Associational Refuge Promotes Short-term Seedling Survival

in *Banksia integrifolia* (Proteaceae)

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Abstract

Long-term changes in vegetation structure and habitat disturbance have impacted stand dynamics in *Banksia integrifolia* coastal woodlands at Wilsons Promontory National Park. This study assesses the impacts of recruitment-limitation on the ability to replace aging or dying trees to maintain healthy stand dynamics. This will better inform strategies to promote successful regeneration and stand resilience. Natural and planted seedling recruitment was followed in three vegetation types (Banksia woodland, Bracken dominated and Coast Teatree shrubland) to determine how differing microsites affect probability of seedling survival. To test for impacts of top-down processes by overabundant herbivores (Swamp Wallaby, *Wallabia bicolur* and Hog deer, *Hyelaphus porcinus*), a fencing/control experiment was also implemented. After four months, the Banksia woodland and Coast Teatree shrubland sites each experienced a greater loss of germinated seedlings compared to the Bracken dominant community. Furthermore, survival was higher when herbivores were excluded in all patch-types.

Associational refuge may explain these results; dense bracken cover may allow seedlings to escape initial browsing as this vegetation type is often avoided by herbivores due to perceived poor nutritional value. This factor should be further investigated to determine whether it is an effective mechanism for promoting long-term persistence both in this setting and in other species experiencing post-dispersal recruitment failure as a result of overabundant herbivores.

Introduction

In several ecosystems in Australia, herbivore populations have increased as a result of changing land use, removal of native predators and provision of water points (Glen *et al.* 2007; Bird *et al.* 2013;; Letnic and Crowther 2013). The increased densities and subsequent browsing pressure exerted by these herbivores has had negative impacts on plants in communities ranging from temperate to semi-arid regions at a small- and large-scale (Brown and Allen 1989; Huntly 1991; Deraison *et al.* 2015). This can cause the local extinction of plant species and compromise the structure, function and development of ecosystems over time (Gordon et al. 2004; Klein 2012).

Herbivore populations are considered 'overabundant' in an ecological sense when they reduce the density of favoured plant species, thereby disrupting the equilibrium between plants and herbivores (Caughley 1981). This can occur at many levels, from an individual organism experiencing repeated defoliation events resulting in it no longer being able to regenerate, as seen in Manna Gums (*Eucalyptus viminalis*) supporting overabundant koala populations at Cape Otway, Victoria (Whisson *et al.* 2016). It may also manifest at the community level, whereby recruitment attempts are hindered by increased herbivory pressure and as a result plant composition or ecosystem function is altered. An extreme example of this is the impact of unregulated Elk populations in Yellowstone National Park (Ripple and Beschta 2012).

In south-east Australia, the primary native herbivores are macropods such as Eastern Grey Kangaroo (*Macropus giganteus)*, Swamp Wallaby (*Wallabia bicolur)* and the Common Wombat (*Vombatus ursinus*) and feral herbivores include deer and lagomorphs. Kangaroos are grazers, feeding predominantly on grasses, whereas wallabies and deer are considered

browsers, consuming herbaceous and woody plant species (Davis *et al*. 2008). In most areas of Victoria, they experience no predation from native predators (Dingos), and do not fit the preferred size-class to be hunted by exotic predators (foxes and cats) (Davis *et al*. 2015; Yugovic 2015). This, in addition to readily accessible water points has led to population densities increasing (Letnic and Crowther 2013). Many populations are now classified as overabundant and regeneration for the plant species that share the landscape have been shown to be compromised. Dexter *et al*. (2013), for example, found that the presence of overabundant Swamp Wallaby resulted in a significant mortality of *Bankisa integrifolia* and *Allocasuarina littoralis* seedlings in coastal forests. Similar outcomes have been observed elsewhere; on Anticosti Island browsing by overabundant white-tailed deer (*Odocoileus virginianus*) accounted for 48% mortality of Balsam fir seedlings (Côté *et al*. 2008).

 While most woody plants do not require a consistent input of new individuals to maintain their populations, long-term recruitment bottlenecks can threaten a population's ability to replace aging and dying stands (Stefano 2003). For example, Cheal (1993) found that there was almost a complete lack of regeneration of long-lived dominant woody species in stock grazed habitat, concluding that extinction for these populations was inevitable. Similar findings were observed in *Alectryon oleifolius, Casuarina pauper* and *Myoporum platycarpum* populations experiencing grazing pressure (Chesterfield and Parsons 1985). Furthermore, while trees can be buffered from damage by herbivores simply by growing to a size out of their reach, this can take several years. Hence, many individuals are either killed before they reach this point or become stunted as they are constantly browsed upon due to high herbivore pressure (Cadenasso *et al*. 2002; Davis and Coulson 2010).

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Many studies have turned to analysing how habitat attributes can influence herbivore foraging decisions and how this can be manipulated to promote plant survival and growth beyond the vulnerable seedling stage (Emerson *et al.* 2012). One mechanism is known as 'associational refuge', which accounts for all the factors that may influence a herbivores decision to forage. This includes the structure of the broader landscape, the nutritional quality as well as chemical and physical defences of focal and neighbouring species, composition of preferred resource to non-preferred in a patch of vegetation and plant composition in neighbouring patches (Atsatt and O'Dowd 1976). Stutz *et al.* (2015) determined that these factors influence different stages of decision making for herbivores when they are foraging. These decisions are defined as: where to search, what it will detect and whether it will consume what it has found. Between each step, the herbivore makes an assessment to determine whether to proceed or abandon its foraging attempt (Fig. 1).
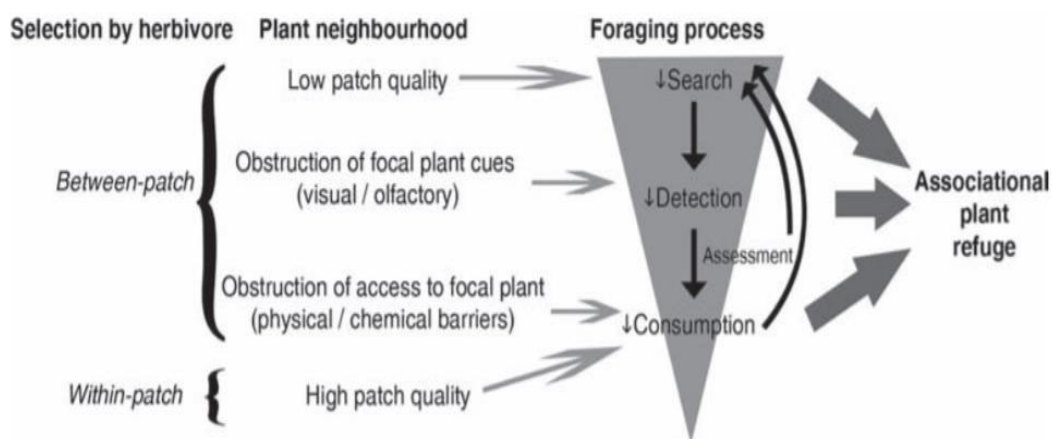

Figure 1. Conceptual diagram depicting the relationship between a herbivores selection process and the plant neighbourhood it may forage in. Associational refuge can be achieved for a focal species if it exists between patches with poor quality as a herbivore will reduce search effort. Alternatively, if a focal plant exists within a patch of high quality a herbivore will consume the species of greater nutritional value relative to the focal plant. Reproduced from Stutz *et al.* 2015.

At the landscape scale, herbivores may prioritise investigating one patch over another due to its structure and the accessibility of high-quality resources (Bennett *et al*. 2020). Browsing herbivores such as Swamp Wallaby and deer are often sympatric because of their overlapping dietary and shelter preferences (Davis *et al*. 2008). They have been observed to prioritise browsing in habitats with overhead canopies as opposed to open grasslands, likely, to reduce detection from predators (Leopole and Wolfe 1970). As a result, plant recruits are more vulnerable to herbivory in those areas. Stutz *et al*. (2015) noted that seedlings that emerged directly under their parent canopy may have been more likely to be detected than seedlings emerging in neighbouring open canopy vegetation patches.

At an individual scale, some plant defences are more effective at repelling herbivores than others. For example, Bracken (*Pteridium esculentum*) is a highly toxic species which occurs widely in south-eastern Australia, from open forests in temperate landscapes to coastal dune-swale systems (Hamilton *et al*. 1990). It contains terpene glucosides with carcinogenic properties such as Ptaquiloside and Ptesculentoside, both of which are capable of alkylating amino acids and DNA (Fletcher *et al*. 2011). As a consequence of its toxicity, it is largely avoided by herbivores and 'fern parklands' are formed (Dexter *et al*. 2013). They are densely packed and can obscure a herbivores direct view of the understorey as well as mask the scents of preferred food sources which reduces detection ability. Therefore, there is a positive effect of dense bracken patches on browsing delay of coexisting seedlings (Stutz *et al*. 2015).

The concept has been investigated in numerous settings e.g. shrubs protecting seedlings or grasses protecting seedlings and have yielded positive results that suggest manipulating habitats at a small scale by planting protective species beside vulnerable individuals could

reduce their susceptibility to herbivory (Jensen *et al*. 2012; Good *et al*. 2014). Furthermore, this can also facilitate recruitment survival at the landscape level, as seen by García and Ramón (2003) who reported that *Ilex aquafolium* (Holly) facilitated the survival and growth of *Taxus baccata* seedlings and saplings. Hence, this could be a valuable method for landscapes experiencing recruitment failure of dominant species as a result of overabundant herbivores.

An example of this is thought to occur in coastal grassy woodlands in southern Australia which are experiencing a decline of their dominant tree species –*Banksia integrifolia* (Coast Banksia). Populations are failing to replace aging and dying stands due to an apparent lack of recruitment. Within 25 years, a decline of 42-77% occurred in two Coast Banksia stands on Westernport Bay (Gent and Morgan 2007). At Wilsons Promontory National Park, Coast Banksia has been experiencing recruitment failure and population decline since the 1940s (Bennett 1994), with the expansion of the invasive *Leptospermum laevigutam* into Coast Banksia habitat apparently exacerbating this decline (Morgan and Nield 2011).

