Protea compacta architecture and Cape Sugarbird (*Promerops cafer*) behaviour: a loose connection or tight bond?

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Abstract:

The Cape Floristic Region (CFR) is an extremely old floral region, making it an ideal natural system to examine the relationship between patterns and processes facilitating evolutionary diversification (Verboom *et al.* 2009; Johnson, 2010; Bytebier *et al.* 2011). After initial plant species divergence in pollination mode; secondary differentiation in plant traits, e.g. architecture, flower phenology; may further reduce the cost of competition for pollinators (Van der Niet & Johnson, 2006). The ecological affiliation between plant and pollinator was assessed using the ornithophilous *Protea compacta* (*P. compacta*) and endemic Cape Sugarbird (*Promerops cafer*) at a study site in Kleinmond, South Africa. The Cape Sugarbird makes frequent use of the tall inflorescences of *P. compacta* for territorial display purposes and thus the reciprocal pressure of maintaining the mutualism between these two species is thought to have resulted in the uncharacteristic architecture of *P. compacta*. The effectiveness of bird pollination in *P. compacta* was assessed using experimental treatment of flowers which either allowed or disallowed bird visits. Flowers that received bird visits set significantly more seed ($U=240$; $p<0.05$) than flowers that did not receive bird visits. Plant architecture was measured and found to differ significantly in four variables to *Protea repens*, a common species at the study site that differs in pollination mode. To establish a functional link between flower position, seed set and sugarbird territorial behaviour three artificial *P. compacta* plants were used to quantify the visitation patterns of Cape Sugarbirds. The territorial and courtship display behaviour in Cape Sugarbirds is highly seasonal and resulted in zero birds visiting the artificial *P. compacta* plants.

Keywords: *Protea compacta*, Cape Sugarbird, *Promerops cafer*, architecture, territorial, behaviour, seed set

Introduction:

The Southern African flora found in the Cape Floristic Region (CFR) is extremely diverse for its latitude and is undoubtedly one of the most species rich temperate floras (Cowling *et al.* 1996; Goldblatt, 1997; Linder *et al.* 2005). With its high plant endemism, the CFR is an extremely old floral region, making it an ideal natural system to examine the relationship between patterns and processes facilitating evolutionary diversification (Verboom *et al.* 2009; Johnson, 2010; Bytebier *et al.* 2011). The reason for the high level of speciation of the flora, by some referred to as an "orgy of speciation", can be ascribed to the interaction of various environmental variables (climate, soil type, altitude) and ecological processes (pollination, competition, dispersal) in space and time (Linder, 2003; Van der Niet & Johnson, 2009). The outcome of a system driven by high levels of ecological speciation is an immense diversity of floral and vegetative traits (Johnson 1997; Johnson *et al.* 2005; Pauw 2006; Van der Niet & Johnson, 2009).

Co-evolution is often evoked as a principal explanation in natural systems whereby two or more species (plant and animal) evolve complementary traits in tandem due to imposing selective pressures exerted on one another (Anderson & Johnson, 2008). Generally, in plant-pollinator interactions co-evolution systems are strongly asymmetrical, with more directional selection placed on the plant to conform to characteristics of the pollinator (Anderson & Johnson, 2008; Johnson, 2010). In the CFR, plant responses are in part due to the availability pollinators in space and time (Linder *et al.* 2010; Johnson, 2010; Schnitzler *et al.* 2011). When subject to range expansion or community composition change, plants adapt accordingly to the presence of new pollinators (Johnson, 2006; Johnson, 2010). After initial plant species divergence in pollination mode, secondary differentiation in plant traits, such as architecture, flower phenology, may further reduce the cost of competition for pollinators (Van der Niet & Johnson, 2006). A plant conforming to a pollination mode does so in order to derive fitness benefits, such as increased seed set quality or quantity, with conformation achieved by adapting floral and vegetative traits.

