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

Simon D. Heyes · Steve J. Sinclair · Susan E. Hoebee · John W. Morgan

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Abstract Land clearing of habitat into smaller, isolated remnants is a major driver of plant and animal extinctions globally. In southeastern Australia, once widespread temperate savannas have been subjected to extensive land clearing since European settlement. 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* 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 an Allee effect. The proportion of trees without cones varied between populations; three populations had large numbers of trees (> 40%) lacking mature fertile cones. Managers should focus on minimising 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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S. D. Heyes (✉) · S. E. Hoebee · J. W. Morgan
Department of Ecology, Environment and Evolution, La Trobe University, Bundoora, VIC 3086, Australia
e-mail: s.heyes@latrobe.edu.au

S. D. Heyes · S. E. Hoebee · J. W. Morgan
Research Centre for Future Landscapes, La Trobe University, Bundoora, VIC 3086, Australia

S. J. Sinclair
Department of Environment, Land, Water and Planning (DELWP), Arthur Rylah Institute for Environmental Research, 123 Brown St, Heidelberg, VIC 3084, Australia

Introduction

Fragmentation is a global problem with around 1.5 billion hectares of habitat converted to farmland (IPBES 2019). In temperate southeast 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 and Harris 1999; Yates and 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 and 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 pollinator foraging behaviour (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 and 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 and Parsons 1977; Tolera et al. 2013) or reproductive biology of a species (Ashton 1976; Zammit and 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 a decline in population size in one or more size- or age-classes (Beck 1995; Holdo et al. 2014). Demographic bottlenecks can be caused by disturbance such as a fire that removes the reproductively mature plants from a population (Enright and Lamont 1989) or herbivores that may browse young 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 eventually 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 and 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 and Atchison 2012). However, they are now either locally extinct or verging on extinction due to extensive land clearing and habitat fragmentation (Sinclair and 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 and Enright 2000), ongoing recruitment might be expected if viable seeds are produced continually and 'safe sites' (*sensu* 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 and Vaughton 1991) and an alternative hypothesis is that small populations are vulnerable to small population Allee effects (Lamont et al. 1993).

Methods

Study area

This 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 (Fig. 1). The climate is Mediterranean, with winter-dominant rainfall and summer drought. Mean annual rainfall ranges between 558 and 702 mm, and mean temperatures range from 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.

Study species

Banksia marginata is a shrub or small tree endemic to southeastern 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 and 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 southeast 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 postfire 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

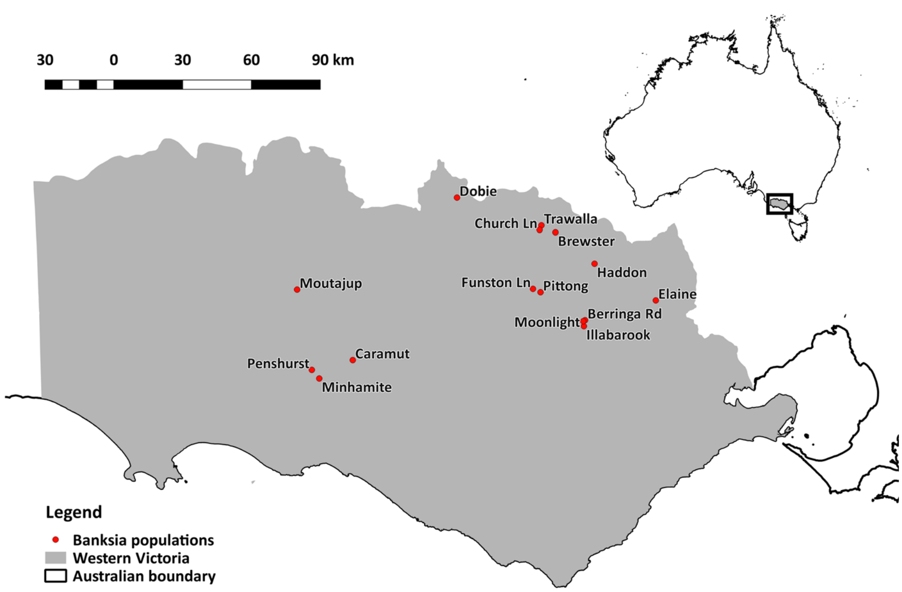


Fig. 1 Map of sampled *Banksia marginata* populations across south-west Victoria, Australia