Bennett (1994) attributed Coast Banksia decline at Wilsons Promontory to herbivores. The aims of the current study were to investigate apparent recruitment failure of *B. integrifolia* at the post-dispersal stage in the coastal grassy woodlands of Wilsons Promontory National Park. There is a large population of both native (Swamp Wallaby) and exotic (Hog Deer) browsing herbivores on the Yanakie Isthmus, both of which target Coast Banksia (Davis *et al*. 2008). Without natural predators, herbivore populations have become overabundant (Jim Whelan *pers. comm.*). It was hypothesised that (1) the overabundance of herbivores was the leading cause for recruitment failure and that (2) *B. integrifolia* seedlings would survive longer in a vegetation type that provided associational refuge from these herbivores.

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Materials and Methods

Study Species

Coast Banksia, *Banksia integrifolia* (Proteaceae) is a long-lived, fire-tolerant tree growing to 25m tall (Hazard and Parsons 1977; George 1996). It occurs along the east and south-east coast of Australia, from southern Queensland to Port-Phillip Bay (George 1996). This includes Wilsons Promontory, the most southern edge of its distribution where it dominates Coastal Grassy Woodlands. It flowers from January to July and releases seed most readily during late summer (Price and Morgan 2003). Its long flowering period makes it a staple resource for many fauna during winter (Law 1994).

Unlike most Banksia, *B. integrifolia* is tachysporous. Rather than relying on disturbance events such as fire to initiate follicle opening and seed release, *B. integrifolia* releases seed spontaneously upon maturation. Seeds are wind dispersed, but often are released while still contained within a cone. This results in many seedlings emerging directly under parent canopies (Witkowski *et al*. 1991). *B. integrifolia* seeds do not survive in the soil long after release (Weiss 1984). Past studies have observed that germinability is generally high regardless of stand age and typically occurs at temperatures under 21°C (Sonia and Heslehurst 1978; Price and Morgan 2003).

Study Sites

The study was conducted from April to July 2020 at the Airstrip and Tin Pot Track on the Yanakie Isthmus, Wilsons Promontory National Park (38.95°S, 142.27 °E). The study sites consist of calcareous sediments of aeolian origin, overlying siliceous sands from the Pliocene Epoch (Bennett 1994).

Across the study areas, three vegetation types were selected to study *B. integrifolia* recruitment dynamics. All vegetation types contained mature, seed-producing Coast Banksia, although density and canopy cover varied. Sites were selected after field reconnaissance and were defined according to their structure and dominant species presence as: (i) Coast Banksia woodland, (ii) Coast Teatree shrublands and (iii) Bracken-dominant.

Climate Trends

Climate on the Yanakie Isthmus is maritime, with a mean annual rainfall of 881mm. Monthly rainfall was above average during the first two months of the study. January and February 2020 experienced 89% and 101% of mean annual monthly rainfall during peak seed release (Fig. 2; Yanakie, station number 85163, 38.79 °S, 146.18 °E, 10 m asl). The mean maximum annual temperature is 16.4 °C. However, the mean maximum annual temperature has exceeded this for the past 20 years as has the mean minimum temperature which is 11.4 °C (Wilsons Promontory Lighthouse, station number 85096, 39.13 °S, 146.42 °E, 95 m asl, 23km south of Airstrip and Tin Pot sites).
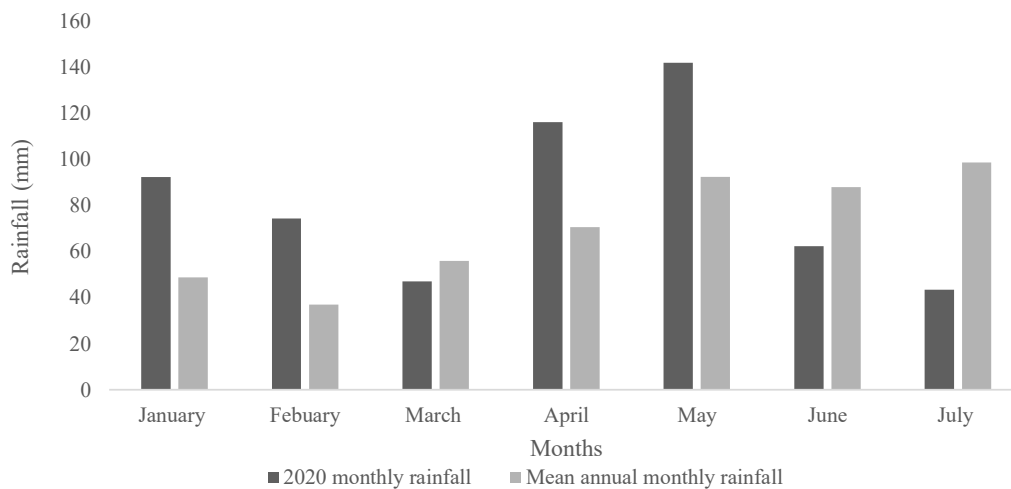

Figure 2. Monthly rainfall during the study period (January 2020 – June 2020) compared to long-term mean monthly rainfall.

Seedling survival according to vegetation type

 To investigate if natural seedling recruitment emergence and survival differed across the three vegetation sites, eight 90 m^2 plots were established in each vegetation type (n =24, Appendix II) in April 2020. First, differences between the three vegetation types were characterized by assessing floristic composition using five 2 m^2 quadrats per plot. Each species was assigned a Braun-Blanquet cover abundance rank in each quadrat. Differences in gravimetric soil moisture between vegetation types was also compared. In May 2020, ten soil samples were collected to 10 cm depth in each plot ($n = 240$). The soils were weighed (wet), air-dried for three months and re-weighed (dry) to determine the gravimetric soil moisture in each of the vegetation types.

 To determine how natural seedling survival varied across vegetation type, I examined the basal diameter of all existing seedlings/saplings within each plot to determine their origin. All individuals found were allocated into one of three groups.

    (i)   2020 recruits (basal diameter < 2.5 mm) ($n = $ 663)

    (ii)   Pre-2020 recruits (basal diameter > 2.5 mm) ($n = 32$)

    (iii)   Older saplings in a suppressed state ($n = 39$)

 All 2020 and pre-2020 seedlings were tagged in April 2020. Survival, height (cm), basal diameter (mm) and number of leaves were recorded monthly for four months to determine seedling performance.

Impacts of Herbivory

 To test for the impact of herbivory on seedling survival, I established an exclusion experiment in April 2020. Three 2 m diameter paired circular plots (fenced vs control) were

assembled in all plots across the three vegetation types. The exclusion plots were constructed with 1.1 m tall fencing with a 2.5 cm wire mesh and four star pickets were used to support the fence structure. The control plots were formed with one star picket and a measuring tape with radius matching the fenced plots. All 2020 seedlings within this area were marked and the picket was later removed. A total of 122 Banksia saplings sourced from local seed (Fishermans Creek, the far north-west of Wilsons Promontory) in 2018 and grown by a local nursery (Friends of the Prom) were also planted ($n = 48$ in Coast Banksia woodlands, $n = 48$ in Coast Teatree shrublands, $n = 26$ in Bracken-dominant patches). This was done to test whether taller, older and woodier individuals were just as vulnerable to herbivory as new recruits.

The survival and growth of the seedlings (height (cm), basal diameter (mm) and number of leaves) and evidence of damage caused by herbivores (e.g. leaves notably ripped/removed, broken stems or seedlings missing with remaining tag obviously chewed on) was recorded at monthly intervals for four months. Furthermore, the number of times an individual seedling experienced damage (was foraged) before being killed was recorded to determine how many attempts of foraging it took for recruits to be removed from the population.

To identify herbivore presence in the three vegetation types, five plots in each vegetation type were randomly selected and one camera trap (RECONYX HC600) was established in each in May 2020 for one month. The traps were set to an advanced setting of five rapid-fire shots in sequence with a delay of 15 seconds between each set of captures. The cameras were attached to trees or star pickets at a height of 1-1.5 m from the ground. After one month, the cameras traps were removed and the species captured by the cameras were identified and the number of times they were observed was counted.

Statistical Analysis

To test for differences in floristic composition between vegetation types the Braun-Blanquet cover abundance values were converted to mid-point percent cover. A mean abundance of the individual species in each plot was calculated by combining the total abundance of each species across the quadrats in each plot then dividing it by five (the number of quadrats per plot). Using PRIMER v7, an ordination (Non-metric Multidimensional Scaling) was conducted to investigate variation in floristic composition within and among vegetation types. Dissimilarities between all samples were based on the Bray-Curtis dissimilarity index. An ANOSIM was used to test differences in floristic composition between vegetation types excluding the dominant vegetation types – Bracken, Coast Banksia and Coast Teatree. A log transformation was performed on the data prior to performing all tests to account for common and rare species (Clarke 1993**)**. Underlying differences in floristic composition between vegetation types were observed (Appendix III). To test for differences in gravimetric soil moisture between vegetation types a one-way ANOVA was used on square-root transformed data (Appendix IV).

A repeated measure two-way ANOVA was used to determine if differences in seedling survival, height (cm), basal diameter (mm) and number of leaves was significant between the three vegetation types and two treatments across time (natural and planted seedlings were tested separately). Log transformation was performed on height and number of leaves data to satisfy ANOVA assumptions of equal variance. The normality assumption was not met through statistical analysis but extent of skewness in descriptive histogram plots was accepted and the F-statistics were still considered robust (Blanca *et al.* 2017). The same tests were applied to measurements of growth in Banksia saplings, though sapling survival was only used for descriptive analysis (Appendix V).

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A two-way chi-square test was used to determine if there was a different proportion of 2020 recruits, pre-2020 recruits or saplings in a suppressed state in each vegetation type. Pearson's chi-square test was used to determine whether the number of seedlings removed/killed as a result of herbivory was different to that of seedlings that died of other causes. Determining whether there was a difference in number of foraging attempts between sites is described by observing the proportion of seedlings killed upon being attacked by a herbivore one, two, three or four times.

The camera trap data was separated into individual species which then underwent analysis. The total number of captures for each species was divided by the total number of cameras and their corresponding trap days:

$$\text{Number of captures for individual spp.} = \frac{\text{total count of each individual spp}}{\text{total cameras in vegetation type } \times \text{ total trap days}}$$

All statistical analyses were performed on IBM SPSS Statistics or Microsoft Excel 2020.