Ornithophily refers to a suite of plant floral and vegetative adaptations to bird pollination (Faegri & van der Pijl, 1979; Hargreaves *et al.* 2004). Highly mobile, birds potentially increase the pollen outcrossing of plants conforming to this pollination mode (Mostert *et al.* 1980; Wright

et al. 1991). The bright pink flower bracts, dilute nectar, diurnal flowering and lack of scent of many Proteaceae can almost certainly be associated with ornithophily (Rebelo, 1987; Hargreaves *et al.* 2004). The ecological affiliation between birds and members of the Proteaceae has been well documented (Rebelo, 1987; Calf *et al.* 2003[a,b]; Hargreaves *et al.* 2004; Johnson *et al.* 2009). One bird in particular, the Cape Sugarbird (*Promerops cafer*), is intimately linked with many proteas, such that sugarbirds are virtually exclusively restricted to stands of proteas (Rebelo *et al.* 1984; Hockey *et al.* 2005; Altwegg & Underhill, 2006). This close affinity between bird and plant has been fine-tuned to such a degree that life cycle and phenological stages of both are now closely synchronised (Calf *et al.* 2003[a,b]; Hockey *et al.* 2005; Altwegg & Underhill, 2006). The longstanding connection between the Cape Sugarbird and ornithophilous protea species resulting in steady ecological reliance on one another can only have been achieved through mediated selective pressures.

The ornithophilous *Protea compacta* has uncharacteristic architecture (tall and spindly) and is frequently visited by male sugarbirds, not only for food acquisition but also for courtship or territorial displays, which alludes to a potential mutualistic relationship between plant and pollinator. *P. compacta* has a low degree of branching, with each branch terminating in a single flower. Flowers are terminal in *P. compacta*, the plant produces few flowers, and therefore few seeds. This suggests that there should be a good reason to explain the architecture, which appears to be structurally costly. Territoriality of male sugarbirds during the breeding season is high, with territorial behaviour mostly taking place in flight or on tall perches (Calf *et al.* 2003[b]; Hockey *et al.* 2005). Facilitating the perching behaviour (territorial or courtship) of male sugarbirds would be a novel adaptation by *P. compacta* when wanting to attract a suitable pollinator.

To establish if *P. compacta* does indeed facilitate the perching behaviour of Cape sugarbirds the project aimed to 1) determine the effectiveness of bird pollination in *P. compacta*, using seed set as a proxy for reproductive success, 2) quantify the architecture of *P. compacta* to infer the influence of bird pollination mode on plant structure, and 3) quantify the visitation patterns of wild populations of Cape Sugarbirds in order to establish a functional link between plant architecture and flower seed production of *P. compacta*. The following are key questions put forward by the study:

1.) How is the seed set of *P. compacta* affected when allowed or disallowed visits by bird pollen vectors?
2.) How does plant architecture vary between co-occurring protea species that differ in pollination mode?
3.) How does flower position influence Cape Sugarbird visitation patterns?

Methods: Study species, site and methods

Study species' (Cape Sugarbird and Protea compacta)

Endemic to the Cape Floristic Region of South Africa, the Cape Sugarbird (*Promerops cafer*) is locally common in mesic mountain environments (Hockey *et al.* 2005). Bird density varies between 0.5 birds/ha in tall closed protea shrublands and 4.1 birds/ha in tall sparse protea shrublands (Fraser, 1989; Hockey *et al.* 2005). Largely restricted to nectar producing stands of Proteaceae, sugarbirds depend on proteas for almost all resources (Rebelo *et al.* 1984; Hockey *et al.* 2005; Altwegg & Underhill, 2006). Substantial quantities of nectar (from approximately 300 flowers per day) are consumed daily by the birds to meet energy requirements; diet may also be supplemented by invertebrates especially when breeding or moulting (Hockey *et al.* 2005; Tjørve *et al.* 2005). Sugarbirds are sedentary during the breeding season (March – August) which coincides with the flowering peak of many protea species (Calf *et al.* 2003[a,b]; Hockey *et al.* 2005; Altwegg & Underhill, 2006). Thus many protea species are effectively pollinated by sugarbirds as a result of the link between food preference and protea flower phenology (Hargreaves *et al.* 2004; Hockey *et al.* 2005). In the non-breeding season sugarbirds become nomadic, due to the spatial distribution of resources in the landscape (Hockey *et al.* 2005; Altwegg & Underhill, 2006).

