 142°30' E	Central Victorian Volcanic Plain	Quaternary basalt (Buckland and Stuart-Smith, 2000)	628	127
Pittong	PIT	37°41' S, 143°27' E	Central Victorian Upland	Granite (Thost and Stuart-Smith, 2000)	617	143
Minhamite	MIN	37°59' S, 142°20' E	Central Victorian Volcanic Plain	Quaternary basalt (Vandenberg, 1997)	702	>500

### ***Study species***

*Banksia marginata* (Proteaceae) is a widely distributed, highly variable shrub to small tree from south-east Australia (Collins, 2009; Taylor, 1988). Flowering occurs from March, with inflorescences forming on old nodes; some individual plants exhibit cauliflory, where inflorescences develop on the main trunk and branches (S. Heyes pers. obs., 2017). Unlike many other *Banksia*, the flowering sequence is neither acro- nor basipetalous; instead, flowers have been observed opening randomly (S. Heyes pers. obs. 2016). Inflorescences then develop a cluster of dry woody follicles (fruit) that form a woody cone approximately 12 months later. Cones can contain as many as 150 follicles, with each follicle containing two papery, winged seeds that are separated by a dehiscent woody septum. The follicles of *B. marginata* are not serotinous on the western plains of Victoria, with seed released annually in late summer (S. Heyes pers. obs.).



**Figure 10.** *Calyptorhynchus funereus* (Yellow-tailed Black Cockatoo) (A) foraging in *Banksia marginata* at Clarence, NSW. (Photo by Carol Proberts) and (B) Dunkeld, Victoria (Photo by Neil Scott). The litter of broken cones and follicles (C) here from Clarence, NSW is typical of foraging by *C. funereus* and was found at all our study sites.

### ***Seed predation***

In December 2017, field visits were undertaken to quantify the impact of pre-dispersal seed predation on the crop of newly developing cones at the four study sites. Sites were randomly sampled to represent two eastern and two western populations, however two sites were initially rejected after cones were found to have been removed and the

smallest populations were excluded due to sample sizes. Six branches were randomly sampled throughout the canopy of 10 randomly sampled trees at each site ( $n = 60 \times 4 = 240$ ), with each branch tagged and numbered. Due to the retention of dead flowers on cones, under-developed follicles can often be obscured and difficult to distinguish visually from unfertilised inflorescences. Therefore, each cone was inspected by hand to confirm the presence of developing follicles. There was some evidence that seed predation had already begun across all sites, with freshly discarded cones below trees and damage to branches where they had been removed. As a result, the subsequent data is conservative, as an under-representation of total cone removal within a season. The sites were revisited in March 2018, coinciding with typical seed release from follicles and dispersal. A count of all cones remaining on tagged branches (undiscarded) was obtained; three branches at PIT could not be found during the final count.

While discarded cones were recorded at our sites, we did not directly observe *C. funereus* handling cones. Nevertheless, the predation of *B. marginata* seed by *C. funereus* has been observed in New South Wales and Victoria (Figure 10), as well as Tasmania. This suggests *B. marginata* is an important food source and that seed predation of this species by these birds is widespread.

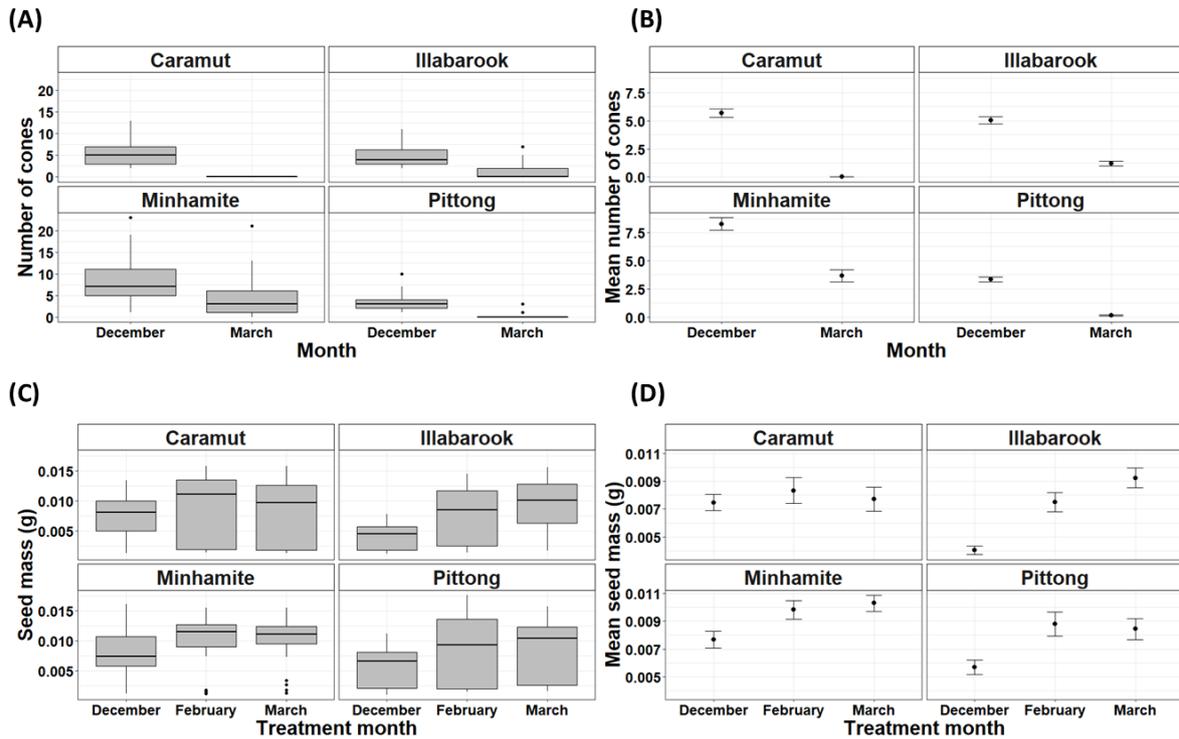
### ***Seed fitness***

To assess the effects of pre-dispersal seed predation on seed fitness, we ran an experiment between December 2018 and March 2019 to investigate how early- and late-visits by granivores may affect seed mass and germinability of seed from cones that had been removed from tagged branches but then discarded. To mimic the effect of cockatoo removal on seed fitness and release, 10 trees were selected, and six cones were caged to prevent seed predation with a fine mesh bag (totalling 60). Seed predation was heavy at

CAR and this method was not possible at this site. Therefore 60 cones were randomly sampled across the entire population and caged using the same method. Cones were then removed from trees in each of December (n=20), February (n=20) and March (n=20) to simulate the removal and discarding of cones by cockatoos. These were then placed in paper bags to dry and allow follicles to open and release seed. The number of follicles opened and closed were counted for each of the three treatments for the Pittong population only to determine if early removal affected the proportion of follicles that opened. This was done after cones of other populations were disposed of and we realised that cones removed early did not release much seed naturally.