RESULTS

There was a significant difference in the proportion of different aged Coast Banksia individuals between vegetation types, with a higher number of observed 2020 recruits to expected (χ^2 (4, 733) = 14.897, $p < 0.05$). Furthermore, there was a higher number of pre-2020 recruits and suppressed saplings in the Bracken dominant vegetation type than expected (Fig. 3).
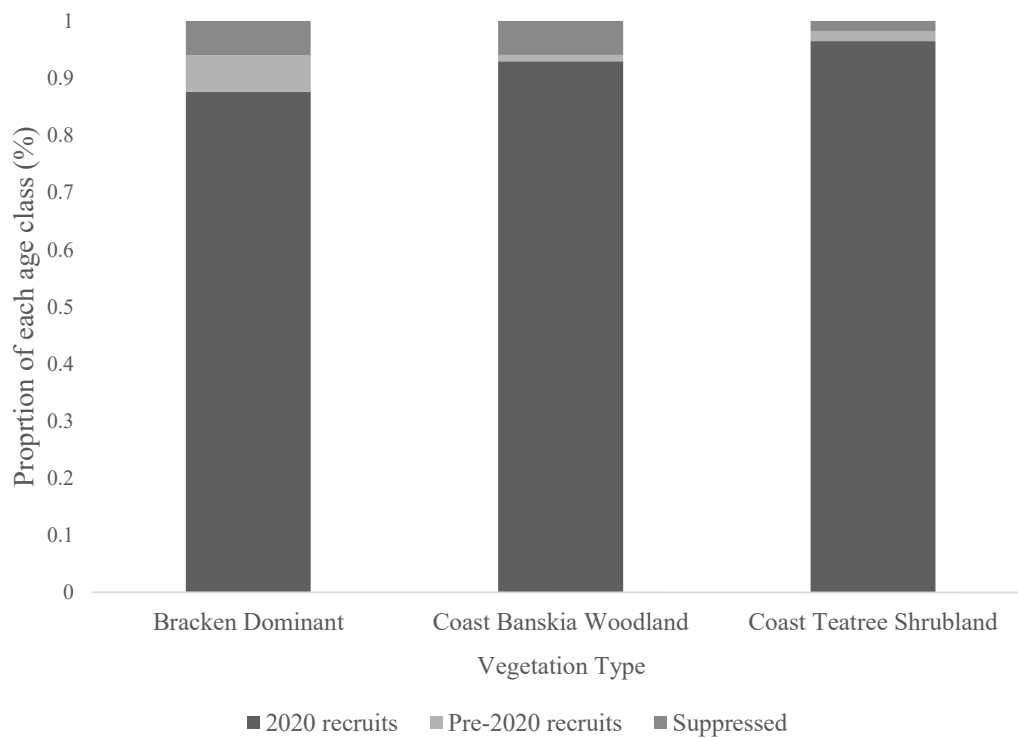

Figure 3. Proportion (%) of natural Coast Banksia tagged in each age class (2020 recruits, pre-2020 recruits, suppressed) between vegetation type.

Seedling count changed significantly over time ($F(1.57, 58.083) = 30.818$, $p < 0.01$, Greenhouse-Geisser). The main effect of vegetation type on seedling count was also significant ($F(2, 37) = 8.029$, $p < 0.01$). The significant effect was found to be dependent on Bracken dominant vegetation type, which had a higher mean number of seedlings compared to Coast Teatree shrubland and Banksia woodland (Fig. 4). There was no interaction between vegetation type and time (Greenhouse-Geisser, $p > 0.05$).

Treatment was found to have a significant main effect on seedling count ($F(1, 37) = 8.579$, $p < 0.01$). There was a significant interaction between treatment and time (Greenhouse-Geisser, p-value < 0.01). Mean seedling count decreased markedly in all control plots over time compared to seedlings in fenced plots.
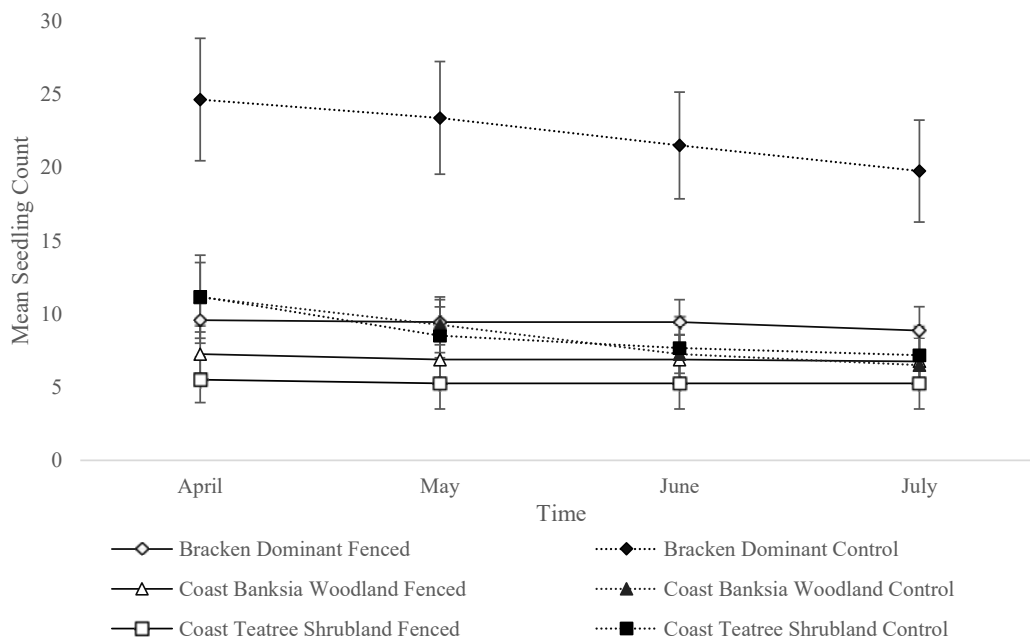
Figure 4. Mean (±SE) number natural banksia seedlings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Coast Banksia Woodland, Coast Teatree shrubland) across time.

Height changed significantly over time (F (2.556, 966.294) = 23.769, p-value < 0.01, Greenhouse-Geisser) and was significantly different between vegetation types ($F(2,378)$ = 15.286, p-value < 0.01). The significant effect was driven by a greater mean height in Bracken dominant vegetation type compared to Banksia woodland and Coast Teatree shrublands (Fig. 5). There was a significant interaction effect between time and vegetation type (Greenhouse-Geisser, p-value < 0.01).

The difference in height between treatments did not change significantly ($F(1,378)$ = 2.647, p-value > 0.05). However, treatment did have a significant interaction effect with time (Greenhouse-Geisser, p-value < 0.01). Seedlings in the all vegetation types exhibited a distinct separation in growth between those in fenced plots to those in control by the end of the study period.
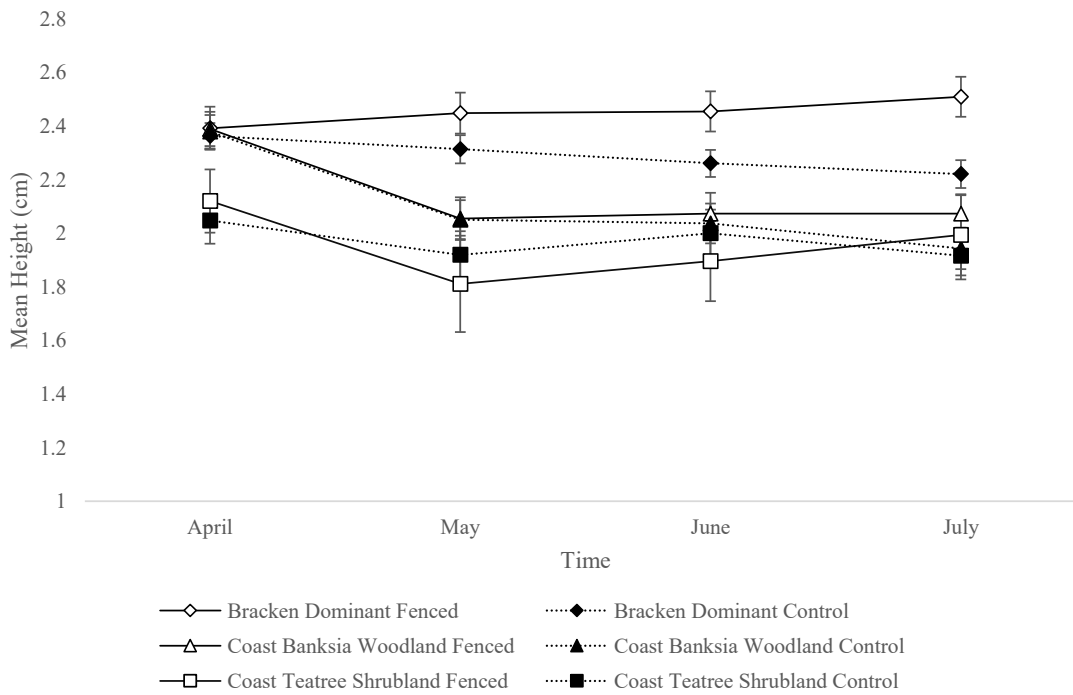

Figure 5. Mean Height (±SE) with log transformation of natural banksia seedlings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Coast Banksia Woodland, Coast Teatree shrubland) across time.

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Basal diameter changed significantly over time ($F_{(2.821, 1066.158)} = 29.678$, p-value < 0.05, Greenhouse-Geisser). There was a significant main effect of vegetation type on basal diameter ($F_{(2,378)} = 10.276$, p-value < 0.01). The significant effect was found to be dependent on the Coast Teatree shrubland vegetation type having a smaller mean basal diameter compared to Bracken dominant and Banksia woodland (Fig. 6). There was no interaction between vegetation type and time (Greenhouse-Geisser, p-value > 0.05).

