

RESEARCH PAPER

An invasive alien Proteaceae lures some, but not all nectar-feeding bird pollinators away from native Proteaceae in South African fynbos

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ABSTRACT

- Invasive alien plants often influence pollinator visitation to native plants when sharing pollinator guilds. It is of conservation concern when the invasive alien plant is characterized by floral resources that attract pollinators, thereby reducing the reproductive success of native species. This is well studied for insects, but whether the same is true for bird pollinators is largely unknown. We address this by considering the impact of an invasive alien plant (*Banksia speciosa*) on visitation rates of nectar-feeding bird pollinators to native *Protea compacta* in the Cape Floristic Region of South Africa.
- We determined bird pollinator visitation rate to *B. speciosa* and *P. compacta* over 21 h of observation at three sites. We also quantified how visitation rate influenced reproductive success of both study species through different breeding experiments.
- Sugarbird visitation to *P. compacta* was significantly lower in the presence of *B. speciosa*, while there was no effect for sunbirds as they mostly avoided *B. speciosa*. *Protea compacta* had higher nectar volumes and sucrose per flower than *B. speciosa*. Sucrose per hectare was higher in all *P. compacta* plots compared to *B. speciosa*. Neither study species is pollen limited and they are self-compatible to some extent. But pollinator visitation enhanced seed production in both species.
- We show here that the invasive alien *B. speciosa* flowers attract sugarbirds – but not sunbirds – away from native *P. compacta*. The long-term effect of reduced pollinator visitation may reduce the fitness of *P. compacta*, but the long-term demographic impact is unknown and would require further study.

INTRODUCTION

Competition for shared resources, including pollinators, is one of the most common forms of interactions between native and invasive plant species (Bjerknes *et al.*, 2007), especially when floral traits overlap (Gibson *et al.*, 2012). Often, invasive alien plants are characterized by showy floral displays and copious rewards that attract pollinators and reduce visitation to native flowering plants, especially when they act as magnet species (Chittka & Schürkens, 2001; Traveset & Richardson, 2014). Conversely, invasive alien plants can also increase overall attraction and thereby facilitate the visitation of pollinators to native species within the invaded area (Morales & Traveset, 2009). Overall, fitness may be influenced by the degree of competition between native and invasive flowering plants for pollinators (Van Kleunen *et al.*, 2010) and this may aid the invasion potential of alien plants in the introduced range (Pimentel *et al.*, 2005; Vilà *et al.*, 2011).

Globally, approximately 87.5% of flowering plants depend on animal pollination for seed production (Ollerton *et al.*, 2011). Animal pollinators also enhance seed production in

pollen-limited species, especially in areas with high plant species diversity (Vamosi *et al.*, 2006). For invasive alien plant species, an increase in seed production due to high visitation by native pollinators will enhance invasiveness in the novel range (Geerts & Pauw, 2009; Razanajatovo *et al.*, 2016). Most pollination studies that have addressed competition between native and invasive alien plants have adopted experimental approaches, such as using potted plants to study these interactions (see *e.g.* Kandori *et al.*, 2009; Flanagan *et al.*, 2010) and less often test this in a natural setting (but see Vilà *et al.*, 2009; Gibson *et al.*, 2012). The grand-scale transplant experiments provided by the introduction of alien species can teach us much about competition for pollinators. This is well studied for insect pollinators (see Jakobsson *et al.*, 2009; Parra-Tabla *et al.*, 2019), but not so for bird pollinators (but see Richardson *et al.*, 2000; Ollerton *et al.*, 2012). Such an opportunity is presented when an alien bird-pollinated plant species is introduced and invades parts of the world with native bird pollinators.