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 and 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 (Considine 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 Log_{10} transformed. We then calculated a regression Log_{10} (d_i) as the independent variable and 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 and Rayson 1957) rather than 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 at low frequency (between 0 and 6 clones). Where true clonal species are involved, care needs to be taken when interpreting population dynamics using this method.

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 χ^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.

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).

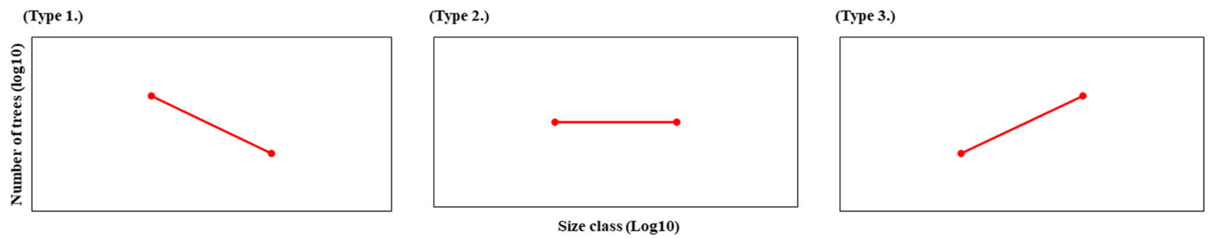


Fig. 2 Conceptual model of three predicted stand types using Condit analysis. Type 1: Recruitment not limited. Type 2: Recruitment moderately limited. Type 3: Recruitment severely limited

Results

Stand dynamics encompassed all Condit slope types (Fig. 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 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 (Fig. 5a; F (1,13) = 28.38, $p < 0.001$, $r^2 = 0.69$) 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 the proportion varied between populations; three populations did 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 ($p < 0.05$); three populations (Moutajup, Trawalla and Caramut) stood out,

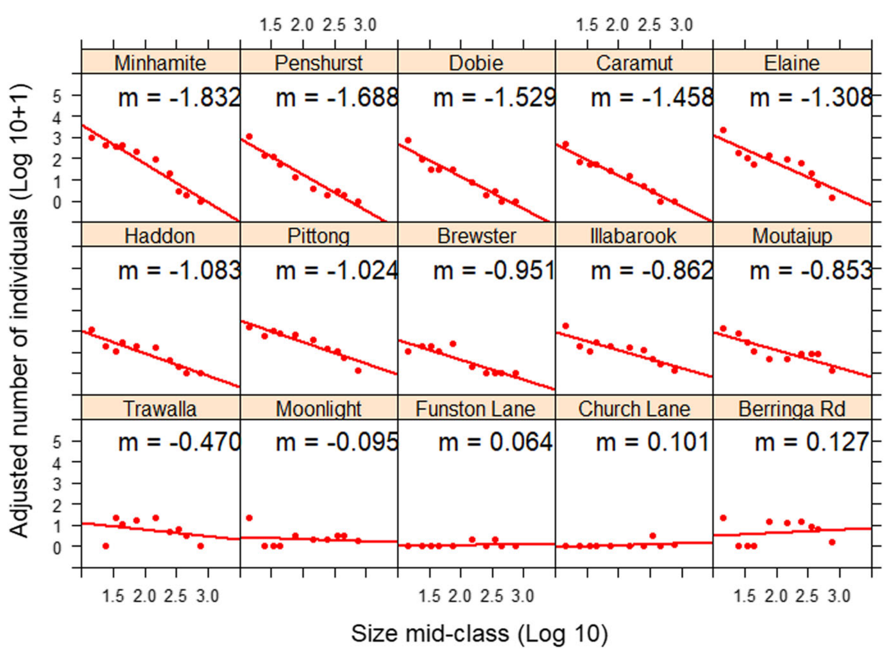


Fig. 3 Condit slope outputs for 15 analysed populations. Regressions are arranged from highest negative value (recruitment not limited) through to the highest positive value (substantial recruitment limitation). The x-axis represents the mid-point of the size class and has been Log10 transformed. The 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