Once removed, seeds (n = 100) were randomly sampled for each treatment at each population. A subset of 40 of the 100 seeds were weighed to obtain the seed mass (mg) to determine if the timing of removal affected mean seed mass.

Prior to germination, seeds cleaned using a wash of dilute sodium hypochlorite (1% NaClO) and rinsed using distilled water. They were germinated on Whatman grade 1 filter paper with 10 seeds per petri dish in 10 petri dishes moistened with 5 mL distilled water and sealed with Parafilm to prevent water loss. Petri dishes were then randomly positioned into a Thermoline Control Climate cabinet (18 °C; 12 hrs light and dark cycling). Germinants were counted every 7 days for 8 weeks, with germination defined by emergence of the radical. If petri dishes were drying, a supplementary 1 mL of distilled water was added, and the dishes resealed with Parafilm.



**Figure 11.** Boxplots (A) and confidence intervals (B) showing loss of *Banksia marginata* cones from branches in 10 trees at each study site. Boxplots (C) and confidence intervals (D) of seed mass across the treatments and the four study sites showing lower mean seed mass of seed when cones were removed early.

### Data analysis

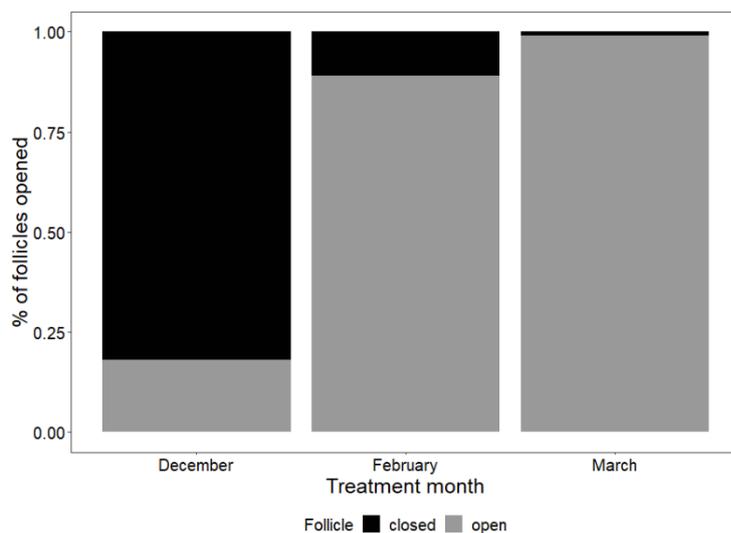
Cone loss between December and March at the four sites were compared using a two-way ANOVA. The proportion of opened and unopened follicles was analysed using  $\chi^2$  test of homogeneity. A two-way ANOVA was applied to compare seed mass for the December, February and March treatments at each site to determine if treatments had an effect on seed mass, followed by Tukey's HSD post-hoc test to investigate between treatment differences. Confidence intervals of the means were also calculated and plotted. All analysis and graphics were performed using R computing software (R Core Team, 2018). The germinability, mean germination rate and percent germination over time was plotted and analysed in R using the GerminAR (Lozano-Isla *et al.*, 2019) statistical package. Two-way ANOVA were used to analyse germinability and mean germination rate to investigate differences between the three treatments across the four

sites. Tukey's HSD was used to investigate differences in the interaction between the three treatments for both germinability and mean germination rate.

## RESULTS

Evidence of seed predation was apparent at all sites, from as early as December, with cone crop removal (equating to pre-dispersal seed predation) found at all sites (Figure 11 A, B). This consisted of scars where cones had been removed from the branch at the point of attachment, as well as a litter of discarded cones (both damaged and intact) under trees and removed follicles. Large numbers of cones were removed (56% at MIN; 77% at ILA; 96% at PIT; and 100% at CAR) between December and March and a significant loss of cones was observed ( $F = 306.06$ ,  $p < 0.001$ ). A significant interaction between cone removal and site was also found ( $F = 4.651$ ,  $p = 0.003$ ).

The removal of cones was shown to have a significant effect on seed mass ( $F = 18.269$ ,  $p < 0.001$ ) and further investigation using Tukey's HSD found a highly significant difference when comparing seed mass of the later treatments (February and March) to seed mass from cones removed in December ( $p < 0.001$ ). However, no significant difference in seed mass was found between cones removed in February and March ( $p = 0.79$ ). When looking specifically at CAR using confidence intervals, we see



**Figure 12.** Stacked bar plot showing the effects of early removal of cones on the percentage of follicles that were able to open and release seed. Foraging visits by Yellow-tailed Black Cockatoo in December is likely to have a much larger effect on seed availability than later foraging visits.