In the Cape Floristic Region (CFR) of South Africa, bird pollinators are crucial for the maintenance of the Cape's floral

diversity by pollinating about 4% of the flora, yet it appears that pollinators, and in particular nectar-feeding birds, are threatened (Kearns *et al.*, 1998). The bird-pollinated plant and nectar-feeding bird mutualism is threatened by frequent fires (Van Wilgen, 2009; Geerts *et al.*, 2012), roads (Geerts & Pauw, 2011a), beekeeping (Geerts & Pauw, 2011b), habitat fragmentation (Geerts & Pauw, 2009; Geerts, 2016), climate change (Mackay *et al.*, 2017) and potentially invasive species (Mangachena & Geerts, 2017). The dominant overstorey species in fynbos are Proteaceae, of which approximately 25% depend on nectar-feeding birds for pollination. However, this highly specialized form of interaction is rather simple as only four species of nectar-feeding bird act as important pollinators (Geerts, 2011). At small spatial scales, Proteaceae nectar, rather than vegetation structure, determines the distribution and abundance of the nectar-feeding bird community (Geerts *et al.*, 2020). There is some evidence to suggest that additional nectar in the landscape benefits the nectar-feeding bird community (see Le Roux *et al.*, 2010; Schmid *et al.*, 2015; Gray and Heezik 2016; Le Roux *et al.*, 2020) but whether this indeed increases the number of nectar-feeding birds has not been quantified. Invasive alien species may alter nectar quantity at landscape scale through addition of nectar (Le Roux *et al.*, 2010, 2020) or even through nectar replacement that may occur when invasive species spread rapidly and outcompete native flowering plants. This is important when considering the possible pathways through which invasive alien flowering plants alter the quantity and properties of floral rewards at landscape scale, influencing the visitation rates as well as the community of pollinators in the invaded areas.

Here we investigate whether the addition or replacement of nectar by the alien invasive *Banksia speciosa* R. Br. influences the nectar-feeding bird community and their dependant native plants in the CFR. We selected the invasive *Banksia speciosa* and the native *Protea compacta* R. Br. since they co-occur, flower simultaneously and are both bird-pollinated (Paton & Turner, 1985; Collins & Rebelo, 1987; Steenhuisen & Johnson, 2012) and visited by Cape sugarbirds and sunbirds (Mostert *et al.*, 1980; Moodley *et al.*, 2016). Approximately 14 species of the genus *Banksia* were introduced from Australia to South Africa for floriculture (Moodley *et al.*, 2013). Two of these, *B. ericifolia* L.f. and *B. integrifolia* Meisn., have become invasive, while species such as *B. speciosa* have become naturalized in some areas of the CFR based on climate suitability, propagule pressure and ability of this species to adapt to land-use and other anthropogenic disturbances in this region (Honig *et al.*, 1992; Geerts *et al.*, 2013; Moodley *et al.*, 2014).

Because of the co-occurrence and overlapping flowering period of *B. speciosa* with native *P. compacta*, as well as the production of copious amounts of nectar by *B. speciosa* (George 1999; Moodley *et al.*, 2016), which often attracts nectar-feeding birds, we hypothesize that *B. speciosa* will compete with the native, co-flowering *P. compacta* for nectar-feeding bird pollinators (Catford *et al.*, 2009; Traveset & Richardson, 2014), and by doing so reduce seed set in *P. compacta*. Alternatively, *B. speciosa* can facilitate the overall visitation of nectar-feeding bird pollinators to *P. compacta* (Morales & Traveset, 2009). We thus ask the following questions: (i) does the addition of *B. speciosa* to the landscape change nectar-feeding bird communities; (ii) does the invasive *B. speciosa* influence nectar-feeding bird visitation rates to the native *P. compacta*; and (iii) does the

altered visitation rate to native *P. compacta*, if any, reduce seed set of *P. compacta*?

MATERIAL AND METHODS

Study area

Study sites were located at Soetanysberg (34°44'667 S, 19°52'931 E) and Bergplaas (34°43'585 S, 19°52'488 E) in the Agulhas National Park, Western Cape Province, South Africa. The area experiences a Mediterranean-type climate characterized by cold wet winters and warm dry summers. It receives mean annual rainfall of 452 mm. The mean temperature ranges between 13.5 °C and 20.6 °C for the cool and warm months, respectively (Richards *et al.*, 1995).