Cape Sugarbirds are sexually dimorphic, with the male birds often displaying their ornamental tails before the onset of the breeding season (Hockey *et al.* 2005; Altwegg & Underhill, 2006). Once paired up, the birds become highly territorial with both male and female assisting in territory defence and actively displace competitors in an attempt to secure the necessary resources for themselves and their offspring (Calf *et al.* 2003). Peak egg-laying dates are from April to May, when resources are sufficient but effectively egg-laying can take place during any part of the year if nectar resources are abundant (Broekhuysen 1959; Hockey *et al.* 2005). Typically a clutch of two eggs is laid, which is incubated by the female and once the eggs hatch the male and female provide food to the chicks (Broekhuysen 1959; Hockey *et al.* 2005).

P. compacta (also known as the Bot River protea), a lanky shrub, grows between 3m and 5m tall and is largely restricted to coastal slopes and flats of the south-western Cape (Manning, 2007). Inflorescences are situated on the distal extremities of branches and are cup-shaped

with a mixture of white and pink involucral bracts (Manning, 2007). Each inflorescence consists of multiple flowers forming the flower head. Each flower has a single ovule, thus allowing only one seed to be produced per flower (Hargreaves *et al.* 2004). *P. compacta* flowers during the austral winter from April to September.

Study site:

The study was carried out in the Western Cape of South Africa in the town of Kleinmond. The study site comprises a massive stand of *Protea compacta* with a profuse population of Cape Sugarbirds and is situated on the south coast foothills of the Hottentots-Holland mountain range within the Kogelberg Biosphere Reserve (KBR) which borders the town (Fig. 1). The KBR is the "hottest" local biodiversity hotspot forming a component of the global Cape Floristic Region (CFR) hotspot and is managed by Cape Nature in accordance with the internationally accepted rules of biosphere reserve management (Myers *et al.* 2000; Grant & Samways, 2007). Plant endemism is high in the KBR as it is home to 1654 plant species of which 150 are endemic (Goldblatt, 1997; Grant & Samways, 2007). The KBR is parallel (30km east) to the Cape Point National Park and forms the south eastern boundary of False Bay. It stretches inland towards Bot River and north towards Grabouw, comprising a core area of 31629 ha and total area of 103629 ha (34°04' to 34°24'S; 18°48' to 19°12'E) (UNESCO). The climate of the KBR is typically Mediterranean; hot dry summers and cool wet winters, with a prominent oceanic influence (Bond and Goldblatt 1984; Grant and Samways, 2007). Rainfall occurs predominantly in winter and has a strong orographic component which varies with the local topography (Grant and Samways, 2007).

The landscape at the study site is dominated by multiple stands of *P. compacta*, each varying in density. *P. repens* and *P. lepidocarpodendron* are also common but less prominent, as is the surrounding matrix composed of various flowering fynbos taxa (Ericaceae, Restionaceae and Bruniaceae). At the site, common bird species apart from sugarbirds include the Orange-Breasted Sunbird (*Anthobaphes violacea*), Lesser Southern Double-Collared Sunbird (*Cinnyris chalybeus*), Malachite Sunbird (*Nectarinia famosa*), Cape Grassbird (*Sphenoeacus afer*), Cape Weaver (*Ploceus capensis*), Karoo Prinia (*Prinia maculosa*) and the Cape Siskin (*Pseudochloroptila totta*).