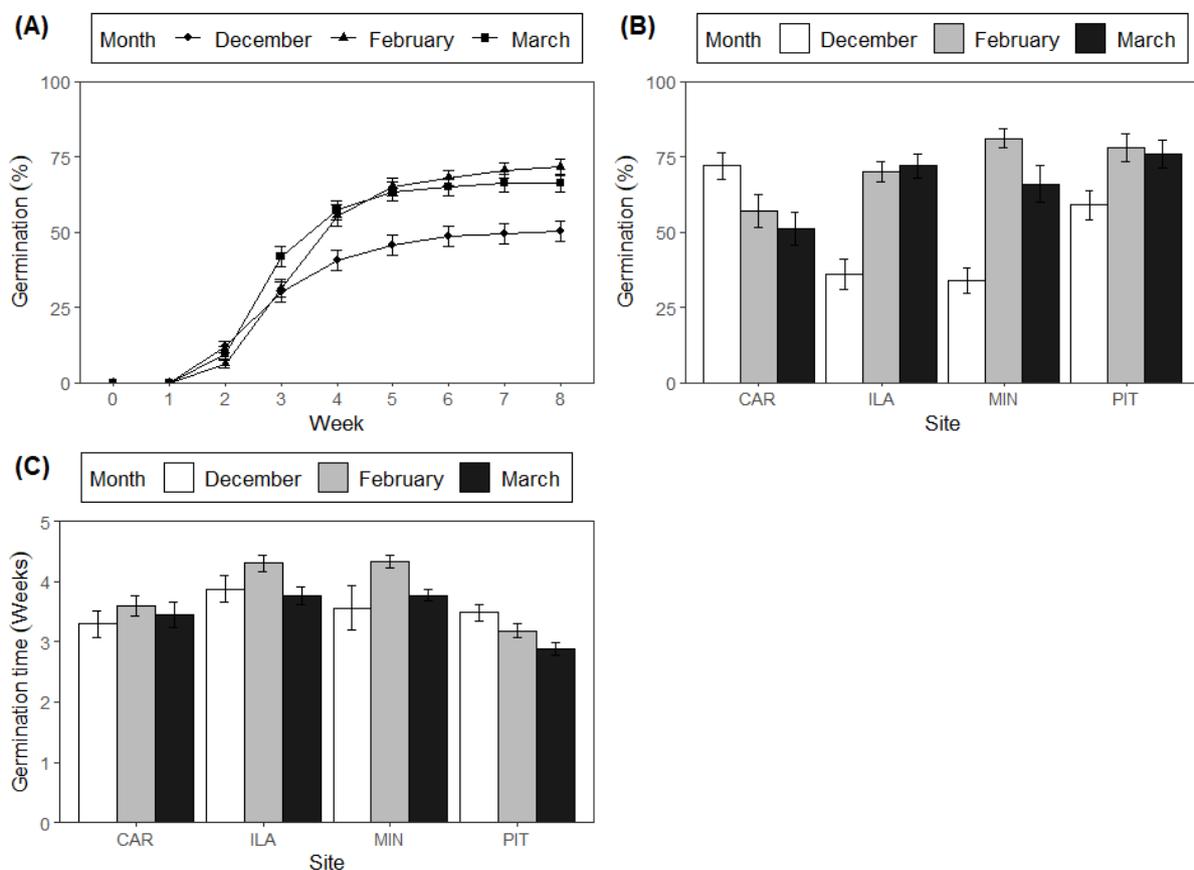
that there appears to be no significant differences between treatments at Caramut (Figure 11 D, December [0.006, 0.008], February [0.006, 0.010], March [0.006, 0.009]). There was also a significant effect on the ability of follicles to open and release seed and a highly significant association was found when cones were removed and follicles opening ( $\chi^2 (2) = 1119.4, p < 0.001$ ). Far fewer follicles opened in December treatment (18%)

**Table 2.** Seed mass and germination percent and speed for all sites and the treatments.

Site	Treatment	Mean seed mass (g)	Lowest germination %	Mean germination %	Highest germination %	Mean germination time (weeks)
CAR	December	0.0074	50	72	90	3.29
	February	0.0083	30	57	80	3.59
	March	0.0076	10	51	70	3.44
ILA	December	0.0040	20	36	60	3.87
	February	0.0074	50	70	80	4.30
	March	0.0092	60	72	100	3.76
MIN	December	0.0076	20	34	60	3.56
	February	0.0098	70	81	100	4.33
	March	0.0102	30	66	90	3.76
PIT	December	0.0056	40	59	90	3.48
	February	0.0088	60	78	100	3.18
	March	0.0084	50	76	100	2.87

compared to the February (89%) and March (99%) (Figure 12). The germination of seeds was higher in the February and March treatments in three out of four populations (Figure 13). Conversely, CAR had a higher mean percent germination for the December treatment (72%) than subsequent treatment months (February (57%) and March (51%)). The lowest mean germination was at MIN (34%) in the December treatment while the

highest was MIN (81%) in the February treatment (Table 2). The effects of the harvest month on germination was highly significant ( $F = 22.560, p < 0.001$ ), as was germination between sites ( $F = 4.286, p = 0.006$ ) and there was a highly significant interaction between sites and treatment ( $F = 11.072, p < 0.001$ ). Tukey's HSD post-hoc test found highly significant differences when comparing both March and February late treatments to the early December treatment ( $p < 0.001$ ). There was a significant difference ( $F = 5.082, p = 0.007$ ) between the treatments and a highly significant difference between sites ( $F = 13.119, p < 0.001$ ) for mean germination time. While mean germination time in February, when compared to December, was significant ( $p = 0.008$ ), there was no significant difference when mean germination time in March was compared to mean germination time in December ( $p = 0.75$ ).



**Figure 13.** Testing for the effects of cone removal at different times (December, February and March) on seed germination variables: percent germination over time (A), percent germination (B) and germination time (C).

## DISCUSSION

*Calyptrorhynchus funereus* is an important pre-dispersal seed predator capable of removing large proportions of the crop of *Banksia marginata* cones. The proportion of cones removed by cockatoos in our study was particularly high compared to studies of seed predation in *Banksia* elsewhere, though entire crops were not being removed at all sites and therefore we reject the hypothesis that entire crops are removed at least in the sites we studied. But, cone removal by *C. funereus* in our study was greater than 50% and, for two sites, over 90% of the seed crop was removed. Whereas, work on *B. attenuata* by Scott and Black (1981) found the highest removal rates by Carnaby's Cockatoos to be 35% of cones and Witkowski *et al.* (1991) found cone removal by cockatoos for *B. baxteri* and *B. speciosa* to be 20% and 10%, respectively. At our study sites, where small remnant stands of *Banksia* are embedded in a dryland grazing matrix, we found a litter of broken and damaged cones from previous years under trees, and anecdotal observations by seed collectors suggests that this seed predation has been an ongoing phenomenon. It is still unclear if the large proportion of cones being removed is consistent across years; the results from short-term studies such as this do need to be interpreted carefully. If removal is high over many years then this may be a significant contributor to recruitment limitation.