Treatment did not have a significant effect on basal diameter ($F_{(1, 378)} = 0.939$, $p > 0.05$). There was no significant interaction between treatment and time (Greenhouse-Geisser, p-value > 0.05). All seedlings experienced growth regardless of whether they were damaged by herbivores or if other individuals in each population were removed/killed with the exception on seedlings in the Banksia woodland control treatment.
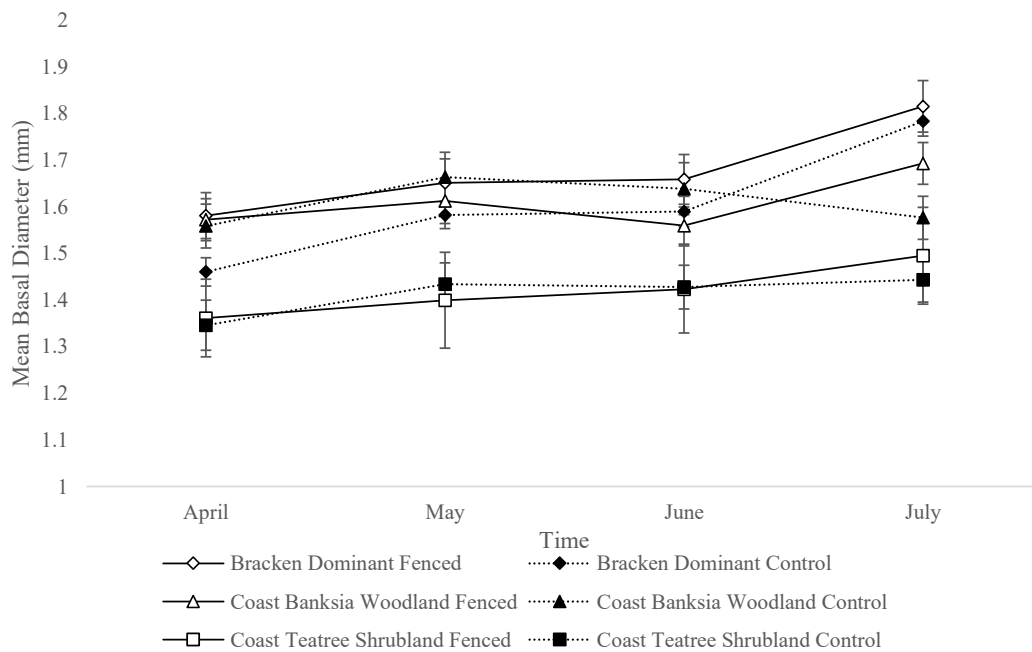

Figure 6. Mean (±SE) basal diameter of natural banksia seedlings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Coast Banksia Woodland, Coast Teatree shrubland) across time.

Mean leaf number changed significantly across time ($F(2.043,747.908) = 13.519$, p-value < 0.01) and between vegetation types ($F(2,366) = 14.286$, p-value < 0.01). The significant effect was driven by a greater mean height in Bracken dominant vegetation type compared to Banksia woodland and Coast Teatree shrublands (Fig. 7). There was also a significant interaction effect between time and vegetation type (Greenhouse-Geisser, p-value < 0.01).

The difference in leaf count between treatments did not change significantly ($F(1,366) = 1.444$, p-value > 0.05).However, treatment and time did have a significant interaction effect, with seedlings in control plots losing leaves while seedlings in fenced plots maintained or gained leaves across time (Greenhouse-Geisser, p-value < 0.01). Seedlings in the Bracken dominant vegetation type exhibited a distinct separation in leaf gain/loss between those in fenced and control plots.
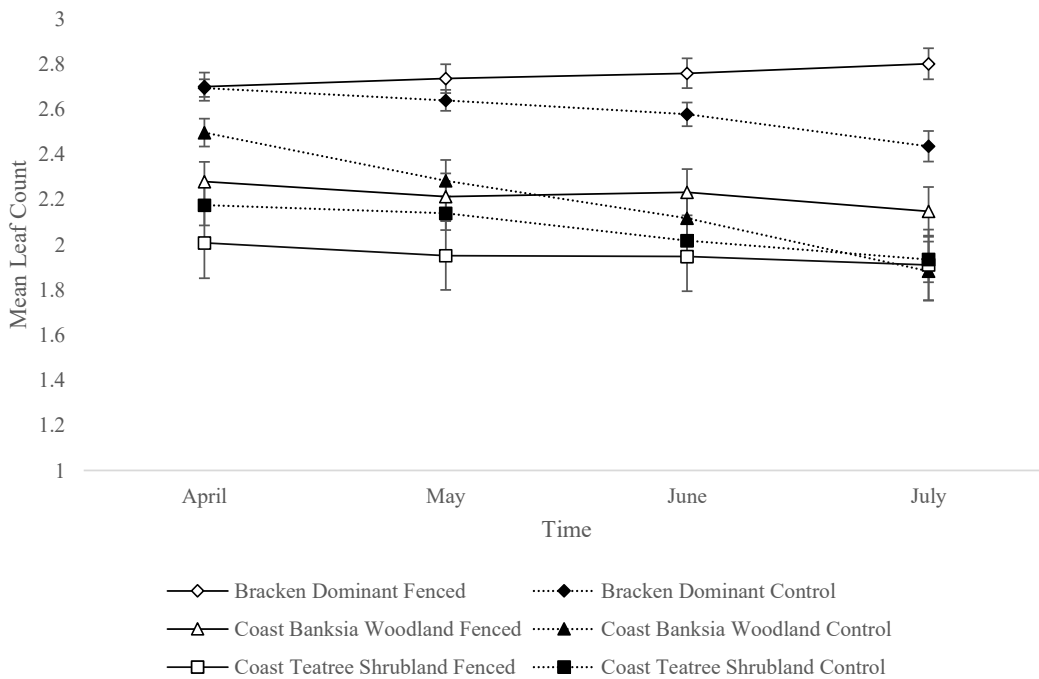

Figure 7. Mean number of leaves (±SE) with log transformation of natural banksia seedlings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Coast Banksia Woodland, Coast Teatree shrubland) across time.

The number of Coast Banksia killed by herbivory was not significantly greater than the number killed by unrelated causes when compared between vegetation types (χ^2 (2, 147) = 0.721, $p > 0.05$). A greater proportion of seedlings died of causes unrelated to herbivory in the Coast Teatree shrubland vegetation type compared to Bracken Dominant and Coast Banksia Woodland vegetation (Fig. 8).
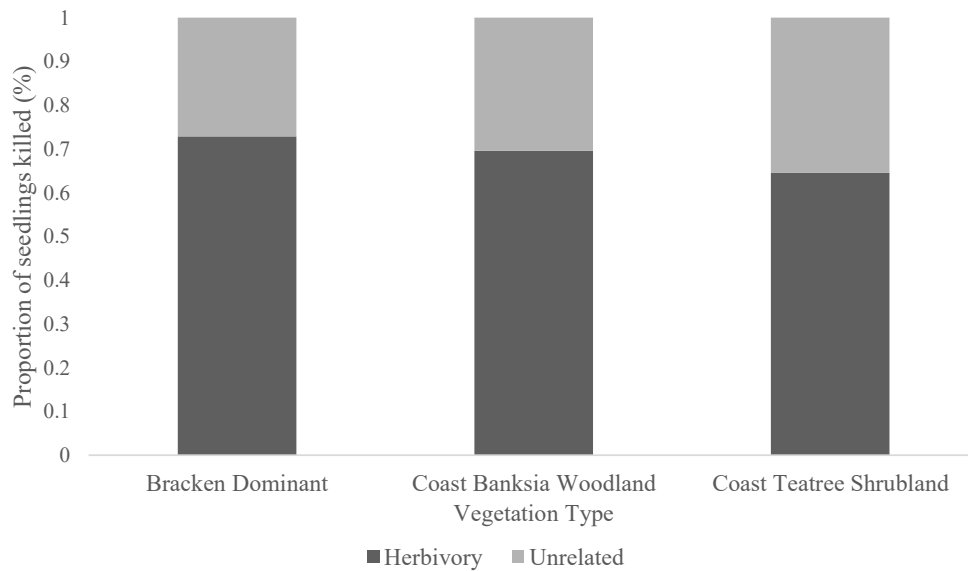

Figure 8. Proportion (%) of natural banksias killed as a result of herbivory or unrelated causes between vegetation types (Bracken Dominant, Coast Banksia Woodland, Coast Teatree shrubland).

The highest proportion of seedlings were killed after only one attack by herbivores regardless of vegetation type. No seedling survived more than three attacks (Fig. 9).
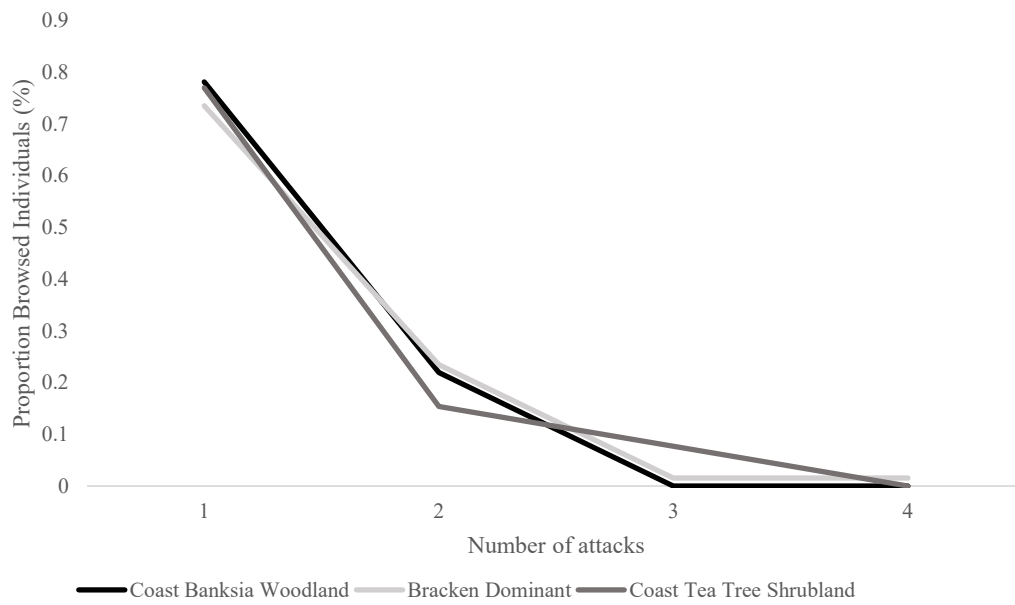

Figure 9. The proportion of seedling killed on the first, second, third or fourth attack from herbivores in each vegetation type (Bracken Dominant, Banksia Woodland, Coast Teatree shrubland).