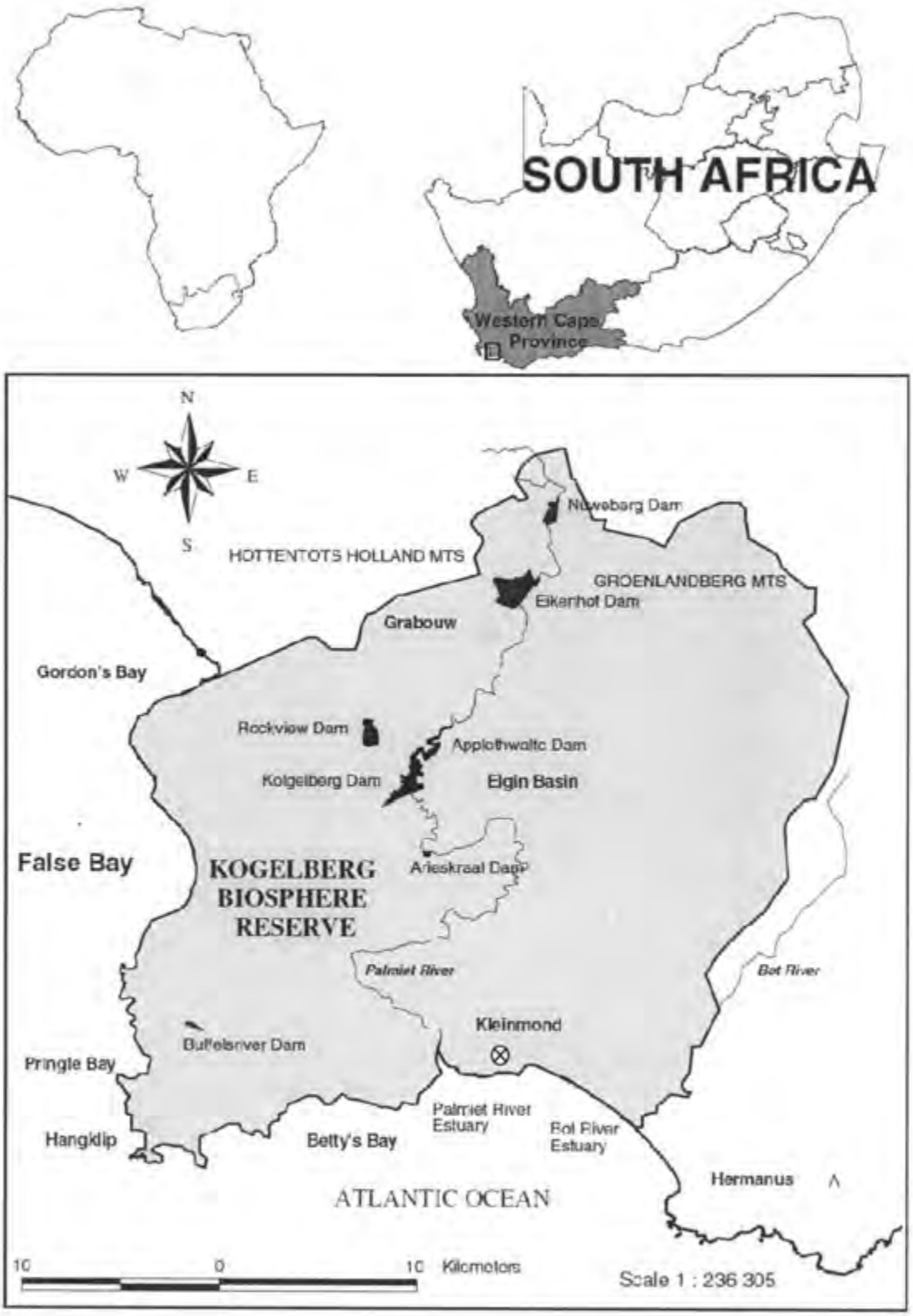

Figure 1: Position of the Kleinmond study site (x) located within the Kogel Biosphere Reserve (KBR). Adapted from Grant & Samways (2007).

Sample methods

Seed production and pollinator effectiveness:

To determine the effectiveness of bird pollination in *Protea compacta*, the number of seed produced per inflorescence served as a proxy for reproductive success. In May 2011 thirty *P. compacta* plants were randomly selected across the site and on each plant two inflorescences of similar age (pre-flowering) were chosen. On one of the inflorescences birds were excluded using a fitted mesh-cage enclosure (treatment, n=30), whilst the other inflorescence was left exposed to birds (control, n=30). Once senesced (approximately 4 months later in September 2011) all sixty inflorescences were collected dried and the seeds counted. A successful seed was plump and moist compared to unsuccessful seeds which were dry and shriveled.

