Nectar distribution and nectarivorous bird foraging behaviour at different spatial scales

by

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own original work, that I am the authorship owner thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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Abstract

While foraging strategies of animals may be shaped by the distribution of their food resources, these strategies in turn also affect the ecology and evolution of their resources. In this regard, African systems, of all the different bird-pollination systems worldwide, have been least studied. I investigated the relationships between these aspects at population, community and landscape levels in the bird-pollination systems of the Cape Floristic Region. This biodiversity hotspot in the southwest of South Africa contains an unusually high number of bird-pollinated plant species relative to the number of pollinating bird species.

Chapter 2 describes how I experimentally tested which nectar resource traits affect sunbird foraging behaviour at the small scale within populations. Sunbirds' behaviour was largely determined by visual signals and distances between nectar resources. The birds showed flower colour preferences, but no flower constancy (selective foraging only on one flower type).

The foraging behaviour of pollinators seems to influence plant community assembly. With the use of null models, I show in Chapter 3 that communities of Proteaceae, a diverse and dominant plant family in the Cape Floristic Region, are structured both by competition for and facilitation of pollination. This was deduced from the non-random structure of the plant communities with respect to pollination syndromes and style lengths, which are proxies of the degree of pollinator sharing and of interspecific pollen transfer.

While species traits were important driving forces of community assembly in natural habitat, I show in Chapter 4 that species and habitat traits may also be important factors structuring bird communities in novel environments such as human settlements. Through a questionnaire, I determined how well different species of nectarivorous birds are adjusting to urban environments and which traits facilitate and prevent this adjustment. Nectar-generalist birds were successful exploiters of urban resources and were most abundant in gardens with large vegetated areas, bird baths and feeders. Nectar-specialist birds were less successful at adjusting, due to their high dependence on nectar. The presence of sugar water feeders and the number of indigenous bird-pollinated plants in gardens best predicted the communities of nectar-specialist birds. All nectarivorous birds were negatively affected by dispersal barriers.

Lastly, in Chapter 5, I use biome-wide atlas databases for birds and proteas to show how nectar distribution affects bird abundances at a landscape scale. The non-significantly different flowering phenology patterns throughout the biome suggest that nectarivorous birds would not

need to migrate seasonally. Instead, birds may be sustained within mountain ranges all year round by the complementary flowering of species of different genera. Low floral abundances in the dry months of the year may still produce resource bottlenecks and this may encourage birds to forage in areas of human settlement.

Though we have gained insight into some of the relationships between African nectarivorous birds and their nectar resource distributions in space and time, there is still much to learn. There is also an urgent need to understand the effects of land-use change on the long-term persistence of nectar-feeding birds of the Cape Floristic Region.

Opsomming

Die voedingsstrategieë van diere kan gefatsoeneer word deur die verspreiding van hul voedselbronne, maar terselfdertyd kan hierdie strategieë die ekologie en evolusie van hul voedselbronne affekteer. In hierdie opsig is Afrika sisteme, van al die verskillende voëlbestuiwingssisteme wêreldwyd, die minste bestudeer. Ek het die verhoudings tussen hierdie aspekte in die voëlbestuiwingsisteme van die Kaapse Blommeryk op populasie-, gemeenskaps- en landskapsvlak ondersoek. Hierdie biodiversiteit-brandpunt in die suid-weste van Suid-Afrika huisves ‘n ongewone groot aantal voëlbestuifde plantspesies teenoor die aantal voëlbestuiwerspesies.

Hoofstuk 2 beskryf hoe ek eksperimenteel getoets het watter nektarbroneienskappe die voedingsgedrag van suikerbekkies op klein skaal binne populasies affekteer. Suikerbekkies se gedrag is grootendeels bepaal deur visuele seine en die afstande tussen nektarbronne. Die voëls het blomkleurvoorkeure getoon, maar nie blomkonstantheid (selektiewe voeding op een blomtipe) nie.

Die voedingsgedrag van bestuiwers blyk plantgemeenskapsamestelling te affekteer. Met die gebruik van nulmodelle, wys ek in Hoofstuk 3 dat gemeenskappe van Proteaceae, ‘n dominante plantfamilie in die Kaapse Blommeryk, deur beide kompetisie vir en fasilitering van bestuiwing gestruktureer word. Dit is afgelei uit die nie-ewekansige struktuur van plantgemeenskappe met betrekking tot bestuiwingsindrome en styllengtes, wat ‘n maatstaf is van interspesifieke stuifmeeloordrag en die mate waartoe plante bestuiwers deel.