Banksia speciosa is a perennial woody shrub that grows up to 8-m tall (George, 1981; Richardson *et al.*, 1990). The cream to pale yellow hermaphroditic and protandrous flowers are grouped into a long inflorescence of 4–12 cm (George, 1981; Fig. 1A). The selected native species, *Protea compacta*, is a non-sprouting serotinous shrub of up to 3.5-m tall that is endemic to the fynbos (Rourke, 1982; Rebelo, 2001). The pink and white flowers of *P. compacta* are grouped into large inflorescences.

Field observations were conducted at three sites with similar veld age during July and August 2016, which are the peak flowering months for *B. speciosa* and *P. compacta*. Native vegetation invaded by a 2-ha stand of *B. speciosa* (the *Banksia* site, Fig. 1A) and an adjacent 1.5-ha monospecific stand of native *P. compacta* (Fig. 1B), termed the *Protea* experimental site, were used as study sites. A *P. compacta* stand of 1.8 ha was located 2.6 km away and used as a control site. *Protea compacta* was the most abundant native bird-pollinated flowering plant species at both the experimental and control sites. However, in the *Banksia* site, *B. speciosa* was the dominant bird-pollinated species. The abundance of *P. compacta* was similar between the experimental and control site (with 32 and 33 plants per 25 m², respectively), while *B. speciosa* had fewer stems per area (24 stems per 25 m²), although the plants were larger.

Nectar-feeding bird abundance

To determine nectar-feeding bird abundance and richness in invaded and uninvaded sites, a 10-min point count method was used (Bibby *et al.*, 2000). Due to small stand size at both sites, only one fixed point was established within each stand. Bird observations were conducted between 7:00–12:00 h – when nectar volume was highest – on good weather days without rain and little or no wind. Birds are more active in the morning when nectar volume is highest (Kalinganire *et al.* 2001) and flower visitation tends to decrease after midday (Sun *et al.*, 2017). Sites were sampled multiple times per day in an alternating manner for 8 days, spread out over the peak flowering period. The species and number of individual nectar-feeding birds seen within a 40-m radius from the observer were recorded. Bird observations were carried out by two observers per site with Nikon 8 x 42 binoculars, and we merged data collected by the two observers for statistical analysis.

Nectar-feeding bird pollination rates

To determine nectar-feeding bird visitation rates, the number of bird visits to 20 focal inflorescences was recorded for 30 min

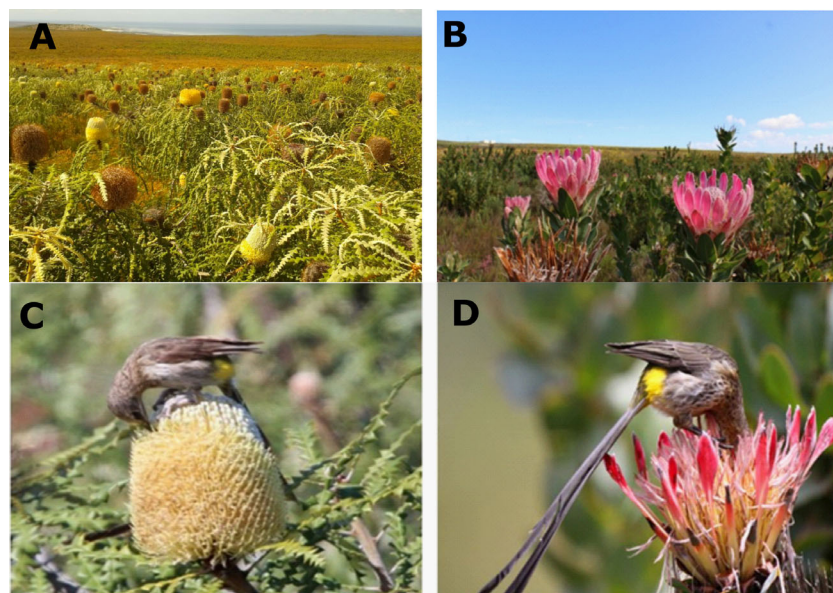


Fig. 1. (A) Density of *B. speciosa* across the *Banksia* site, (B) homogenous distribution of *P. compacta* across the *Protea* control site, (C) Sugarbird feeding on nectar from an alien *B. speciosa* inflorescence, (D) male Cape sugarbird feeding on *P. compacta* nectar. A-Ernita van Wyk; B, C-Sjirk Geerts D- Laimi Erckie.