Plant architecture:

To objectively quantify the architecture of the two dominant protea species, *P. compacta* and *P.repens* which differ in pollination mode (bird and insect respectively), the following measurements were taken at the study site:

Plant height (m); Basal diameter (cm); Number of flowers present on a 2cm thick branch; Number of branching tips on a 2cm thick branch; Branches per single year of growth; Wet weight of flower (g) – this will be used as a proxy for flower size.

Bird observations:

The study made use of three artificial *P. compacta* style plants with natural inflorescences in order to quantify the visitation patterns of Cape Sugarbirds. Naturally occurring *P. compacta* plants could not be used because plant height and flower position could not be standardized between samples, and because pseudoreplication of bird visits appeared to be a problem when observing fixed *P. compacta* stands. The artificial plants were constructed from electrical conduit pipe, consisting of a main stem (4.5m high) with six branches (55cm long). Branches were fitted in opposite pairs at the following heights: bottom - 1.5, middle - 3m and top - 4.5m and terminated in a flower holder (see Appendix 1). Six similar aged *P. compacta*

inflorescences were placed in each flower holder before the "plant" was erected in a suitable location for observation.

A total of six morning (07:00-08:30) observations were conducted in the duration of the study. In the morning sugarbird activity is generally higher and therefore offers the best opportunity for observations. On a single morning the following sample protocol was followed: In order to prompt more visits by the birds a sample consisted by placing all three "plants" a distance of 10m apart in an area (territory) frequented by Cape Sugarbirds. Using binoculars observations took place at a comfortable viewing distance. If a Cape Sugarbird visited any of the inflorescences on the three "plants" it was counted as one replicate. The position of the inflorescence visited was recorded e.g. bottom, middle and top, as well as the birds behaviour e.g. preening, resting, displaying, vigilance, feeding. Once the bird moved off, the three "plants" were then moved (at least 75m) to a new location to collect the next replicate.

Statistical analyses:

Seed production and pollinator effectiveness:

Using the experimental flower manipulation data a non-parametric Mann-Whitney U-test was performed in Statistica V.10. to test for a difference in the amount of seed produced. Variables included in the analysis were control (exposed) and treatment (enclosed).

Plant architecture:

All architecture data was compiled in Microsoft® Excel. The data was then analysed using various graphical techniques available in Microsoft® Excel. All data did not conform to any degree of normality and therefore a non-parametric Mann-Whitney U-test was performed in Statistica V.10. to test for a difference in the following variables of the two protea plants: Branches per single year of growth; Number of branching tips on a 2cm thick branch; Number of flowers present on a 2cm thick branch. Similarly a Kolmogorov-Smirnov test was performed to test for a difference in wet flower weight (g); plant height (m) and basal diameter (cm) of the two protea plants.

Results:

Seed production and pollinator effectiveness:

Seed production between the control and treatment flowers were significantly different ($U=240$; $p<<0.05$). Flowers that were excluded from bird visits did not produce any seed (n=30), whilst 46% (n=14) of the flowers that received visits from birds produced seed (Table 1). Of the flowers that were pollinated (n=14), the mean number of seed produced per flower was 4.85 (± 2.71) (Table 1).

Table 1: Seed production of *P. compacta* flowers when experimentally exposed (control) or enclosed (treatment) to bird pollinators.

	Sample size (n)	Total seed set	No. of flowers pollinated	Mean seed set of pollinated flowers
Treatment	30	0	0	0
Control	30	68	14	4.85

Plant architecture:

A significant difference existed in four of the measured plant architecture variables of *P. compacta* and *P. repens* (Table 2). Generally *P. compacta* for a given basal diameter (Table 2, Fig. 2) is taller than *P. repens*, has a less branches, less branching events per year and less flowers but does not differ in mean flower weight (size). *P. compacta* and *P. repens* show marginal overlap in plant structure and life strategy variables (See Appendix 1).

Table 2: Summary of plant architecture attributes of *P. compacta* (n=30) and *P. repens* (n=30) used in the study. All values in the table represent the sample mean of the attribute.