The high degree of fragmentation of remnants, and the small population sizes of *Banksia* on the western volcanic plains might, in part, explain why we observed high cone removal, with fewer cones being removed at the largest population (MIN). It could be that fragmentation poses only a limited barrier to a highly mobile seed predator like *C. funereus*. Once birds have arrived at a population, they satiate themselves on the entire crop, rather than moving between populations. This hypothesis is difficult to test because the amount of land clearing since European settlement is exceptionally high and

unfragmented patches of *B. marginata* on the western volcanic plains do not exist. High rates of seed predation by parrots have also been recorded for small fragments of Cerrado in Brazil (Francisco *et al.*, 2002; Pizo and Vieira, 2004), but the effects of fragmentation on seed predation per se is less clear when the broader literature is examined (Chacoff *et al.*, 2004; Chen *et al.*, 2017; Fleury and Galetti, 2006; García and Chacoff, 2007; Herrerías-Diego *et al.*, 2008; Mendes *et al.*, 2016; Pizo and Vieira, 2004).

Seed predation affects both the release of seed from discarded cones and the fitness of discarded seed, particularly for seed that has been removed early. Earlier removal had a noticeable negative effect on germination and seed mass for the majority of sites. One site (CAR) was the exception and the highest mean germination for seed from cones that were removed early. It is possible that the difference in the result at CAR was due to differences to the sampling method that was used at this site. Despite this, cones that have been removed early showed that most follicles were unable to release the seed. Regardless of seed quality, if seed is unable to be released then those cones removed earlier are not contributing seed for recruitment. We also noticed that seed that had been released from follicles in the cones removed in March had failed to properly develop a seed coat and that many of these seeds became affected by mould. It is possible that the seed coat functions to protect the seed embryo from pathogens prior to germination, which was investigated in agricultural crop species as far back as 1921 (Hurd, 1921) and has been found in herbaceous woodland species (Warr *et al.*, 1992). Given so few seed are released, low germination and susceptibility to pathogens, seed from cones removed early by seed predators face an almost insuperable barrier to successful natural germination.

Our experiment shows that timing of foraging appears to be important and can affect the amount of seed that is released from the follicles, as well as subsequent seed quality (seed mass and germination). We still do not know what time of the year the cockatoos are doing the bulk of their foraging. We observed some birds visiting stands as early as December and saw evidence of foraging, such as scars on the trees where cones had been removed, as well as recently removed cones below the trees. If much of the cockatoo foraging is early (i.e. before fruit maturation), then their contribution to recruitment limitation is likely to be high, especially given so few follicles open when cones are removed early and the released seed has lower germination. If foraging is staggered, then both more seed would be released, and higher quality seed would be available for recruitment. Despite the obvious negative impacts of cockatoos on *Banksia* seed availability, Cockatoos may also act as inadvertent seed dispersers (Tella *et al.*, 2019). How effective this inadvertent dispersal is in fragmented landscapes is questionable, with many fruits likely to be dropped into hostile patch types such as cropped and grazed paddocks.

Clearly, birds can be strong filters on regeneration, compounding effects of small population size (Allee Effects), habitat isolation (genetic inbreeding), and habitat quality. However, managing small populations of *B. marginata* will be problematic. Yellow-tailed Black Cockatoos are reported to be experiencing a significant decline on the south-east Australian mainland (Ehmke *et al.*, 2015) and clearly *B. marginata* is an important food plant for this bird. Novel approaches, such as netting and caging plants, may increase seed rain and subsequent opportunities for seed regeneration, however it would limit food sources for foraging birds and care needs to be taken if this approach were to be used. Increasing patch size and their connectivity may alleviate seed limitation in smaller populations, but further evidence is required to understand if this

approach would prove fruitful at landscape scales. Further work is now required to determine peak foraging activity across western Victoria, as well as to understand whether foraging intensity is related to patch size, and whether seed predation is consistent across multiple years.

## CHAPTER 4

### Conclusion and Synthesis

#### INTRODUCTION

Tree decline in rural Australia, often as a result of habitat fragmentation, has been demonstrated in a range of species (Dorrrough and Moxham, 2005; Lamont *et al.*, 1993; Mogoutnov and Venning, 2014; Prior *et al.*, 2011; Ross and Brack, 2015). As small fragmented populations, many trees are vulnerable and persistence is compromised by small population sizes, Allee effects (Allee, 1931; Odum and Allee, 1954) and altered biotic interactions (Llorens *et al.*, 2012). This can manifest at the genetic level with inbreeding depression (Severns, 2003) or it may affect the number of available mates (Pickup and Young, 2007; Young *et al.*, 2000a). Allee effects in small populations can also affect critically important plant-animal mutualistic/antagonistic relationships, such as the simplification of pollinator assemblages in fragments (González-Varo *et al.*, 2009) and the over exploitation of food resources by seed predators in small or fragmented populations of plants (Francisco *et al.*, 2002; Kurkjian *et al.*, 2017).

Prior to European settlement, *Banksia marginata* savannas were once extensive throughout the western plains of Victoria (Hateley, 2010; Sinclair and Atchison, 2012) but many of these remnants now exist in small linear fragments. Despite many populations persisting in small isolated fragments, I demonstrated that the majority of populations observed are continuing to recruit new individuals into stands.

## ***Chapter 2. How widespread are recruitment bottlenecks in fragmented populations of the savanna tree *Banksia marginata* (Proteaceae)?***

This chapter sought to test the hypothesis that a failure to set seed and recruitment-limitation was a widespread phenomenon in *B. marginata* fragments. Despite the highly fragmented nature of many populations, the majority of stands were found to be recruiting and only three populations were experiencing severe recruitment-limitation. However, the smaller fragmented stands are exhibiting evidence for demographic Allee effects, with Condit slopes falling sharply when populations fall below 100 individuals. We also see a similar effect when we look at the proportion of trees not setting seed in relation to population size.