at each site. Birds were only considered as potential pollinators once they made contact with the flower's receptive part. Sites were observed at least twice per day and were sampled in an alternating manner to eliminate any temporal bias in observations. Each site was sampled for a total of 7 h, resulting in a total of 21 h of observations conducted during the winter season, which is the peak flowering period of our two study species. Total bird visitation observation was low, but many flowers observed during this period had 20 inflorescences (> 100 flowers each) that were observed simultaneously. Unlike other pollination studies, nectar-feeding bird abundance was also recorded for 21 h. Also, with observations spread out over multiple weeks, and at least 40 h spent on nectar measurements and hand-pollination of flowers in these populations, during which anecdotal bird observations was conducted, the sampling period was sufficient.

Nectar properties and availability

To determine the quantity of floral nectar rewards available to nectar-feeding birds, a representative 5 × 5-m plot was established at each site. The number of open inflorescences in each plot was counted. In *Protea* inflorescences, the outer ring of the flowers matures first, followed by the inner rows of the flower. We therefore measured nectar volume and concentration (from ten inflorescences from different plants) in open flowers ($n = 14$) across the middle of the inflorescence, totalling 140 flowers per study site, thereby effectively sampling flowers across all ages (Geerts *et al.*, 2020). This controls for differences in nectar volume between flowers of varying age in an inflorescence. Inflorescences were collected early in the morning from study sites and nectar was extracted in the laboratory using 5 μ l or 40 μ l microcapillary tubes. Nectar sugar concentration was determined with a 0–50% handheld refractometer. All nectar measurements were transformed to milligrams (mg) of nectar sugar (sucrose equivalents). The standing crop of nectar, which provides an estimate of the nectar available to pollinators at a given time, was measured early morning when the

birds are most active (Kearns & Inouye, 1993). The average nectar volume and concentration per flower was then calculated and multiplied by the total number of flowers in the inflorescence then multiplied by the total number of inflorescences per 5 × 5-m plot and scaled up to nectar (mg nectar sugar) per hectare.

Breeding system experiments

To determine whether *P. compacta* is pollen-limited when nectar-feeding bird pollinators are lured away by *B. speciosa*, exclusion of pollinators and pollen addition experiments were conducted. Between 15 and 30 plants of each species were randomly selected in the *Banksia* site, *Protea* experimental site and *Protea* control site, and randomly allocated to one of the three treatments: (a) one inflorescence still in bud phase was bagged with fine-mesh nylon bags to exclude all pollinators, (b) another inflorescence, also in bud phase was tagged, and once flowers opened, hand-pollinated with pollen from multiple donors (rubbing pollen onto the receptive stigma with a 25-mm paint brush), (c) one inflorescence was tagged as a control and left uncovered to allow access by pollinators. Similar-sized and -aged inflorescences were selected to ensure consistent maturity across inflorescences for the different treatments. Infructescences were harvested 6 months after flowering to determine seed production. Follicles of *B. speciosa* were opened by heating infructescences in an oven for between 2–30 days at 120 °C and seeds counted. Seeds of *P. compacta* were counted immediately upon harvesting their infructescences.

Data analysis

To understand how floral visits to the invasive *B. speciosa* and native *P. compacta* are affected by differences among taxonomic groups as well as the general ecology of the four nectar-feeding bird species recorded in this study, we separated the analysis into two broad groups using data from visitation rates

of sugarbirds as well as visitation rates of the three sunbird species.

We pooled visitation and abundance data for all sampling periods that occurred on the same day for each group. Visitation frequency was converted to visitation rate per inflorescence per hour and this was used to explore the pattern of visitation among bird species across study sites. The Shapiro-Wilk's test was performed on all data to test for normality. We conducted non-parametric Kruskal-Wallis tests to determine differences in nectar-feeding bird abundance, flower visitation rate per inflorescence per hour, nectar volume and sucrose per flower among study sites. A Dunn's test was used to determine significance among paired study sites.