	Protea compacta	*Protea repens*	**Significant difference ($p<0.05$)**
No. of branches. single year $^{-1}$ of growth	0.06	3.5	Yes
No. of branches. 2cm diameter branch^{-1}	5.9	20.7	Yes
No. of flowers. 2cm diameter branch^{-1}	4.46	11.66	Yes
Wet weight of flower (g)	35.33	39.65	No
Plant height (m)	2.6	1.4	Yes
Basal diameter (cm)	4.37	3.81	No

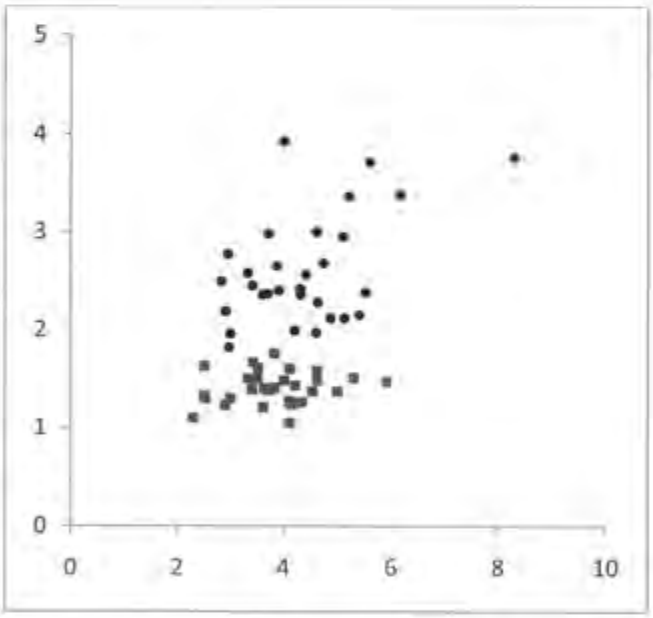

Figure 2: Relationship between basal diameter of the main stem and plant height for *P.compacta* (black circle; n=30) and *P. repens* (grey square; n=30). X-axis = Basal diameter (cm); Y-axis = Plant height (m).

Bird observations:

The three artificial *P. compacta* plants remained unvisited on all six morning observation sessions during the study period. Cape Sugarbirds were observed in the general vicinity but made no attempt to visit any of the flowers placed in the flower holders (n=18). During one morning observation session a female Cape Weaver bird visited all six flowers on one of the "plants", similarly two flowers on another "plant" were visited by a Fork-tailed Drongo (*Dicrurus adsimilis*). In the event that a sugarbird did visit any one of the placed flowers, the following record sheet was available for capturing visitor information (See Appendix 2).

Discussion:

Pollinator generalisation has been argued to be the rule in the mode of pollination amongst angiosperms, rather than specialisation (Ollerton, 1996; Johnson and Steiner, 2000). Reproduction among generalist species is highly dependent on setting seed and therefore necessitates the need to attract an array of pollinators for a successful transfer of genes to ensue among generations (Johnson and Steiner, 2000). A generalist approach is best suited to plants that are subject to fluxes in the most affective pollinator, thus they do not rely solely on any one pollinator (Johnson and Steiner, 2000). This study demonstrated the sole importance of birds as pollen vectors in a member plant of the Proteaceae family - *P. compacta*.

Seed production in *P. compacta* was negatively affected when inflorescences were excluded from bird visits, as flowers produced no seeds (Table 1). Of the control inflorescences that were exposed to birds only 47% of them produced seed which clearly shows that seed production in *P. compacta* is pollen limited and that other available pollen vectors are inefficient. One would expect a more generalist approach taken by *P. compacta* to ensure seed production, however if a more specialised approach guarantees bird visits and effective pollination then the life strategy is justified. *P. compacta* pollinator fluxes may not occur as drastically as peak flowering time is closely coupled with the breeding season of the Cape Sugarbirds (Calf *et al.* 2003[a,b]; Hockey *et al.* 2005; Altwegg & Underhill, 2006). Treatment inflorescences that were excluded from birds, had no subsequent insect pollination or self pollination taking place further corroborating a specialist lifestyle suited towards bird pollen vectors. *P. compacta* has significantly less flowers in comparison to *P. repens* which is equally abundant at the study site and insect pollinated, this clearly illustrates two contrasting approaches in pollination mode (Table 2 and Appendix 1B).