Terwyl spesies-eienskappe belangrike dryfkragte was in gemeenskapsamestelling in natuurlike habitat, wys ek in Hoofstuk 4 dat spesie- en habitateienskappe ook belangrike faktore kan wees in die strukturering van voëlgemeenskappe in nuwe omgewings soos menslike nedersettings. Ek het deur ‘n vraelys bepaal hoe goed nektarvretende voëls in stedelike omgewings aanpas en watter eienskappe hierdie aanpassing fasiliteer of verhoed. Nie-spesialis nektarvretende voëls was suksesvolle uitbuiters van stedelike bronne en was die volopste in tuine met groot beplante areas, voëlbaddens en -voerders. Nektarspesialis voëls het minder suksevol aangepas, weens hul hoë afhanklikheid van nektar. Die teenwoordigheid van suikerwatervoerders en die aantal inheemse voëlbestuifde plante in tuine was die belangrikste bepalers van nektarspesialis voëlgemeenskappe. Alle nektarvretende voëls was negatief geaffekteer deur verspreidingshindernisse.

Laastens gebruik ek in Hoofstuk 5 bioomwye atlasdatabasisse van voëls en proteas om te wys hoe nektarverspreiding voëlgetalle op die landskapsvlak affekteer. Die nie-beduidende verskille in blombloeiingspatrone regdeur die bioom suggereer dat nektarvretende voëls nie seisoenaal hoef te migreer nie. Voëls kan regdeur die jaar binne bergreekse onderhou word deur komplimentêre bloeipatrone van spesies van verskillende genera. Die lae getal blomme in die droeë maande van die jaar kan steeds voedselbronbottelnekke veroorsaak en dit mag dalk voëls aanmoedig om in menslike nedersettings voedsel te soek.

Alhoewel ons insig oor die sommige van die verhoudings tussen Afrika nektarvretende voëls en die verspreiding van hul nektarbronne in tyd en ruimte gegroei het, is daar steeds baie om te leer. Daar is ook ‘n dringende behoefte om die effek van veranderings in landgebruik op die langtermyn-voortbestaan van nektarvretende voëls van die Kaapse Blommeryk te verstaan.

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Chapter 1: General introduction

The availability and distribution of resources often shape the foraging strategies of animals (Sulikowski & Burke 2011; Beerens, Noonburg & Gawlik 2015). At the same time, the behaviour of animals may influence the ecology and evolution of their resources (Stiles 1981). These reciprocal effects are commonly found within biotic communities and may sometimes scale up to the landscape level (Wisz *et al.* 2013). These interactions may be particularly strong in mutualistic relationships, where both partners depend on each other to different degrees (Wisz *et al.* 2013). In fact, the ecological and evolutionary interactions between animals and their resources have been a central topic of pollination mutualism studies, and the hummingbird-pollination system has been relatively well explored in this regard (Abrahamczyk & Kessler 2015). However, African bird-pollination systems require more investigation (Rodger & Balkwill 2004), particularly in the light of current land-use changes potentially affecting bird-plant interactions (Phillips, Hopper & Dixon 2010).

The mutualistic relationships between nectarivorous birds and bird-pollinated plants make their persistence and population viability through the next few centuries of global change highly interdependent (Cronk & Ojeda 2008). Bird-pollinated plants rely on nectarivorous birds for their reproduction and can adapt to them to optimise their fitness (Meléndez-Ackerman & Campbell 1998). In fact, bird-pollinated plants appear to have converged on a suite of traits that promote successful pollination by birds and thus, a bird-pollination syndrome can be identified (Faegri & Van der Pijl 1979). The most common traits of this syndrome include reddish flowers, relatively large volumes of dilute nectar, a lack of scent, and a sturdy perch (for all nectarivorous birds except hovering hummingbirds) (Cronk & Ojeda 2008).

Nectar-specialist birds show a similar dependence on nectar-bearing flowers, as nectar provides their primary food source. The main groups of nectar-feeding birds differ among geographical regions: Hummingbirds (Trochilidae) occur in North and South America, honeyeaters (Meliphagidae) occur in Australasia and sunbirds (Nectariniidae) and sugarbirds (Promeropidae) are the dominant pollinators in Africa and Asia (Cronk & Ojeda 2008). These birds have evolved morphological, behavioural and physiological traits to aid their nectar foraging. This includes long, narrow bills (often curved), that fit the most common morphology of bird-pollinated flowers, and tongues that very efficiently extract nectar by means of an elastic micropump mechanism (Rico-Guevara, Fan & Rubega 2015). Furthermore, nectar-specialist birds have small body sizes due to the physiological constraints of a nectar diet (Nicolson & Fleming 2003). Their foraging strategy depends mainly on visual cues and spatial memory, due to the depletion and slow replenishment of nectar in flowers (Gill & Wolf 1977; Hurly & Healy 1996; Sulikowski & Burke 2012). Besides nectar-specialist birds, there are also many bird species that secondarily or occasionally feed on nectar, classified as nectar generalists (Johnson & Nicolson 2008; Brown, Downs & Johnson 2010a). Strong evidence exists which shows that these nectar-generalist birds are important pollinators of certain plants (Arena, Symes & Witkowski 2013) and that these plants have evolved a different set of traits from those plants that are dependent on nectar-specialist birds (Johnson & Nicolson 2008).