To determine differences in number of seeds produced per plant species across study sites for *B. speciosa* and *P. compacta*, we applied a generalized linear model, specifying quasi-Poisson error to account for overdispersion of data. All statistical tests were conducted using R (R Core Development Team, 2017).

RESULTS

Nectar-feeding bird abundance

A total of 465 bird visitations from four nectar-feeding bird species, the Cape sugarbird (*Promerops cafer* Linnaeus 1758), Orange-breasted sunbird (*Anthobaphes violacea* Linnaeus 1766), Southern double-collared sunbird (*Cinnyris chalybeus* Linnaeus 1766) and Malachite sunbird (*Nectarinia famosa* Linnaeus 1766), were recorded. Among study sites, Cape sugarbird were significantly more abundant in the *Banksia* site compared to other sites (Kruskal-Wallis chi-square = 13.90, $df = 2$, $P = 0.001$; Fig. 2A). There was no significant difference in Cape sugarbird abundance between *Protea* control and *Protea* experimental sites. Unlike sugarbirds, sunbirds were significantly less abundant in the *Banksia* site compared to the *Protea* sites (Kruskal-Wallis chi-square = 9.74, $df = 2$, $P = 0.008$; Fig. 2A). There was no significant difference in sunbird abundance between *Protea* control and *Protea* experimental sites.

Nectar-feeding bird pollination rates

Banksia speciosa received three times as many visits by nectar-feeding birds per inflorescence per hour as *P. compacta*. Visitation rate of sugarbirds was significantly higher in the *Banksia* site, followed by *Protea* control site, and lowest in the *Protea* experimental site (Kruskal-Wallis chi-square = 19.35, $df = 2$, $P < 0.001$; Fig. 2B). Among study sites, visitation rate of sunbirds was significantly lower to *B. speciosa* compared to *P. compacta* sites (Kruskal-Wallis chi-square = 11.99, $df = 2$, $P = 0.003$; Fig. 2B). There was no significant difference in visitation rate of sunbirds to *P. compacta* in *Protea* control and *Protea* experimental sites.

Nectar content

Banksia speciosa nectar volume per flower (mean \pm SE = 3.3 ± 0.13 , 0.5–6.0 μ l) was significantly lower than that of *P. compacta* (Kruskal-Wallis chi-square = 24.897, $P < 0.05$, $df = 2$, 24.26 ± 0.62 , 5–58 μ l). Nectar volume per inflorescence

was also significantly lower for *B. speciosa* (53.55 ± 11.01 , 11.5–141.5 μ l) compared to *P. compacta* (Kruskal-Wallis chi-square = 22.986, $P < 0.05$, 366.25 ± 28.1 , 198–445 μ l). Total amount of sucrose per hectare was 80.64 g, 222.73 g and 934.94 g in *Banksia*, *Protea* experimental and *Protea* control sites, respectively. Sucrose per flower was significantly lower in *B. speciosa* (0.61 ± 0.03 , 0.08–1.88 mg) compared with *P. compacta* (Kruskal-Wallis chi-square = 23.205, $P < 0.001$, $df = 2$, 5.23 ± 0.21 , 0.82–16.27 mg).

Breeding system

Pollen addition by hand did not significantly increase seed production of *B. speciosa* or *P. compacta* among all study sites ($F = 2.55$, $P = 0.092$, $df = 2$), showing that neither plant species was pollen-limited. The number of seeds produced by *B. speciosa* and *P. compacta* was significantly lower in pollinator-excluded flowers (*Banksia* $F = 8.19$, $df = 2$, $P = 0.0007$ and *Protea* control sites $F = 11.63$, $df = 2$, $P < 0.0001$; Fig. 3). In contrast, there was no significant difference in the number of seeds produced among treatments in the *Protea* experimental site ($F = 1.55$, $df = 2$, $P = 0.22$; Fig. 3). Overall, there was no significant difference in natural seed set between *Protea* control and experimental sites ($t = 1.5$, $P = 0.14$).