Many reproductively mature trees did have an absence of cones across all populations, and this was highest at Caramut, with 76% of mature trees missing fruit. By contrast, at Illabarook, only 7% of mature trees were missing fruit. It is unlikely that missing fruit is due to the complete absence of pollinators given observations of multiple pollinator guilds on other *Banksia* species (Cunningham, 1991; Ramsey, 1988; Vaughton, 1992). A litter of broken cones beneath many trees, as well as widespread observations of Yellow-tailed Black Cockatoos (*Calyptorhynchus funereus*) foraging on *B. marginata* cones, suggests that these large avian granivores may be responsible for reducing seed set in small populations (see Chapter 3).

Despite the large proportions of trees that do not have seed, many of the populations are recruiting, as evidenced by high Condit scores. However, there are some caveats to this good news. The extinction debt hypothesis states that after fragmentation, the presence of some species within the fragmented habitat is transient and that extinction may occur many decades to even centuries after fragmentation (Tilman *et al.*, 1994). This may mean that, despite evidence of recruitment, stands of *B. marginata*

could be experiencing a slow decline and research elsewhere has found that fragmented *B. marginata* populations are at risk of significant decline in genetic diversity (Miller *et al.*, 2020). Perhaps even more important than long-term processes for these small populations is the threat of stochastic extinction due to climate change. Heatwaves, drought and water stress may contribute to rapid decline in trees (Allen *et al.*, 2010; Matusick *et al.*, 2013), including *Banksia* as has been increasingly observed in south-west Australia (Canham *et al.*, 2009; Steel *et al.*, 2019).

### ***Chapter 3. Effects of pre-dispersal seed predation on fruit crop and seed fitness in a highly fragmented savanna tree***

This study found that fruit removal was particularly high (>50%) across all four stands of *Banksia marginata* compared to similar studies in other *Banksia* species (Scott and Black, 1981; Witkowski *et al.*, 1991); indeed, one population of *B. marginata* experienced 100% removal of fruit.

When foraging, *C. funereus* discard a lot of partially damaged cones with unopened follicles containing seed. This Chapter sought to investigate how foraging at different times during cone development (December, February and March) would affect the seed from cones that have been discarded. It was found that most follicles (82%), when cones were removed early (December), would not open under ambient conditions. Early removal also affected seed mass and germination; seed also appeared to be more affected by mould during germination than the seed from later removed cones. Many of the early removed seed were white and appeared to have poorly developed seed coats and it is possible that seed coats may play a role in protecting the embryo from pathogens in the soil during germination.

## **FUTURE RESEARCH**

*Banksia marginata*, despite its widespread distribution, has been poorly studied and clearly there are many gaps that warrant further investigation. In this next section, I highlight some future research directions that appear important to pursue.

### ***Long-term recruitment dynamics***

Recruitment may be an ongoing but infrequent process. Higgins (2000) suggest that recruitment in savannas may be infrequent but occasionally very successful (the ‘storage effect’ of Chesson and Huntly, 1989), while background mortality of adults is low and ongoing. This might be particularly important as climate warms and rainfall becomes less predictable in south-east Australia. Long-term revisitation studies can be used to monitor stand dynamics and are a useful way to determine if populations are undergoing longer-term population decline (Gent and Morgan, 2007). Ongoing seed addition experiments, and seed addition and transplant experiments are a useful way to test if germination and/or seedling survival is constrained across seasonal climate variation. Most *B. marginata* stands are in grassy ecosystems and grass dominance has long been thought to constrain both tree growth and recruitment in savanna (Scholes and Archer, 1997). It would be useful to know if grass competition plays a role in facilitating this, particularly in dry seasons.

### ***Other causes of recruitment limitation***

It is unlikely that recruitment-limitation is limited by a single factor per se; multiple causes of limitation are likely be involved. Further work to understand the role of different herbivores on seedling survival is needed. The overabundance of some herbivores, such as the European rabbit (*Oryctolagus cuniculus*), as well as native

herbivores, are important causes of recruitment limitation in many native plant species (Bird *et al.*, 2012; Dexter *et al.*, 2013; Di Stefano, 2003; Tiver and Andrew, 1997). Their effect on seedling survival will need to be resolved if successful management of remaining populations is to be realised. Understanding microsite availability across linear fragments is also necessary. Most *Banksia marginata* stands, particularly those containing old trees, are on linear fragments that are bordered by rail lines or roads and intensively managed agriculture. Ongoing recruitment is likely to be limited to linear strips because suitable microsites for emergence and early seedling survival might be limited to localised patches within these linear reserves. Understanding patterns of seed dispersal and suitability of microsites across linear fragments will help to understand which population might be dispersal- and microsite-limited, and will help to identify the conditions (microsites) necessary to advance restoration efforts.

### ***Yellow-tailed Black Cockatoo foraging behaviour***

The study on seed predation rates seems to indicate that, in this ecosystem, Yellow-tailed Black Cockatoos are an important cause of seed loss where some stands suffer more predation than other stands. Further study is now needed to determine why some stands might be suffering from higher rates of seed predation. Yellow-tailed Black Cockatoos might be selecting sites that are closer to roosts or, alternatively, some sites may be preferred for other factors such as higher numbers of boring insects (Scott and Black, 1981).

This study examined the timing of foraging on germination and seed release in discarded cones and the results suggest that early foraging can affect the release of seed from the cones as well as seed germination. There is now a need to determine the frequency of visits across the year; if the birds are foraging early, then we can conclude

that seed predation is an important cause of seed loss even in cones that remain discarded and uneaten.

## **MANAGEMENT DIRECTIONS**

Many populations of *Banksia marginata* are small and, as a result, they are subject to small population Allee effects, inbreeding depression (Miller *et al.*, 2020) and, as demonstrated in this thesis, reduced recruitment. The threshold for higher Condit slopes (recruitment) appears to be around 100 individual trees, and seed predation appears to be an important cause of recruitment-limitation. It is possible that an Allee effect exists for seed predation, and smaller populations are more likely be impacted than larger populations. Therefore, land managers should focus on reintroducing plants into smaller populations in an attempt to raise populations over this minimum threshold. Miller *et al.* (2020) examine ways to do this, including sourcing seeds from climate-adapted populations to improve the resilience of stands to future, climate-impacted stochastic events.