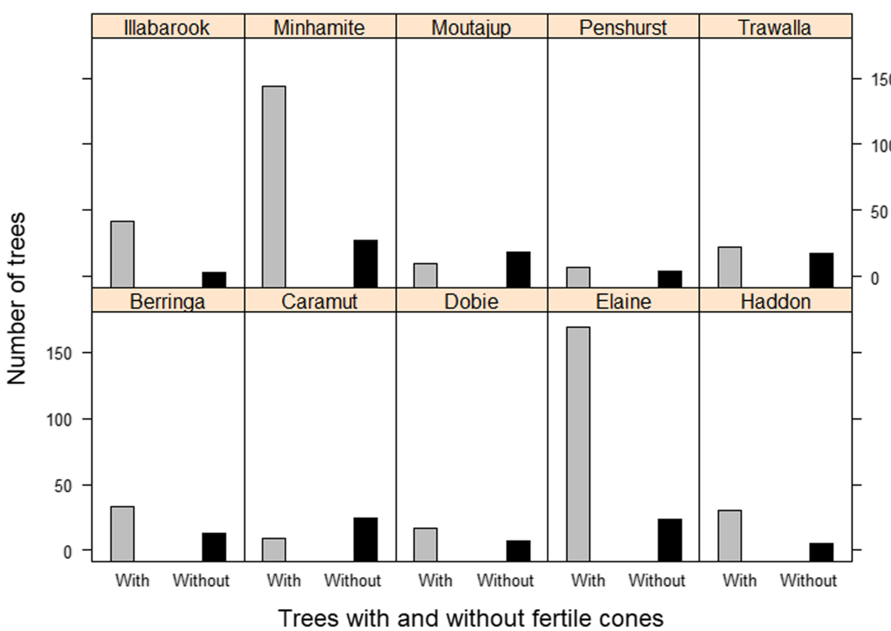
with the most comparisons that were significant and these populations were also found to have high proportions of mature trees without cones (Fig. 4). The results of the linear regression suggest no significant relationship between population size and the percentage of trees without fertile cones (Fig. 5b; $F(1,8) = 1.42$, $p = 0.27$, $r^2 = 0.15$) 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 policymakers 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, with reports from land managers suggesting 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 Victoria, 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 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)

Fig. 4 Proportion of *Banksia marginata* trees with and without fruit at ten populations distributed across the western plains, Victoria