DISCUSSION

The alien invasive *Banksia speciosa* attracted sugarbirds away from native species, yielding a lower visitation rate of sugarbirds to native *P. compacta* flowers. This is important when considering the impact of invasive *B. speciosa* on the pollination of native flowering plant species that share similar pollinators. However, we did not find a decline in seed production in *P. compacta* occurring in close proximity to *B. speciosa*. This may be because of the higher visitation rate of sunbirds in the *Protea* site compared to the *Banksia* site. Sunbirds are also effective pollinators of *P. compacta* and they may supplement the reproduction of *P. compacta* when sugarbirds are scarce. Also, a reduction in pollinator visitation does not always result in a parallel decline in seed set (Lundgren *et al.*, 2013), especially when flowering plants are adapted to different pollination modes, such as autogamy whereby pollination is achieved even when pollinator visitation rate is low.

Floral rewards, especially nectar, play a critical role in attracting pollinators to ensure effective pollination (Carr *et al.*, 2015; Prasifka *et al.*, 2018). Although the amount of nectar produced per flower is important to support the energy requirements of birds, more importantly, the quantity of nectar per hectare – which largely depends on flower abundance – is critical for the overall attraction and maintenance of birds at landscape scale (Nottebrock *et al.*, 2017). Despite the similar density of *P. compacta* in the experimental and control site, we observed a large difference in the total amount of sucrose per hectare between the two sites, with higher sucrose per nectar sample recorded in the control site. Since dense stands of *B. speciosa* form thickets, this may reduce the access of *P. compacta* to sunlight, which is critical for nectar production (Nocentini *et al.*, 2013). Also *B. speciosa* may compete with native *P. compacta* for other abiotic factors, such as soil nutrients, space, water and other