Across western Victoria, there is renewed effort to restore *B. marginata* savanna across the landscape (Stevenson, 2018). Seed supply, from both natural stands and seed production areas, might be impacted given the number of cones and seed removed by Yellow-tailed Black Cockatoos. In Chapter 3, we found that caging individual cones was a successful way to protect cones from the birds and this method could be implemented to ensure seed availability for some of these projects. However, as these trees are also important seed sources for granivores, seed collection should be conservative and avoid overexploitation of seed in any given population.

This thesis came about because of the widespread concern for the ongoing landscape conservation of tree-form *B. marginata* on the basalt plains of western Victoria. Anecdotally, the species was considered to be (a) not producing seed and (b)

not recruiting new individuals into stands. While both statements are true, my research (and data) has shown that these claims were over-stated. There is every reason to sympathetically manage and expand existing stands to contribute to in situ landscape conservation of these forgotten savannas. But clearly, landscape-scale conservation of the Silver Banksia savanna will need a sustained, landscape restoration effort, to identify suitable locations in which to replant and then sourcing seeds to undertake this recovery. An adaptive management strategy seems prudent, building on the knowledge gained in this thesis about stand dynamics and biotic interactions.

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# APPENDICES

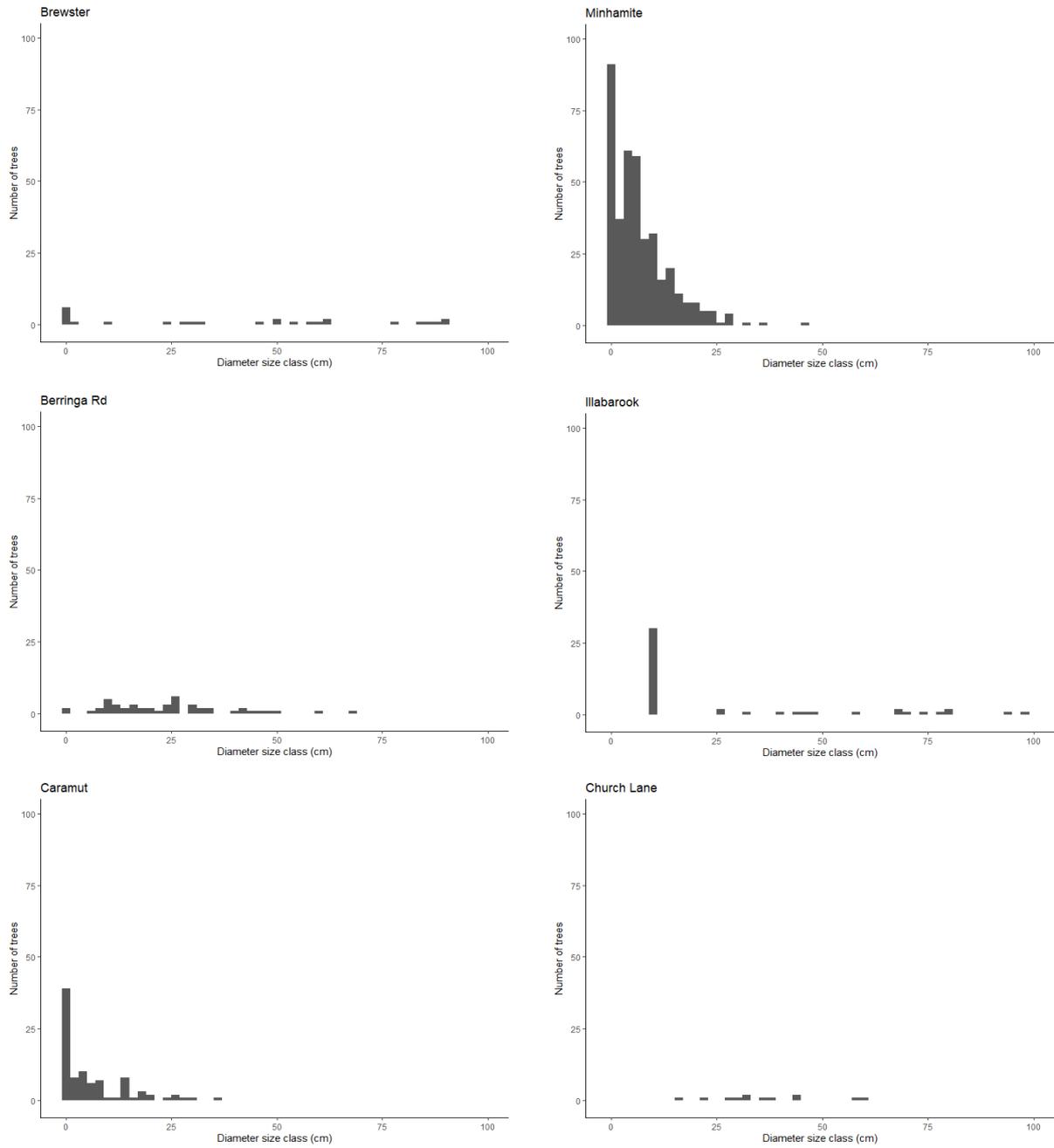
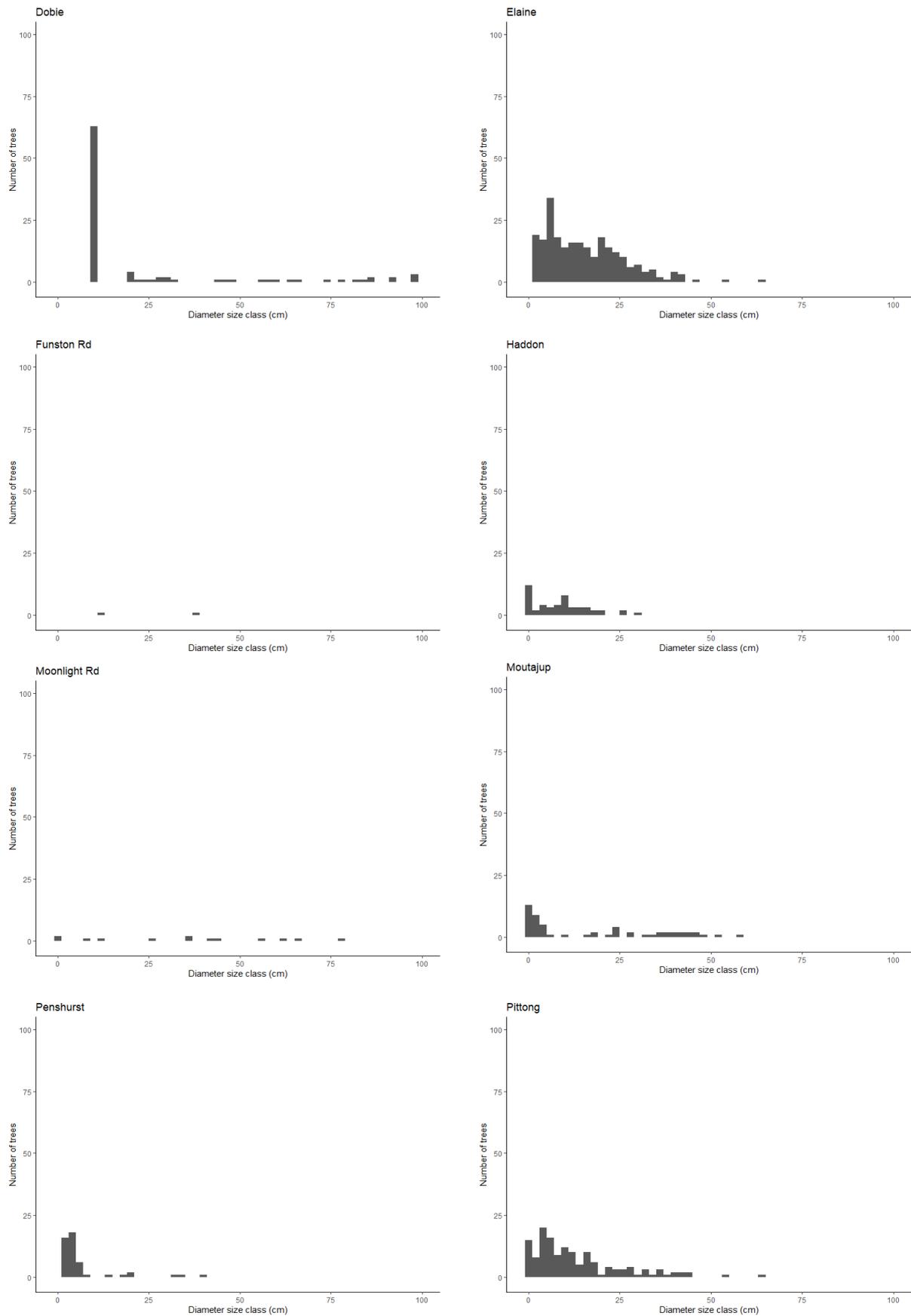
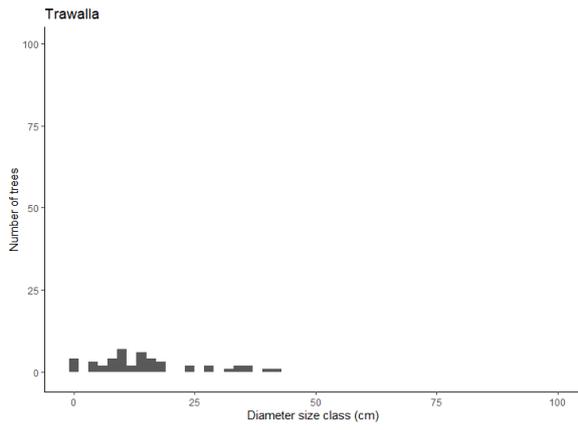