The general architecture of *P. compacta* and *P. repens* differed significantly in most of the variables measured (Table 2). Clearly both plants exhibit diverging life strategies as a consequence of pollination mode. *P. compacta* invests resources to a much greater degree than *P. repens* into growing taller for a given basal diameter and also produces less branches and flowers. This architecture might seem odd, given the need to attract sufficient pollinators for a successful transfer of genes to ensue among generations. However if *P. compacta* is able to facilitate the characteristic territorial and courtship behaviour of Cape Sugarbirds by

providing tall vantage points at vital times during the year, this architecture will ultimately pay off - guaranteeing pollination. Sugarbirds, as their name suggests have a high energy diet and in between episodes of acquiring or defending territories which form the greater part of morning and midday (Calf et al. 2003[b]), the birds will undoubtedly need to feed and in turn will pollinate *P. compacta*. The nectar produced by *P. compacta* will provide a rich food resource that can be used between daily activity bouts. From a Sugarbird's perspective a plant that provides food as well satisfies behavioural demands will be regarded as favourable in terms of energy expenditure and life goals.

Inflorescences that are situated on the distal extremities of the longest branches may help facilitate increasing seed set. These flowers should receive a high number of visits by sugarbirds as they provide the tallest vantage point. Plant architecture may not support the long distance gene flow between *P. compacta* populations as birds are highly territorial however *P. compacta* plants contained within a sugarbirds territory will receive adequate pollen outcrossing. If being taller and having long branches terminating in a flower is an adaptation towards attracting bird pollen vectors then; *P. compacta* would benefit by increased rates of outcrossing mediated by Cape Sugarbird territorial behaviour and in exchange Cape Sugarbirds are provided with the ideal vantage point to satisfy behavioural and physiological demands.

Quantifying the visitation patterns Cape Sugarbird was unsuccessful using the artificial *P. compacta* plants. This was in part due to the timing of the observations, which did not coincide with sugarbird breeding activity and peak flowering time of *P. compacta*. Observations took place only in the latter part (August) of the breeding season and into the non-breeding season (September - October), subsequently the birds had already acquired mates, occupied territories and were raising young. Thus the need for tall perches, which *P. compacta* provides, was not a necessity to facilitate breeding behaviour. The issue of whether the general appearance of the artificial *P. compacta* plants was unsuitable to attract birds and restricted observations does not apply as the "plants" did receive visits from two other bird species namely the Cape Weaver and Fork-tailed Drongo.

Conclusion:

The study showed that seed production in *P. compacta* is pollen limited and that other pollen vectors (rodents and insects) do not pollinate *P. compacta*. *P. compacta* and *P. repens* exhibited different life strategies mediated by the general plant architecture. Whether the architecture of *P. compacta* has evolved to influence the visitation patterns of Cape Sugarbirds by attempting to encourage more visits or vice versa is equivocal, as the study was unable to provide the necessary evidence. The results of this study point at three immediate priorities for future research 1) acquiring a robust set of Cape Sugarbird visitation observations at different times of the year; 2) quantifying seed production between high and low inflorescences; 3) and quantifying pollen load and removal rates between male and female sugarbirds. All three of these variables should be fairly easy to quantify and will provide invaluable evidence in establishing whether a loose connection or tight bond exists between the "pollinator friendly" architecture of *P. compacta* and the territorial Cape Sugarbird.