Many species were identified in camera trap captures (Appendix VI). The most common were kangaroos, and primary browsers hog deer and wallaby. There was a distinct difference in the number of observations of these species between the Bracken dominant vegetation type and Coast Teatree shrubland and Banksia woodland (Fig. 10).
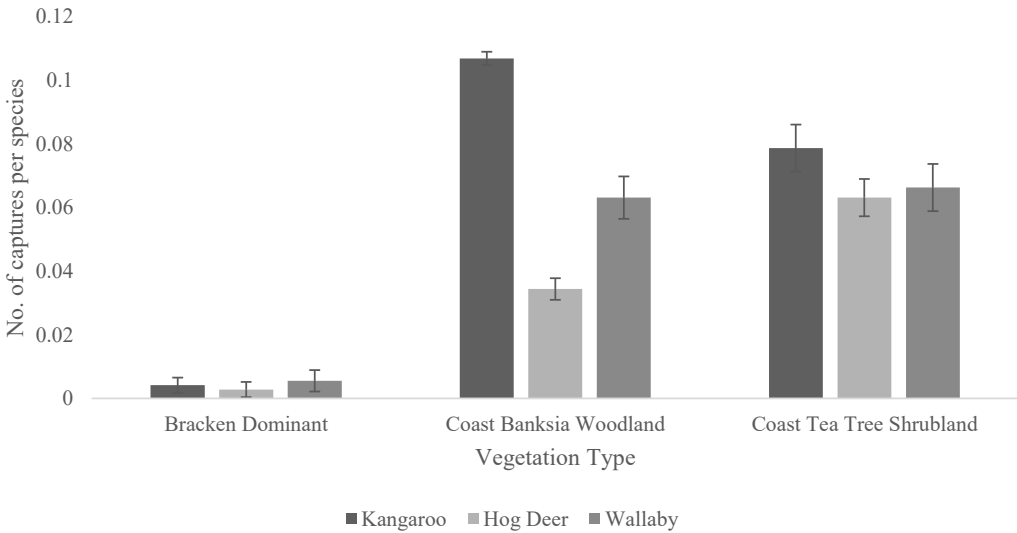

Figure 10. The total number of kangaroos, hog deer and wallabies (±SE) observed according to trap instances between vegetation types (Bracken Dominant, Banksia Woodland, Coast Teatree shrubland).

Discussion

 This study supports the hypothesis that associational refuge promotes seedling survival and growth of *Banksia integrifolia*, at least in the short-term. Variation in seedling survival was identified to be driven by herbivore patch preference. Regeneration of *B. integrifolia* in Banksia woodlands and Coast Teatree shrublands was hindered by high browsing pressure which resulted in reduced growth and increased damage to Coast Banksia seedlings, as well as the complete removal of individuals. By contrast, Banksia seedlings in Bracken dominant patches grew, on average, taller, thicker and retained and grew more leaves during the study period. This indicated that seedlings that emerged in this patch type exhibited a greater capacity to survive and grow than in the other two vegetation types investigated.

Associational effects of vegetation type

 Herbivore foraging behaviour is first and foremost driven by habitat structure and resource availability (Augustine and McNaughton 1998; WallisDeVries *et al*. 1999; Hansen *et al*. 2009). If the structure of a patch increases vulnerability to predation or contains poor species quality, then it is generally avoided (Freeland 1991). This has been observed in numerous studies including Kotler *et al*. (1991), where two gerbil species selectively foraged in bush microhabitats rather than in the open in response to owl presence. The importance of 'bottom-up' process in terms of plant quantity and quality impacts on herbivore heterogeneity and behaviour has also been extensively studied (e.g. Hunter and Price 1992; Underwood 2004).

 In this study, Bracken dominant sites fit both descriptions as a patch of low perceived quality and with increased exposure risk to predators. It represents a habitat with both inadequate shelter available to reduce predator detection (i.e. raptors) and refuge from harsh

weather conditions, but also contains seemingly little palatable food compared to neighbouring vegetation patches (Stephens and Krebs 1986). This is evidenced by the near complete absence of primary browsers (Swamp Wallabies and Hog deer) and indirect grazers (Eastern Grey Kangaroo) in camera trap images compared to Coast Banksia woodland and Coast Teatree shrubland sites. Swamp Wallabies in particular have been shown to exhibit this selective habitat behaviour in response to food and shelter availability (Stefano *et al*. 2009; Swan *et al*. 2009).

 The reduction of herbivores in Bracken dominant patches can be further explained by the presence of dense *Pteridium esculentum* which is highly toxic and non-palatable for consumers (Fletcher *et al*. 2011). The density with which it grows also acts to obscure a herbivores ability to detect other species growing amongst it (Hambäck *et al*. 2000). For example, Swamp Wallabies rely heavily on olfactory cues to detect resources, and the high density of Bracken can act to obscure or block these cues, preventing the herbivore from identifying and following unique scents to preferred food sources (Bedoya-Pérez *et al*. 2014; Stutz *et al*. 2016). As a result, Banksia seedlings that coexisted in this patch type were more likely to survive through associational refuge as a consequence of the repellent-plant mechanism, whereby the presence of bracken repelled herbivores from investigating within patches (Hay 1986; Van Uytvanck 2009; Smit and Ruifrok 2011; Stutz *et al*. 2015).

 Unlike the Bracken dominant patches which had an open canopy, Banksia woodlands and Coast Teatree shrubland sites contained mature, reproductively active *B. integrifolia* individuals. Stutz *et al.* (2015) predicted that in these dense overstorey canopies, focal seedlings were more likely to emerge directly under parent canopies. As a consequence, these seedlings may be more vulnerable to herbivory, as the existence of mature individuals

acts as an indicator of a patch with a high quality resource in high concentrations (Bergvall *et al*. 2006). The closed canopy also hinders dense bracken establishment in the understorey, through light competition (Douterlungne 2013). This can increase a herbivores ability to detect seedlings by reducing visual and olfactory obstructions. This observation can be linked to work conducted by Root (1973),who coined the 'resource concentration hypothesis' in relation to insect-plant interactions and has since been applied to habitat selection for small and large mammalian herbivores (O'Neill *et* al. 1988; Ritchie and Olff 1999; De Knegt *et al* 2007; Schartel and Schauber 2016).

Long-term impact of increased herbivore pressure on patch dynamics

The success of Coast Banksia seedlings in Bracken dominant patches compared to Coast Banksia woodland patches could suggest that associational refuge creates successional patch dynamics in the long-term. Ogden *et* al. (1987) investigated Kauri (*Agathis australis*) forests in New Zealand and found that regeneration relied on gap-phase dynamics. Kauri was most successful at recruiting in gaps between mature forests compared to within forest patches, eluding to a slow transition in patch dynamics within and between vegetation that could take place over centuries, owing to the longevity of Kauri.

Similar assumptions could be made of this study whereby Bracken dominant patches could develop into a Coast Banksia dominant patch as seedlings emerge through the Bracken and grow to maturity. By contrast, Banksia woodland patches could naturally senesce over time, either going on to form Bracken dominant patches, or as a negative but actively occurring outcome, be encroached by invasive *Leptospermum laevigutam.* This is further evidenced by the greater number of pre-2020 recruits and supressed saplings in Bracken patches. Their presence encourages the theory that Bracken patches may be temporary in the long-term. As

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such, present-day Coat Banksia woodland may be the product of a constantly shifting mosaic of patch dynamics across time and space, as observed by Meyer *et al*. (2009) in savanna tree-grass patch dynamics and discussed by Olff *et al*. (1999) in temperate woodland habitats.

 However, the recent introduction of the non-native herbivore Hog Deer and removal of regulating predators like Dingoes could be disrupting this natural progression (Bird *et al*. 2012; Davis *et al*. 2016; Morris and Letnic 2017). An increase in browsing pressure by two species (Hog Deer and Swamp Wallaby) could alter spatial and temporal dynamics of Coast Banksia recruitment, preventing stand establishment in available neighbouring patches. This has been observed in numerous systems (Kouki *et al*. 2004; Ripple and Beschta 2012; Hackworth *et al*. 2018). For instance, the establishment of *Allocasuarina huegeliana* into neighbouring Kwongan habitat was inhibited by browsing of seedlings by kangaroo and tammars in south-west Western Australia (Maher *et al*. 2010).

 Across time, there was a significant difference in the growth and survival of seedlings between plots that excluded or allowed access to herbivores. This was the best indicator that herbivory is a leading cause in seedling removal and subsequent recruitment-bottleneck (Allcock and Hik 2004; Kamler *et al*. 2010). The most reliable indicators of herbivory were seedling number and leaf count, both of which decreased outside of treatment plots. While seedling height did experience significant changes across time and has been used as the main index for impacts of herbivory in other studies (Cadenasso *et* al. 2002), this study found that the impact of herbivory was understated by this measurement. When seedlings were attacked, often they would be completely stripped of leaves while the height of the individual would not change, this was also particularly evident in the older saplings planted. It is not an isolated observation and relates to individual plant part preference of herbivores

as well as chemical and physical plant defences that reduce palatability and can also cause harm to herbivores that consume them (Harper 1977; Lucas *et al*. 2000; Pearse 2011).

 Most Coast Banksia seedlings were killed upon the first attack by a herbivore, indicating that *B. integrifolia* may not contain effective physical or chemical defence mechanisms to deter herbivores at the beginning stages of its life cycle. This also speaks for the efficiency of herbivore decision making when foraging; once a resource is detected, a herbivore will most likely act upon this detection and consume the plant. Past studies investigating the influence of browsing on eucalypt seedlings revealed that browsing severity, rather than repeated foraging events were the most influential factor on seedling growth (Neilsen and Pataczek 1991; Wilkinson and Neilsen 1995). In this study, individuals that survived attacks, but lost biomass, did not show signs of recovery throughout the study period. This indicates that Banksia seedlings that experience herbivory are more vulnerable than those that escape it. However, given the short length of this study, more evidence is required to confirm this observation.

Additional factors influencing seedling emergence and survival
 It is clear that associational refuge and herbivore pressure explained seedling survival and growth, however other factors may have also contributed. Variation in light and competition within patches may have also influenced growth. Howe (1990) found that height and leaf number increased respectively by 616% and 1075% in *Virola surinamensis* juveniles that were established in gaps, compared to the 33% and 222% percent growth of juveniles under canopy cove; this was attributed to light availability. Arrieta and Suárez (2005), also attributed mortality of Holly (*Ilex aquifolium*) seedlings to competition for light. The

combined pressures of competition between species and herbivory could have significant implications for regeneration.