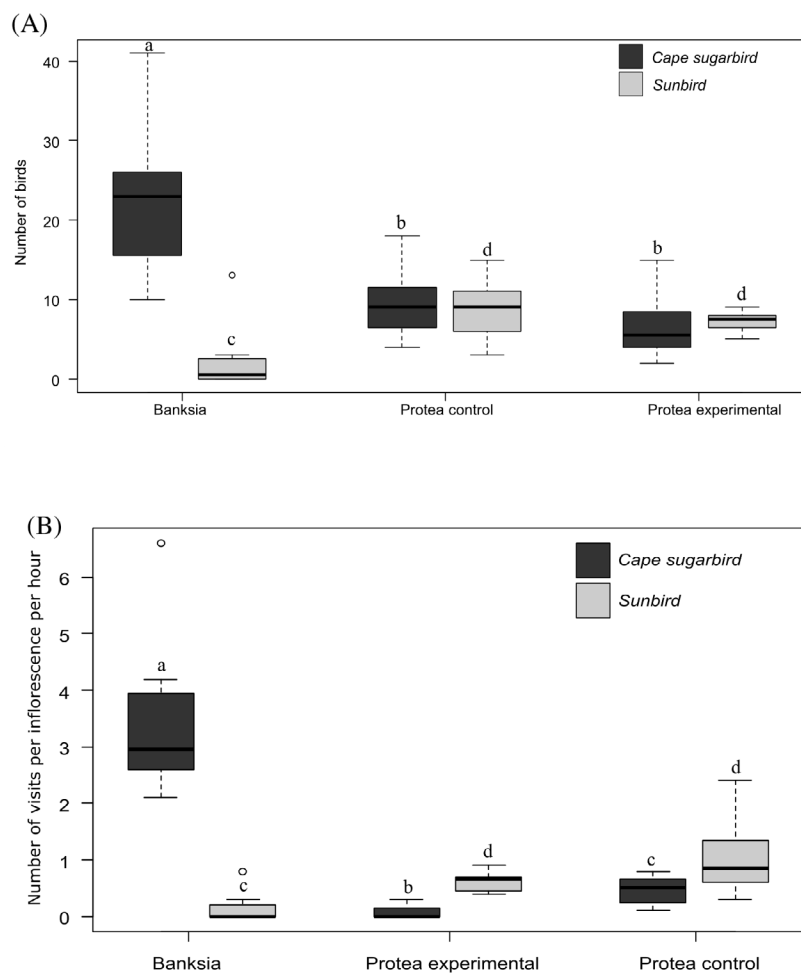


Fig. 2. Differences in (A) abundance and (B) visitation rate per inflorescence per hour of sugarbirds and sunbirds to *B. speciosa* and *P. compacta* across study sites. Boxplots display the median with a solid line, 25th and 75th percentiles in the lower and upper boxes, respectively, data range is indicated by the whiskers. Different letters indicate significant differences among study sites at $P < 0.05$.

factors that may influence the fitness of *P. compacta* in the experimental sites. However, the low nectar per hectare recorded for *B. speciosa* did not explain the high abundance and visitation rates of sugarbirds. This also contrasts with results of Geerts *et al.* (2013), where high nectar volume in *B. ericifolia* doubled the nectar available to birds in the study area. While this could be because of high foraging activity of sugarbirds, measuring flowers in the early morning – as was done in this study – should have circumvented this. Also, measuring nectar in ten inflorescences from different plants and ensuring that flowers sampled ($n = 14$) per inflorescence were representative – by sampling across the inflorescence – reduces the bias of varying nectar volume among inflorescences and plants in both species. Therefore, what drives the high visitation rate of sugarbirds to *B. speciosa* remains to be determined.

The Cape sugarbirds are relatively larger in body size compared to sunbirds, and they also outcompete sunbirds during visits to flowering plants for nectar (Schmid *et al.*, 2016). The difference in the morphology of these two bird species may explain why the abundance and visitation rates of sunbirds were low in *Banksia* and *Protea* experimental sites, where sugarbird abundance and visitation rates were higher compared to

the control site. Cape sugarbirds were highly attracted to invasive *B. speciosa* in this study, and this may aid in the integration of this invasive species into the plant–bird interactions of the CFR (Maruyama *et al.*, 2016). Species-specific floral traits of *B. speciosa* may mediate the high visitation rate of sugarbirds in this study. Unlike the relatively small and slender *P. compacta*, *B. speciosa* is characterized by a sturdy stem suitable to support the relatively large sugarbirds, especially during the breeding period when males display to attract females. Also, insects are often attracted to *B. speciosa* (Moodley *et al.*, 2016), which in turn could attract sugarbirds; particularly during the breeding season – as in this study –, when insects supplement the diet and are an important source of protein for female sugarbirds (Mostert *et al.*, 1980). In addition, stands of *B. speciosa* form denser thickets, which could be important in protecting sugarbirds against predators and harsh weather (Burger *et al.*, 1976). Thickets may also provide more nesting sites for sugarbirds and may further support the preference of sugarbirds for *B. speciosa*.

Floral traits are key influencers of plant–plant interactions, predicting the impact of invasive alien plants on native species, especially when they compete for similar resources such as pollinators (Gibson *et al.*, 2013). This is well researched