Bird pollinators in the fynbos biome of South Africa, a biodiversity hotspot known as the Cape Floristic Region (Myers *et al.* 2000), are of particular importance because a disproportionally high number of plant species rely on them. There are more than 200 bird-pollinated plant species and only 6 bird pollinator species in this biome, which is a much higher plant to bird ratio than in many of the most biodiversity-rich tropical and Mediterranean regions in the world (Rebelo et al., 1984). Only four nectar-specialist bird species are resident in and occur across the whole biome. The Cape Sugarbird *Promerops cafer* and the Orange-breasted Sunbird *Anthobaphes violacea* are endemic to the fynbos (Hockey, Dean & Ryan 2005). Sugarbirds are closely associated with Proteaceae plant species, while these sunbirds are associated with *Erica* plant species (Rebelo, Siegfried & Crowe 1984). Both these plant groups are characteristic elements of the fynbos biome (Cowling 1992). The other two bird species, Malachite Sunbird *Nectarinia famosa* and Southern Double-collared Sunbird *Cinnyris chalybeus*, occur across a large part of southern Africa and forage on a larger variety of plant families (Skead 1967; Hockey *et al.* 2005).

At the fine scale of flower patches, the foraging behaviour of nectarivorous birds is expected to be strongly influenced by visual signals, nectar quality and spatial distribution of flowers. Optimal foraging theory suggests that birds should maximise their energy intake by feeding on the highest energy resource (Montgomerie, Eadie & Harder 1984) and minimising movement distances (Pyke 1981). It has been proposed that nectar-feeding animals can optimise their foraging through selective foraging, visiting only preferred flower types (which are, for example, abundant or highly rewarding) (Waser 1986). This selectivity may be facilitated by visual cues. Sunbirds are capable of associating visual signals with reward quality and can use it to improve their foraging success (Whitfield, Köhler & Nicolson 2014). Whichever foraging strategy pollinators employ, it is thought to ultimately affect floral evolution (Jones & Reithel 2001). In particular, the question whether bird pollinators' preferences explain the common reddish colour of bird-pollinated flowers is still open (Rodríguez-Gironés & Santamaría 2004). These theories and questions can be addressed within the fynbos bird-pollination system where the Orange-breasted Sunbird has a close association with colour polymorphic *Erica* species.

The close relationship between nectarivorous birds and their mutualistic plants suggests that they will affect each other's community assembly. Communities are characterised by limited resources: plants provide a limited nectar resource for pollinators and pollinators provide a depletable pollen transport resource to plants (Pauw 2013). Interactions between species for these limited resources will determine which species can coexist in a community (Silvertown 2004). Stable coexistence can be brought about by niche segregation (Chesson 2000; Silvertown 2004) and positive interactions (Bruno, Stachowicz & Bertness 2003). Niche segregation allows co-occurring species to use resources differently, and consequently there is stronger competition for a resource between conspecifics than heterospecifics (Silvertown 2004). On the other hand, co-occurring species may also enhance each other's fitness directly or indirectly (Bruno *et al.* 2003). Thus, segregation and/or facilitation of pollinator use and nectar use are expected to enable coexistence (Sargent & Ackerly, 2008). It is recognised more frequently that pollination interactions can structure communities through pollinator filtering, pollination facilitation (a type of filtering) and competition for pollination (Sargent & Ackerly, 2008).

Birds are highly mobile creatures and can be expected to have more dynamic communities that are better predicted by the distribution of their resources than by their interactions. However, the distribution of nectar resources is currently changing, since urbanisation is causing a loss of natural resources and providing a replacement in the form of garden plants and bird feeders (French et al., 2005). Novel urban communities are being formed by bird species that are capable of adapting to the urban environment (Blair 1996). The different responses of birds to urbanisation have been classified according to where the species are most abundant: urban exploiters (highly developed sites), urban adapters (intermediately developed sites) and urban avoiders (most natural sites). A number of biological traits have been identified that potentially facilitate birds' urban adaptation (Croci, Butet & Clergeau 2008; Conole & Kirkpatrick 2011). Furthermore, the traits of gardens will determine the specific distribution of and composition of these bird communities (Parsons, Major & French 2006). Understanding the responses of nectarivorous bird communities to these relatively novel resources is of importance as some negative effects of land-use change have already been reported for nectarivorous birds (Pauw & Louw 2012; Mackay 2014).