Similar outcomes were observed in this study. Seedlings not exposed to herbivory in Coast Banksia and Coast Teatree vegetation types experienced limited growth or decreases in height and number of leaves compared to seedlings in fenced plots of Bracken dominant sites. *Leptospermum laevigutam* is considered a highly competitive, invasive species which reduces light availability and has been observed to compete for water and other nutrients with surrounding plants (Lam and Etten 2002). This is supported by the lower gravimetric soil moisture in Coast Teatree sites compared other vegetation types. To understand the extent to which Coast Banksia seedling survival and growth is effected between these three vegetation types, further investigation of below-ground resource competition within and between species is required (Kueffer *et al*., 2007; Bartelheimer *et al*. 2010).

Furthermore, seedlings recruitment and emergence may be dependent on episodic events. This study was conducted during a period of average to above-average rainfall. This could have influenced the total amount of recruitment regardless of vegetation type (Muñoz-Rojas *et al*. 2016). For instance, seedling emergence and recruitment increased threefold for the dominant savanna and woodland tree *Quercus emoryi* in experimental plants that experienced 50% increases in summer precipitation compared to the long-term mean. Of course this can only be proven by repeating this study during years of average rainfall but if correct this will act as an added complexity to factors affecting recruitment success and establishment in Coast Banksia woodlands. As Kraaij and Ward (2006) inferred, above-average rainfall and frequent rainfall events may be required for mass tree recruitment.

Limitations of associational refuge

There are concerns about the effectiveness of associational refuge as a long-term method for promoting species regeneration (Churski *et al*. 2017). Studies have found that some species will begin to outcompete focal seedlings for resources such as light and nutrients depending on how quickly the focal species grows. This was observed by Tolhurst and Turvey (1992), whereby eucalyptus seedling survival was reduced by 50% only ten months after emergence as a result of Bracken competition. This has potential implications for the long-term success of Coast Banksia seedlings. However, Stutz *et al*. (2014) argues that in habitats with overabundant herbivores like this study, the trade-off between reduced seedling loss to herbivory and loss due to Bracken competition is negligible given the low numbers of successful recruits required to maintain or restore open woodlands.

This does not take into account the survival of individuals once they grow beyond the seedling stage. As species outgrow the protective cover of the neighbouring plant providing associational refuge, they become once more detectable to herbivores. In effect, they are killed soon after, or their growth stunted (Cadenasso *et al*. 2002; Davis and Coulson 2010). The effectiveness of associational refuge may also reduce as herbivore pressure increases and the density of their preferred food decreases in the habitat they primaily browse. Herbivores are forced to search elsewhere - in less preferred patches of vegetation - and this can result in the few persisting recruits being detected and removed more readily (Wahl and Hay 1995). As a result, the benefits of associational refuge may only be classified as short-term.

Implications for future management

The decline of Coast Banksia woodland habitat and failed regeneration has been a concern for park management in Wilsons Promontory National Park since it was first observed in the 1940s (Bennett,1994). This study provides evidence that vegetation patch characteristics can have a positive or negative impact on *B. integrifolia* regeneration. Ultimately, in the short-term, associational refuge of Banksia seedlings in Bracken dominant vegetation patches is effective, but excluding herbivores by fencing off individuals had the greater impact on seedling survival and growth. Investigating the impact of removing Bracken from these refuge sites, thereby making Coast Banksia seedlings more readily detectable to herbivores, could reveal how strong the repellent-mechanism and associational refuge is within these patches.

It is important to encourage the survival of seedlings in these Bracken patches to reduce the opportunity of Coast Teatree shrubs from encroaching into these open spaces. Dexter *et al*. (2013) defined these patches as areas where dominant trees have senesced and regeneration had failed. Drawing from this, it could be assumed that these patches were once part of the broader grassy woodland landscape dominated by Coast Banksia. Rather than setting our sights on exclusively preserving seedlings within Banksia woodland patches, these Bracken patches could be the primary areas for regeneration of Coast Banksia. Further research should be dedicated to determining if Coast Banksia can re-establish in these patches, thereby reducing fragmentation, most likely by implementing fences around select individuals until they grow to a height that allows them to escape extensive herbivory.

Acknowledgements

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APPENDIX I

Author Instructions

General presentation
The works should be presented concisely and clearly in English. Introductory material, including a review of the literature, should not exceed what is necessary to indicate the reason for the work and the essential background. All pages of the manuscript should contain line numbering to aid the referees in their task. Authors are advised to note the typographical conventions and the layout of headings, tables, and illustrations exemplified in recent issues of the Journal. Observance of these and the following requirements will shorten the interval between submission and publication.

Title
This should be concise and informative and should contain all keywords necessary to facilitate retrieval by modern searching techniques. Titles including generic or specific names should also contain the name of taxa at higher rank, e.g. Division, Class, Order or Family. Nomenclatural authorities should be omitted from the title. An abridged title that does not exceed 50 characters should also be supplied for use as a running head.

Abstract
This should state concisely, preferably in fewer than 200 words, the scope of the work and the principal findings, and should be suitable for use by abstracting services. Species names mentioned in the abstract should include nomenclatural authorities. Acronyms and references should be avoided.

Text
This should normally be divided into sections, e.g. Introduction, Materials and Methods, Results, Discussion, Acknowledgments, References. All main headings should be in upper and lower case bold type, aligned at the left. Minor headings should be in light italics. The following also should be adhered to: spell out numbers lower than 10 unless accompanied by a unit, e.g. 2 mm, 15 mm, two plants, 15 plants, but 5 out of 15 plants; leave a space between a numeral and its unit; use the ´ise´ construction, not ´ize´; indicate approximate positions of figures and tables on the manuscript.

Synonymies should be indicated by a smaller font size and the first line of each synonymous species should be indented. Where presented, synonymy should immediately follow taxon headings.

Latin diagnoses for new species should be given in English to allow checking by the referees.

Material examined should be the last section presented in each taxon treatment and should be indicated by a minor heading and a smaller font size. Where presented, Etymology and Illustration sections should immediately precede Material examined. For clarity, authors should provide a minor heading, on a separate line, for each section of a taxon treatment, except for the taxon description. This may appear without a heading.

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The contribution of colleagues who do not meet all criteria for authorship should be

References
In the text, references should be listed in chronological order, separated by semi-colons. Use ´and´ to link the names of two coauthors and ´*et al.*´ where there are more than two. Do not use a comma between the author´s name and the date. References after names of taxa, e.g. in synonymies, should include the author´s name followed by a comma, the journal name (suitably abbreviated) in roman type, the volume number followed by a colon, then the page numbers, and finally the year in parentheses. References occurring only in synonymy should not be given in the reference list. Make sure that all references in the text (except synonymies) are listed at the end of the paper and *vice versa*. At the end of the paper, list references in alphabetical order. Give titles of books and names of journals in full.

- *Journal article*
  Lucas EJ, Harris SA, Mazine FF, Bellsham SR, Lughadha EMN, Telford A, Gasson PE, Chase MW (2007) Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* **56**, 1105-1128.

- *Book*
  Hesse M, Halbritter H, Zetter R, Weber M, Buchner R, Frosch-Radivo A, Ulrich S (2009) ´Pollen terminology: an illustrated handbook.´ (Springer: New York)

- *Book chapter*
  Walton TJ (1990) Waxes, cutin and suberin. In ´Methods in plant biochemistry. Vol. 4: lipids, membranes and aspects of photobiology´. (Eds PM Dey, JB Harbone) pp. 105-108. (Academic Press: London)

- *Online reference*
  Radcliffe J, Catley M, Fischer T, Perrett K, Sheridan K (2003) ´Review of plant research biosecurity protocols.´ (Department of Agriculture, Fisheries and Forestry: Canberra) Available at http://www.daff.gov.au/__data/assets/pdf_file/0006/146913/review.pdf [Verified 1 April 2012]

Units
The International System of Units (Système International d´Unités, SI units) should be used for exact measurement of physical qualities and as far as practical elsewhere. Measurements of radiation should be given as irradiance or photon flux density, or both, and the waveband of the radiation should be specified. Luminous flux density units (e.g. lux) should not be used. Do not use the double solidus in complex groupings of units, e.g.mmol/m^2/s; use the negative index system instead, i.e. mmol m^{-2} s^{-1}.

Mathematical formulae
Correctly align and adequately space all symbols. Avoid two-line mathematical expressions

wherever possible especially in the running text. Display each long formula on a separate line with at least two lines of space above and below it.

Tables

These should be numbered with arabic numerals and be accompained by a title. The title should be in bold upper and lower case and should be in a separate paragraph from the headnote. Tables should be arranged with regard to the proportions of the printed page (1 column 8.5 cm width, 2 columns 17.5 cm width). Include in the headnote, any information relevant to the table as a whole, and where applicable, the levels of probability attached to statistics in the body of the table. Use *, **, *** only to define probability levels. Use footnotes only to refer to specific items in the body of the table; use ^{A} and ^{B} etc. for footnotes. Insert horizontal rules above and below the column headings and across the bottom of the table; do not use vertical rules. If using Microsoft Word, use table formatting to prepare tables (i.e. use table cells, not tabs), otherwise use tabs, not spaces to align columns. The first letter only of headings of rows and columns should be capitalised. Include the symbols for the units of measurement in parentheses below the column heading. Each table must be referred to in the text.

Illustrations

Line diagrams and photographs must be prepared using either a draw or chart/graph program such as MacDraw, Illustrator, CorelDraw, Excel, Sigmaplot, Harvard Graphics or Cricket Graph and files should be saved in one of the following formats: encapsulated PostScript (EPS), Illustrator or Excel (provided the Excel files have been saved with the chart encapsulated in it). The submission of scanned images or illustrations prepared in a paint program, e.g. Photoshop (and PICT and JPEG files) is discouraged, because of the difficulty in making editorial corrections to these files. If illustrations are created in a paint program, save the file as a TIFF or EPS (these files should be 600 dpi for line drawings and 300 dpi for halftone figures).

Refer to each figure in the text, and number each according to the order in which it appears in the text. All lettering must be of a standard suitable for reduction (if necessary) and reproduction. Use a sans-serif typeface (e.g. Helvetica, Univers, Futura) that contrasts with its background, and which will be 1.5-2 mm high when printed. Use hatching not shading in bar graphs.

APPENDIX II

GPS and visual location of plots used in this study (Table 1, Fig. 1).