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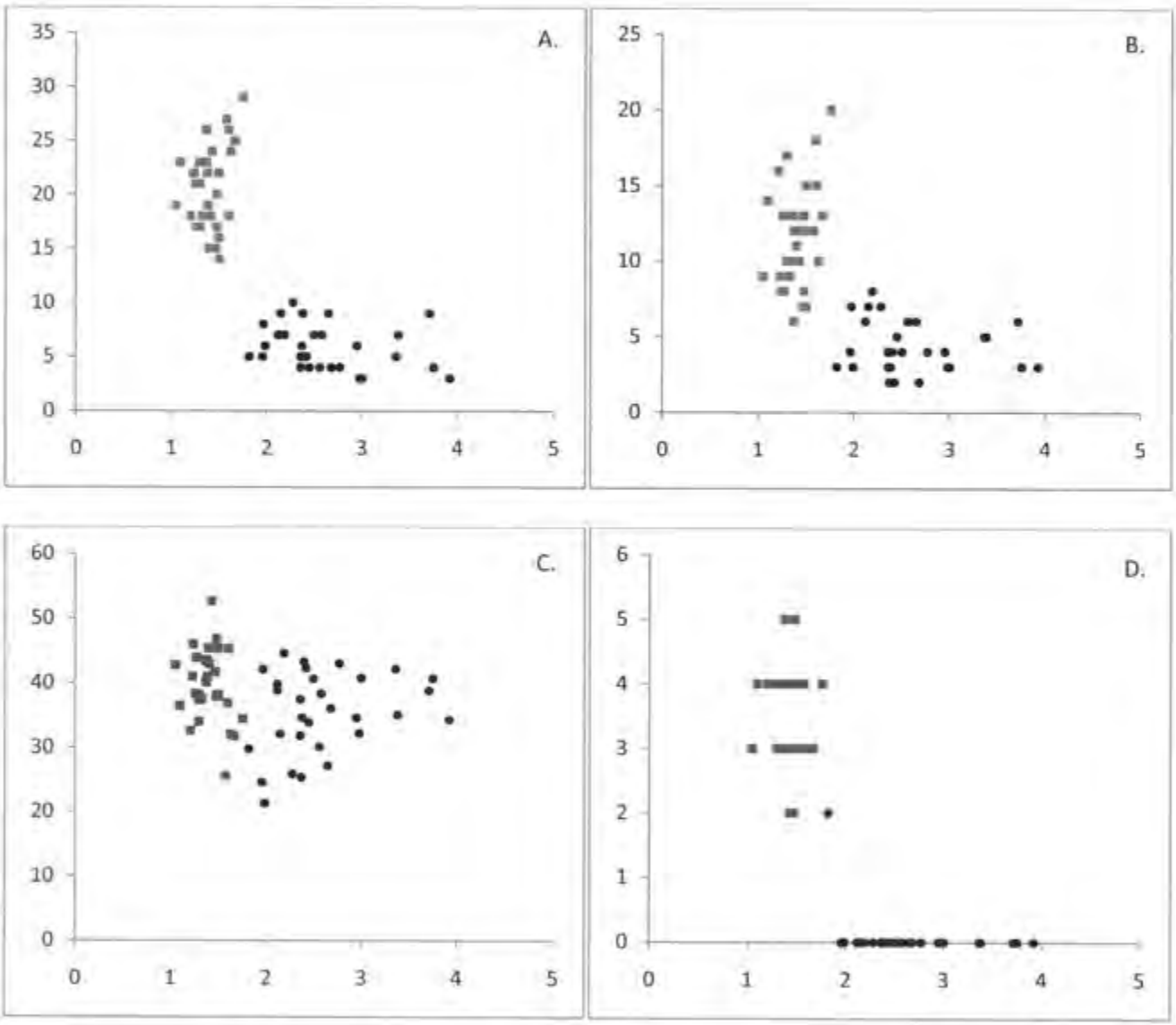
Appendix 1: Graphical representation of plant architecture variables of *P. compacta* (black circle) and *P. repens* (Grey square). In the four graphs the X-axis = Plant height (m) and Y-axis = either A.) the number of branching tips per 2cm diameter branch; B.) the number of flowers per 2cm diameter branch; C.) flower weight (g); D.) the number of branches per single year of growth



Appendix 2: Sugarbird observation record sheet used in the morning sessions at the study site

Observation record sheet										
Site description										
Location (GPS)										
Date										
Time	In									
	Out									
General comments										
	Bird no.	Sex (m/f)	Flower Position(1,2,3)	Feeding	Displaying	Resting	Preening	Fighting	Vigilance	Sequence (.....)