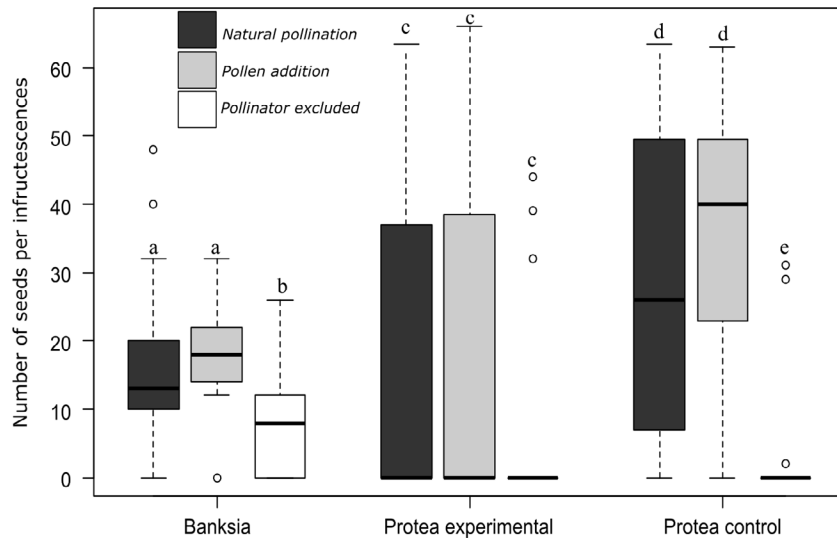


Fig. 3. Number of seeds per infructescence for the different breeding system experiments. Boxplots display the median with a solid line, 25th and 75th percentiles in the lower and upper boxes, respectively, data range is indicated by the whiskers. Different letters indicate significant differences among treatments per species per study site at $P < 0.05$.

for insect-pollinated species (Morón *et al.*, 2009; Gibson *et al.*, 2012) where alien plants alter ecosystem functioning due to reduced fitness of native species in competition. While this study is one of the few studies that has assessed how invasive alien plants influence pollination of native bird-pollinated species, there is an urgent need for a comprehensive assessment addressing the influence of invasive alien species on nectar-feeding birds. The effects of invasive alien plants on the reproductive success of native species through competition for pollinators are often density-dependent (Muñoz & Cavieres 2008). With an increasing number of nectar-rich invasive alien species in the CFR attracting pollinators away from the highly pollinator reliant Proteaceae, ecosystem functions in the CFR may become threatened.

Banksia speciosa is self-compatible and capable of producing seeds through autogamy, as recorded in this study. The ability to reproduce without the intervention of animal pollinators aids in the success of alien species such as *B. speciosa* in its introduced range (Rambuda & Johnson, 2004; Pyšek *et al.*, 2011). Although *B. speciosa* is self-compatible, this study shows the importance of pollinators in enhancing seed production. This supports other studies that have underscored the role of pollinators in increasing seed production of invasive plant species and subsequently enhancing invasiveness (Geerts & Pauw, 2009; Rodger *et al.*, 2010; Moodley *et al.* 2016). Hand pollination did not increase seed production of *B. speciosa* or *P. compacta* in this study, showing that both species are not pollen-limited. Although, pollen addition slightly increased seed set in *P. compacta* in the *Protea* experimental site, this was not significant. The lack of an increase in seed set with hand pollination may be attributed to the typical low seed set in Proteaceae or to the large number of flowers per inflorescence that open sequentially over a long period, limiting the effectiveness of hand pollination.

In conclusion, our results support our hypothesis that invasive *B. speciosa* stands attract sugarbirds away from native *P. compacta* stands; however, this did not reduce the seed set of

the native *P. compacta*. The effect of an invasive alien plant in attracting sugarbirds away from native species may be masked by the presence of sunbirds, which enhance the reproduction and fitness of native *P. compacta* when sugarbird numbers are reduced. Although the overall abundance of sugarbirds is approximately three times that of sunbirds in this study, sunbirds maintained their preference for the native species, especially in the absence of the competitive sugarbirds. This is of significance when considering a reliable pollinator for the persistence of native species in an invaded ecosystem. However, understanding the extent to which invasive *B. speciosa* mediates pollinator visitation to *P. compacta* in the long term requires further investigation. Despite only considering a small pollinator community and having relatively low sampling intensity, this study is one of very few that have assessed the influence of an invasive bird-pollinated plant species on native plant seed production and interactions with native bird pollinators. Since invasive alien plant species are becoming more established in natural ecosystem, competing for resources and integrating into native ecological interactions (Olesen *et al.*, 2002; Morales & Aizen, 2006; Vilà *et al.*, 2009), future studies should assess the role of floral traits and degree of biotic and abiotic resource overlap between invasive and native flowering plant species and how these influence interactions between native plants and nectar-feeding birds. Furthermore, the demographic consequences of a long-term reduction in pollinator visitation should also be considered.

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