Table 1. GPS location of study plots

Plot no.	Bracken Dominant Plots	Coast Banksia Woodland Plots	Coast Teatree woodland plots
1	38°56'58.64"S, 146°17'45.56"E	38°56'57.3"S, 146°17'56.09"E	38°57'08.68"S, 146°16'21.22"E
2	38°56'57.1"S, 146°17'51.87"E	38°56'57.73"S, 146°17'57.1"E	38°57'18.16"S, 146°17'56.1"E
3	38°56'55.76"S, 146°17'55.55"E	38°56'57.92"S, 146°18'01.92"E	38°57'16.51"S, 146°17'54.27"E
4	38°57'09.41"S, 146°17'38.97"E	38°56'58.05"S, 146°17'59.22"E	38°57'05.59"S, 146°16'22.72"E
5	38°57'09.72"S, 146°17'46.24"E	38°56'56.52"S, 146°17'53.47"E	38°57'07.36"S, 146°16'23.07"E
6	38°57'10.78"S, 146°17'47.94"E	38°56'57.63"S, 146°17'55.37"E	38°57'07.00"S, 146°16'21.84"E
7	38°57'11.19"S, 146°17'40.81"E	38°56'58.62"S, 146°17'58.11"E	38°57'07.06"S, 146°16'17.69"E
8	38°56'59.14"S, 146°18'01.94"E	38°57'17.31"S, 146°17'56.31"E	38°57'06.87"S, 146°16'19.89"E

Study Map

All plot locations used in the study:

Yellow tags represent Coast Teatree shrubland sites

Blue tags represent Bracken dominant sites

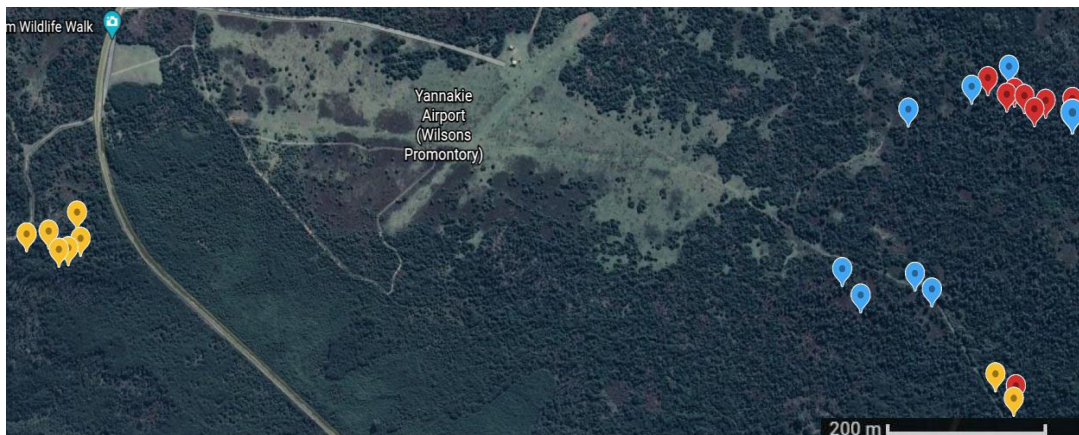Red tags Represent Coast Banksia woodland Sites

Figure 1. Google Earth image of study sites on the Yanakie Isthmus.

APPENDIX III

The MDS plot indicates a clear distinction in floristic composition across the three vegetation types of interest (Fig. 2). The stress was 0.16, indicating that the 2-D plot provides a "fair" presentation of the order of the original similarities.

The ANOSIM test gave a global R statistic of 0.745, with $p < 0.01$ (based on 9999 permutations). Pairwise tests indicated statistically significant differences among all vegetation types (at the 0.05 significance level).

A SIMPER analysis indicated that the similarities within vegetation types were driven by *Poa spp*. The best discriminating species between the three vegetation types were *Cymbonotus preissianus, Phytolacca octandra* and *Ficinia nodosa* which contributed 38% to the average dissimilarity between plots in Coast Teatree shrubland and Bracken dominant vegetation types. *Cymbonotus preissianus* and *Phytolacca octandra* contributed 26% to the average dissimilarity between plots in Coast Teatree shrubland and Coast Banksia woodland vegetation types.
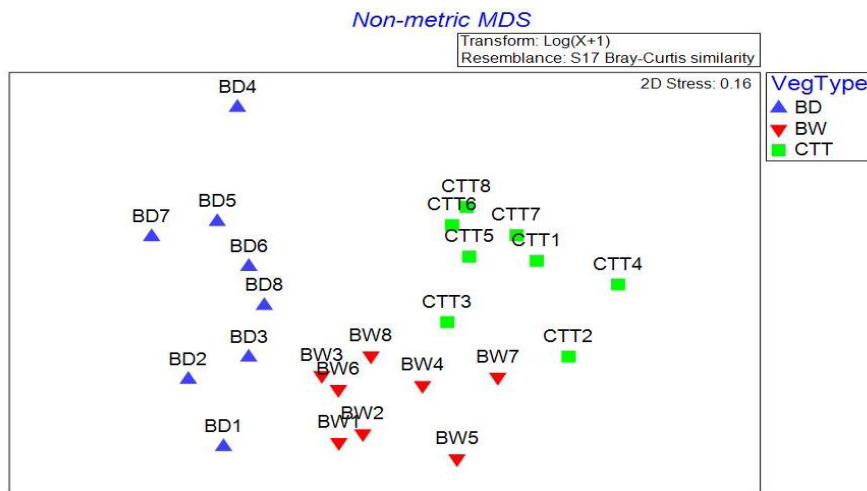

Figure 2. MDS plot of the floristic composition of the eight plots in each vegetation type examined. BD = Bracken dominant, CTT = Coast Teatree shrubland and BW = Coast Banksia woodland.

APPENDIX IV

The gravimetric soil moisture was significantly different between vegetation types ($F_{(2, 240)}$), p-value <0.01). This was driven by the Banksia woodland vegetation type, which had a significantly greater gravimetric soil moisture content than Bracken dominant ($p <0.01$) and Coast Teatree shrubland ($p <0.01$) vegetation types (Fig. 3).
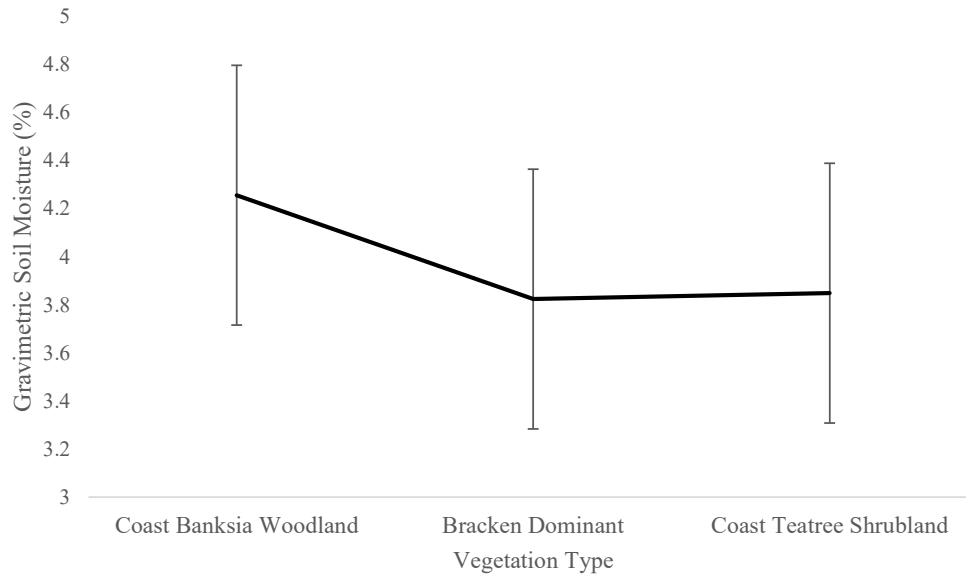

Figure 3. Square-root transformed gravimetric soil moisture content (±SE) in each Vegetation type (Bracken Dominant, Coast Banksia Woodland, Coast Teatree shrubland).

APPENDIX V

The number of saplings used between vegetation types and treatments was not substantial enough to perform statistical analysis. However, given the short time frame a trend of survival between vegetation type and treatment began to emerge towards the end of the study period.

The proportion of saplings outside of fenced plots decreased while saplings in control plots remained relatively stable. Saplings planted in Coast Teatree shrubland sites experienced the greatest loss in number compared to the other vegetation types (Fig. 4).
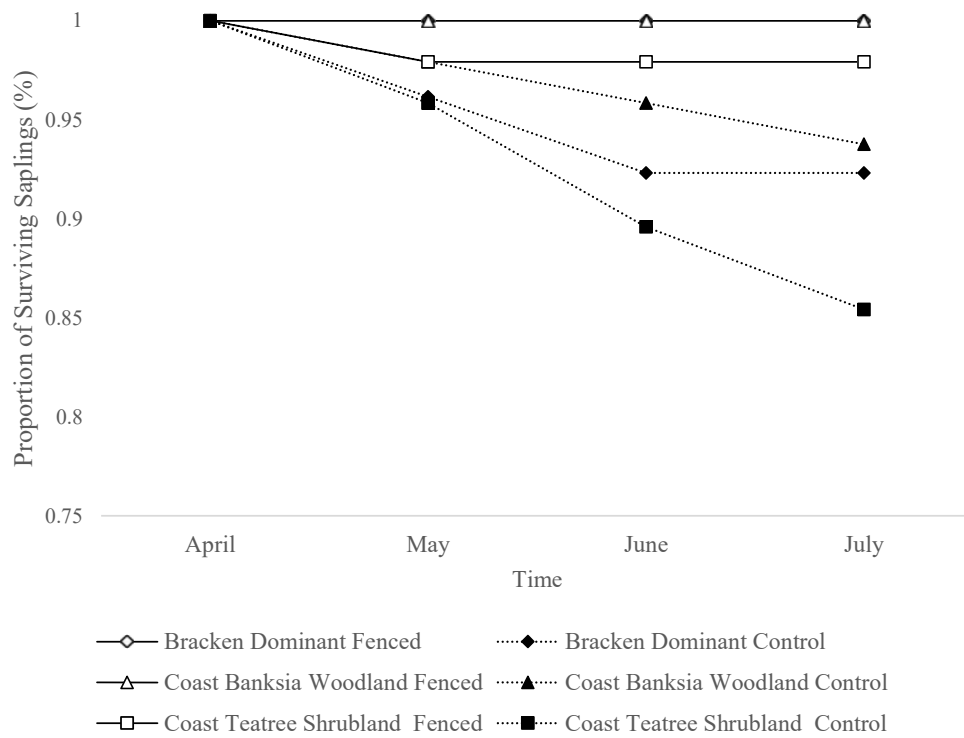

Figure 4. the proportion of surviving saplings between (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Banksia Woodland, Coast Teatree shrubland) across time.