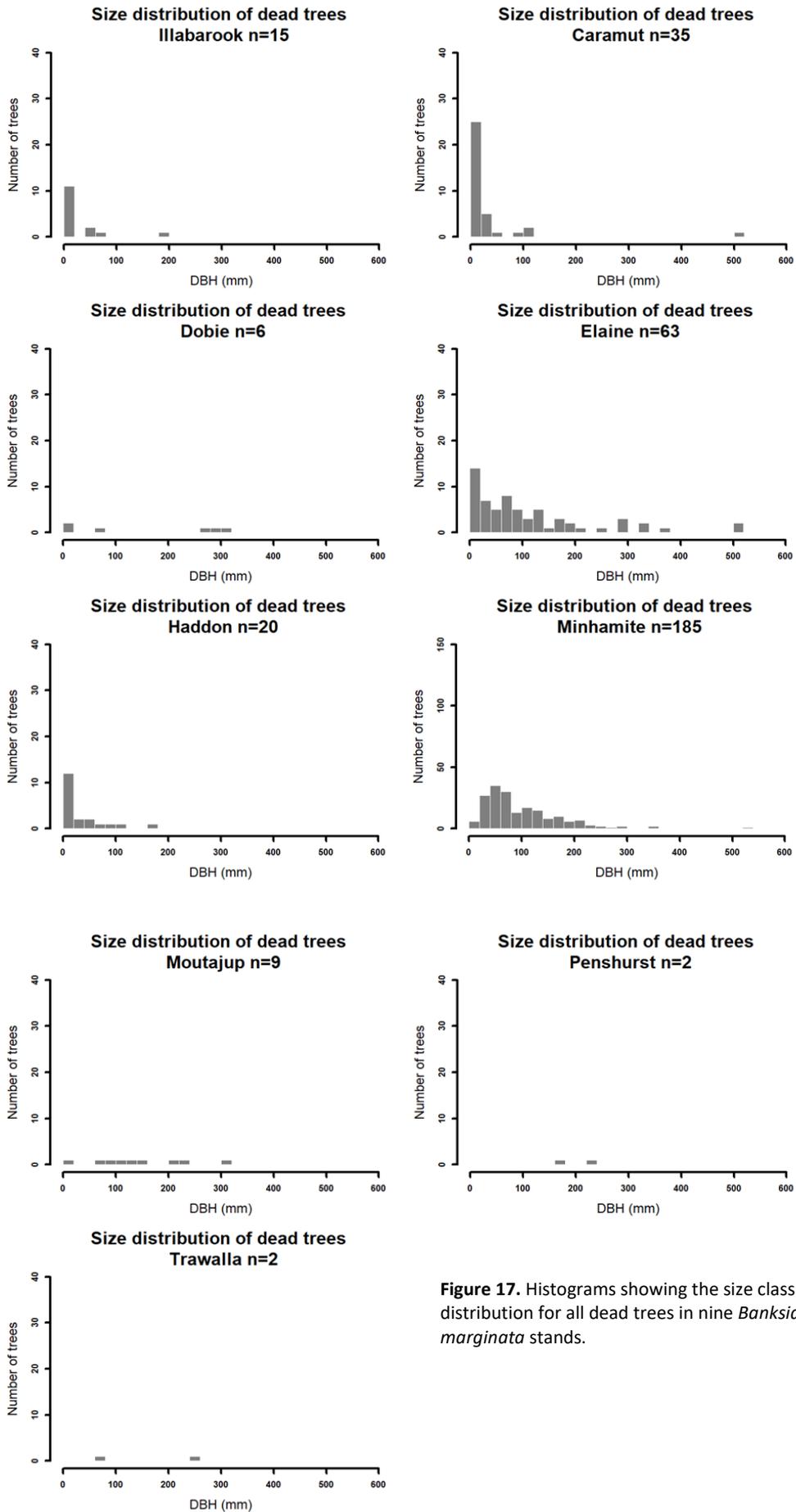
Figure 14. Histograms showing the size class distribution of living trees (1/3)