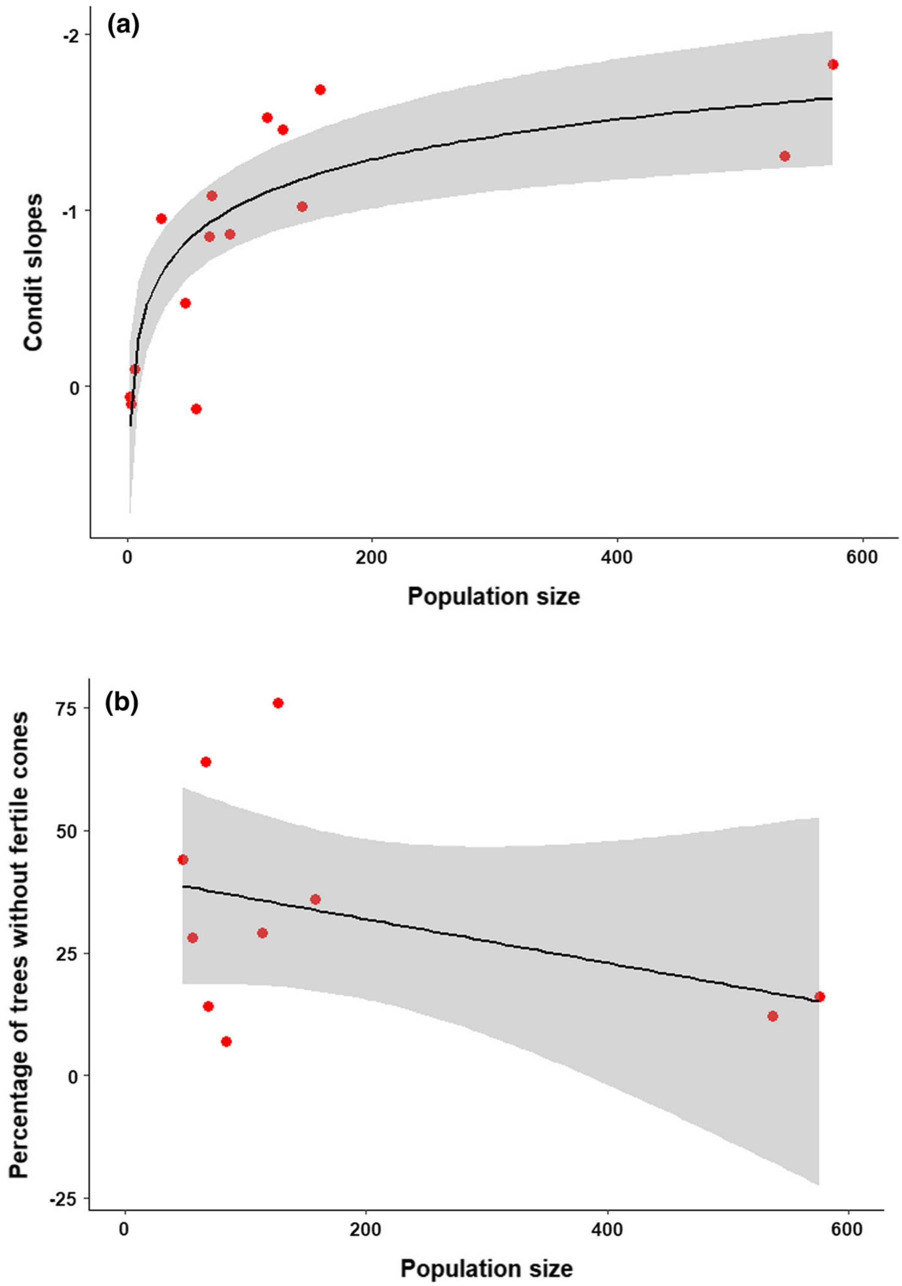


Fig. 5 The relationship between *Banksia marginata* population size and **a** Condit slope values (with a fitted log curve) and **b** percent of trees (> 58 mm DBH) without fruit (with a linear line of best fit)

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 and 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 and Calvo 1991; Nayak and 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 and Brocato 2015; Sankaran et al. 2005; Vadigi and Ward 2013). Grasses both suppress tree growth (February et al. 2013; Riginos 2009) and limit the survival of trees (Morrison et al. 2018; Scholes and Archer 1997), particularly the more vulnerable smaller size classes, where the root zones of trees and grasses are more likely to interact (Holdo and Brocato 2015). Grasses also have the capacity to impact fire regimes, with concomitant effects on tree sapling survival (Haverkamp et al. 2018; Peterson and 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 and 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, changes in vegetation composition over time (Bradshaw and Waller 2016; Dexter et al. 2013; Neave and 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 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 and 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 and 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 and 100% of cones removed (Heyes et al. 2019).

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 and Haridasan 2008), herbivory (MacDougall et al. 2010) or too much/little fire (Gent and 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 and Morgan 2007; Naccarella et al. 2019).

Conclusion

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.

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