The mean height (cm) changed significantly across time ($F(2.077, 213.928) = 19.057$, p-value < 0.01, Greenhouse-Geisser). However, mean height was not significantly different between vegetation types ($F(2,103) = 2.966$, p-value > 0.05) and treatments ($F(1,103) = .225$, p-value > 0.05).

There was also a significant interaction effect between time and treatment (Greenhouse-Geisser, p-value > 0.01). Saplings in control plots experienced a loss in height as a result of foraging by herbivores, whereas the height of saplings in fenced plots remained relatively stable (Fig. 5).
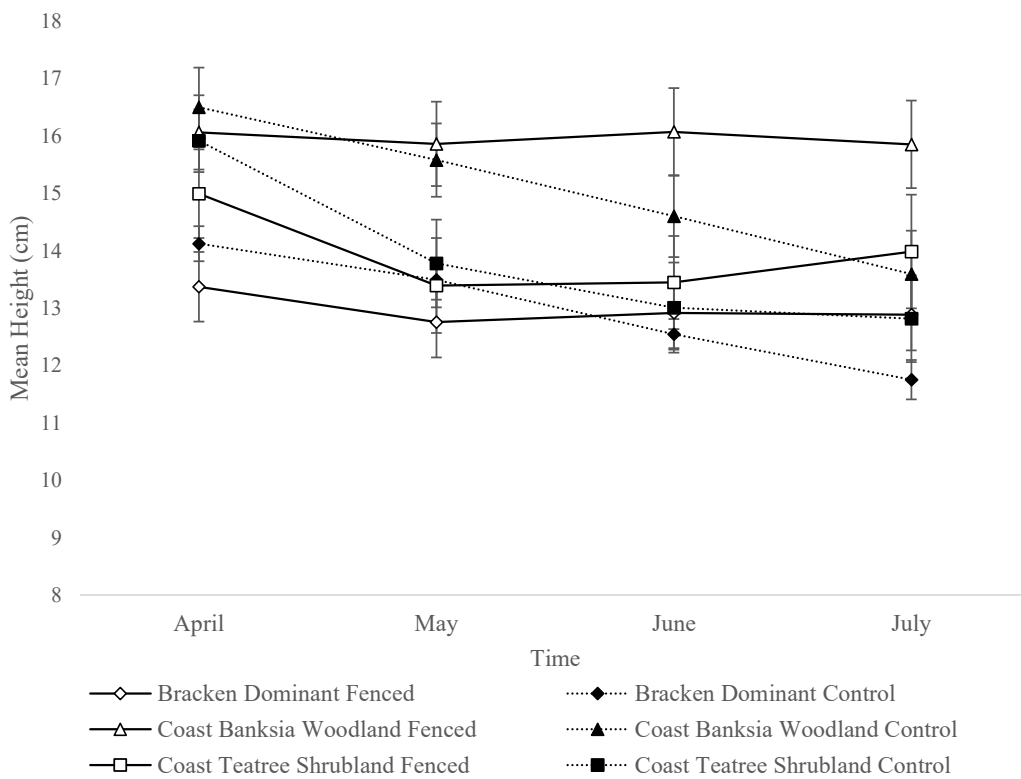

Figure 5. Mean height (±SE) of planted banksia saplings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Banksia Woodland, Coast Teatree shrubland) across time.

The mean basal diameter (mm) was significantly different across time ((F(2.547, 262.320) = 48.371, p-value < 0.01, Greenhouse-Geisser). There was also a significant main effect of vegetation type (F(2,103) = 5.691, p-value < 0.01) but not treatments (F(1,103) = 0.085, p-value > 0.05). However, there was no interaction effect between time and vegetation type (Greenhouse-Geisser, p-value > 0.05).

Time and treatment also did not have a significant interaction effect (Greenhouse-Geisser, p-value > 0.05). All saplings grew regardless of whether they were protected or exposed to herbivores.
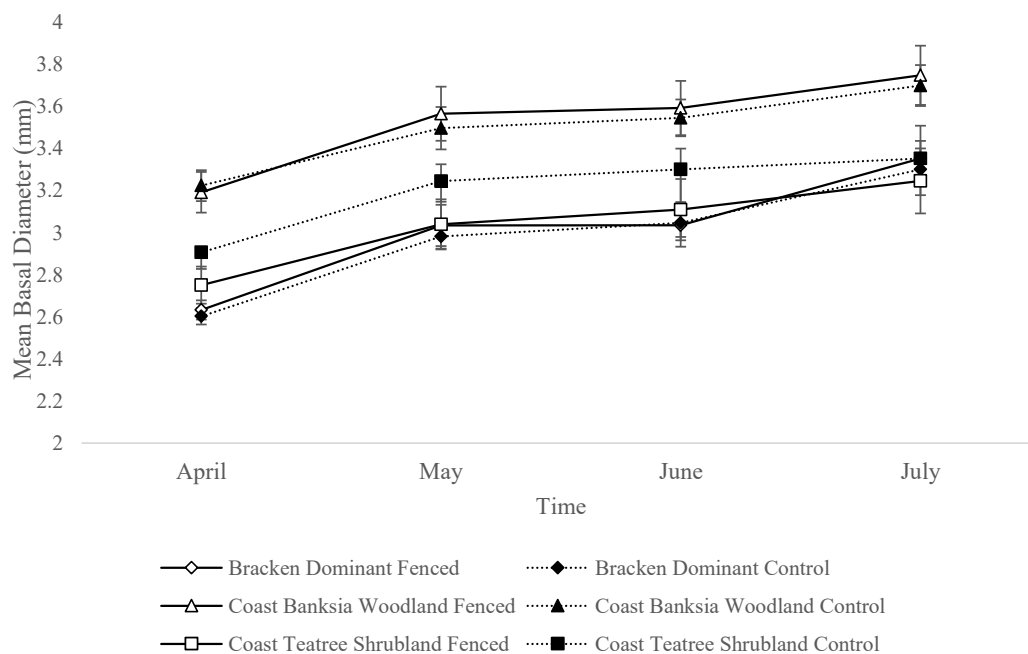

Figure 6. Mean basal diameter (±SE) of planted banksia saplings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Banksia Woodland, Coast Teatree shrubland) across time.

The mean number of leaves was significantly different across time ($(F(2.212, 225.579) = 33.059$, p-value < 0.01, Greenhouse-Geisser). There was also a significant main effect of vegetation type ($F(2,102) = 3.184$, p-value < 0.05) and treatments ($F(1,102) = 4.214$, p-value < 0.05). However, there was no interaction effect between time and vegetation type (Greenhouse-Geisser, p-value > 0.05).

Time and treatment did have a significant interaction effect (Greenhouse-Geisser, p-value < 0.05). Leaf number decreased significantly within control plots, whereas the leaf number of saplings in fenced plots remained relatively stable.
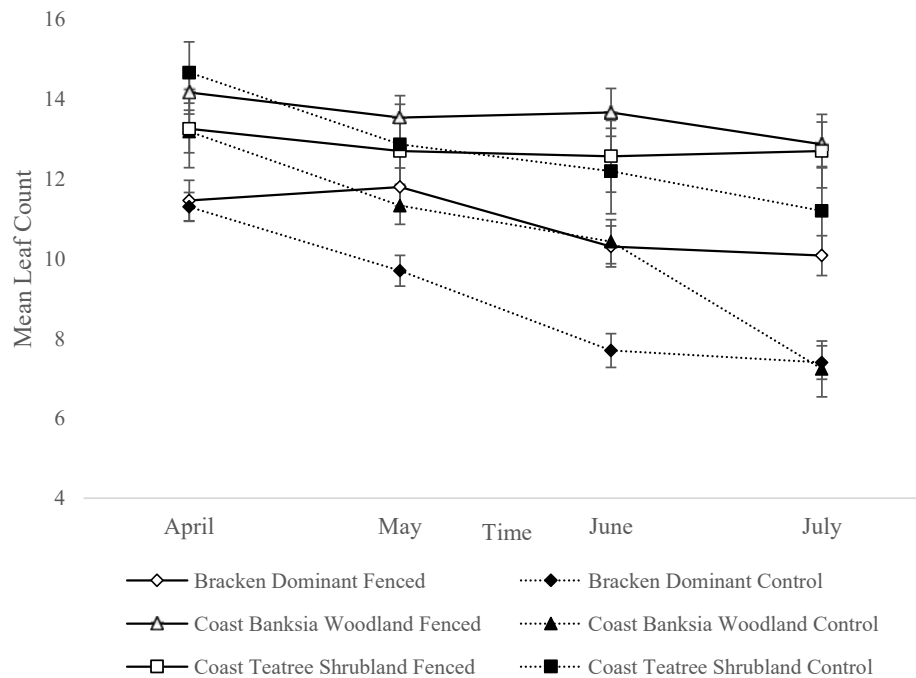

Figure 7. Mean leaf count (±SE) of planted banksia saplings in (a) fenced and (b) control plots with respect to vegetation type (Bracken Dominant, Banksia Woodland, Coast Teatree shrubland) across time.

APPENDIX VI

The species identified and raw number of camera trap captures of each species in each vegetation type for the duration of the camera trap experiment (Table 2).

Table 2. The total number of species captured in each vegetation type

Species	Bracken Dominant	Coast Banksia Woodland	Coast Teatree Encroached
Eastern Grey Kangaroo (*Macropus giganteus*)	3	66	57
Hog Deer (*Hyelaphus porcinus*)	2	23	42
Swamp Wallaby (*Wallabia bicolur*)	4	40	48
Common Wombat (*Vombatus ursinus*)	1	39	25
Emu (*Dromaius novaehollandiae*)	15	10	0
Brushtail Possum (*Trichosurus vulpecula*)	0	3	0
Raven (*Corvus corax*)	0	1	1
Unidentified Bird	2	1	1
Rabbit (*Oryctolagus cuniculus*)	0	3	0
Fox (*Vulpes vulpes*)	0	2	3
Cat	0	0	0
Bat	1	3	1