**Figure 15.** Histograms showing the size class distribution of living trees (2/3)



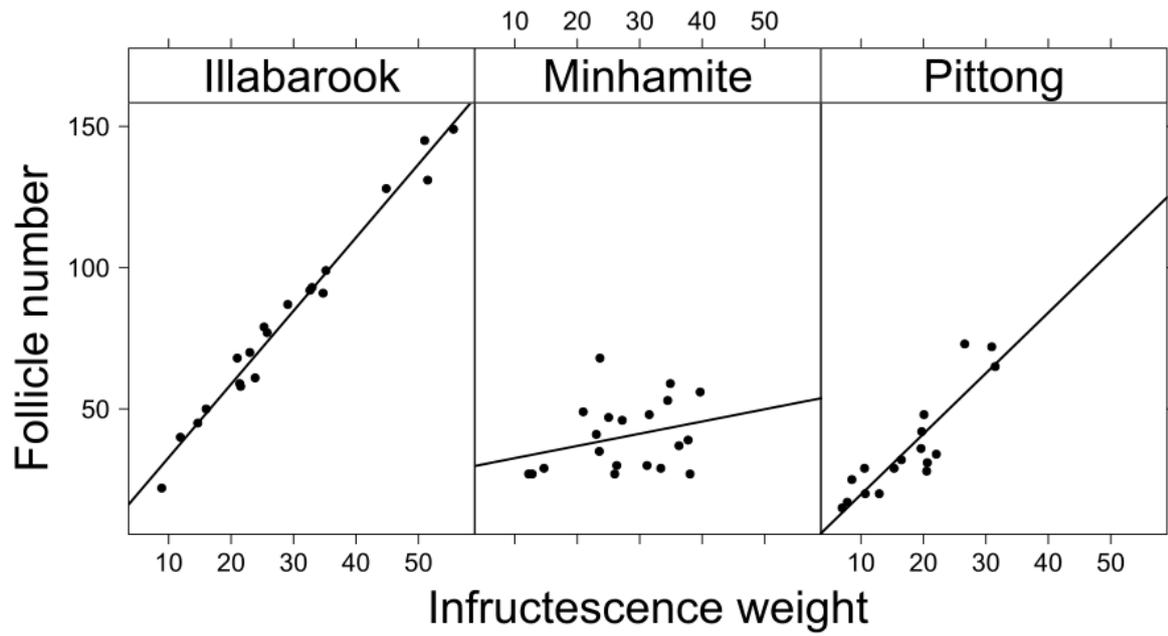
**Figure 16.** Histograms showing the size class distribution of living trees (3/3)



**Figure 17.** Histograms showing the size class distribution for all dead trees in nine *Banksia marginata* stands.

Table 3. Pairwise comparison table from the Fisher's multicomparison test into differences in fruit set from chapter 2.

Trawalla: Berringa	Trawalla: Illabarook	Trawalla: Caramut	Trawalla: Dobie	Trawalla: Elaine	Trawalla: Haddon	Trawalla: Minhamite	Trawalla: Moutajup
<b>0.24</b>	<b>0.000298</b>	<b>0.03221</b>	<b>0.3538</b>	<b>0.000106</b>	<b>0.02407</b>	<b>0.001016</b>	<b>0.2128</b>
	Berringa: Illabarook	Berringa: Caramut	Berringa: Dobie	Berringa: Elaine	Berringa: Haddon	Berringa: Minhamite	Berringa: Moutajup
	<b>0.02548</b>	<b>0.0003101</b>	<b>1</b>	<b>0.02548</b>	<b>0.24</b>	<b>0.138</b>	<b>0.008871</b>
		Illabarook: Caramut	Illabarook: Dobie	Illabarook: Elaine	Illabarook: Haddon	Illabarook: Minhamite	Illabarook: Moutajup
		<b>4.837E-09</b>	<b>0.04706</b>	<b>0.4863</b>	<b>0.3538</b>	<b>0.2128</b>	<b>1.28E-06</b>
			Caramut: Dobie	Caramut: Elaine	Caramut: Haddon	Caramut: Minhamite	Caramut: Moutajup
			<b>0.003411</b>	<b>3.01E-11</b>	<b>3.49E-06</b>	<b>1.23E-09</b>	<b>0.6336</b>
				Dobie: Elaine	Dobie: Haddon	Dobie: Minhamite	Dobie: Moutajup
				<b>0.09545</b>	<b>0.2552</b>	<b>0.2128</b>	<b>0.02877</b>
					Elaine: Haddon	Elaine: Minhamite	Elaine: Moutajup
					<b>0.8294</b>	<b>0.4279</b>	<b>1.02E-07</b>
						Haddon: Minhamite	Haddon: Moutajup
						<b>1</b>	<b>0.000237</b>
							Minhamite: Moutajup
							<b>1.68E-06</b>



**Figure 18.** Scatter plots showing the linear relationship between number of follicles and infructescence weight. Follicle productions can vary within and between sites and can be as high as 150 follicles.