Nectarivorous birds' use of urban nectar resources can be understood by looking at the larger picture of landscape distribution of nectar resources. Flowers are not a consistently reliable resource, because very few plants flower continuously throughout the year and in addition, flower and nectar abundance can vary in the short and long term (Feinsinger, 1976). Flowering phenology is expected to be affected by environmental factors such as rainfall (Cowling 1992) and elevation (Johnson 1993), but also by phylogenetic constraints (Kochmer & Handel 1986; Davies *et al.* 2013). Since birds are highly mobile organisms, they may be able to migrate to wherever resources are available (Feinsinger, 1976). However, this is only feasible where there is sufficient spatio-temporal variation of these resources. In fact, nectar resource scarcities may encourage birds to seek resources in urbanised landscapes (Inouye, Calder & Waser 1991). The spatial relations of such resource scarcities may determine at what spatial scale birds need to forage to sustain themselves all year round (Woinarski, Connors & Franklin 2000). Large scale interactions are more difficult to study due to the challenges of collecting data at such scales. Hence, this level of interactions is less well understood.

Chapter objectives and research questions

Chapter 2: The foraging behaviour of pollinators is thought to affect the evolution of flowers. Pollinators are expected to forage optimally by minimizing movement distances and feeding selectively on rewarding resources. The latter can have significant effects on plant evolution, since selective foraging on one flower type (termed flower constancy) promotes intra-morphotype mating and may lead to reproductive isolation in plant morphotypes. However, antagonistic flower visitors, such as nectar robbers that remove nectar from flowers without pollinating them, may also affect flower evolution. Flower preference and constancy behaviour have only been tested in hummingbirds and require investigation in sunbirds. In this chapter, I determined the flower colour preferences of sunbirds while foraging and tested whether this affects flower evolution. For the experiments, I used an *Erica* species (Ericaceae), which represents the largest genus in the Cape Floristic Region with over 66 bird-pollinated species. Almost half of these bird-pollinated species have multiple flower colour morphotypes (Rebelo & Siegfried 1985). *Erica perspicua* is a marshland species with two flower colour morphotypes that are sympatric and flower synchronously. The pink and white flower colour morphs additionally allowed me to test whether sunbirds show an innate preference for longer-wavelength flower colours. Testing the sunbirds' preferences for pink flowers may shed light on the debate about the reason for the commonness of long-wavelength colours in bird-pollinated flowers. I used field aviaries to experimentally test sunbird behaviour and quantified the natural fitness of the two polymorphs. The female fitness of the morphotypes were measured in terms of pollination rate, fruit set and seed set. Specifically, I asked whether sunbirds (1) show flower preference; (2) show flower constancy; (3) minimise movement distances between nectar sources; and (4) affect morphotype fitness through their choices. In addition, I tested whether antagonistic nectar robbers act as a selective force on flower colour.

Chapter 3: Pollinators may contribute to structuring plant communities through competitive and facilitative interactions between coexisting species. This can be tested by comparing the distribution patterns of pollination-related traits against the patterns of null communities created by null models with specific hypotheses. Null models use certain rules to create communities in which traits are randomly distributed. When the observed community patterns differ significantly from the null community patterns, it suggests that communities may be structured by the processes that were tested. Clustering of similar pollination-related traits in the same communities suggests pollination facilitation processes affect community assembly. Low levels of co-occurrence of similar traits indicates that competitive interactions prevent the coexistence of functionally similar species.

The well-studied Proteaceae, a dominant family in the fynbos biome, provide a good opportunity to test the influence of pollinators on community assembly. Four main pollination syndromes exist in this family, and can be identified by floral morphological features: bird-, insect-, wind- and non-flying mammal-pollination syndrome. Furthermore, the style length of Proteaceae flowers is expected to be an accurate indicator of pollinator use. By assessing the patterns of pollination syndromes and style lengths in small (500 m diameter plots) and large

(8 x 8 km grid cells) communities, I could gain insight into the pollination interactions shaping these communities. The patterns of the three major genera (*Protea*, *Leucospermum* and *Leucadendron*) were also tested separately. I used the extensive Protea Atlas Project data to analyse patterns of over 28 000 communities containing 334 Proteaceae species. I aimed to answer whether (1) pollination syndromes are non-randomly structured; (2) style lengths are non-randomly distributed and (3) the patterns differ in different genera and in each pollination syndrome group.

Chapter 4: Land-use change, such as urbanisation, is affecting biotic communities. Determining which species and habitat traits most strongly influence community assembly may enable us to predict and mitigate negative land-use change effects. Nectarivorous bird species worldwide show varied tolerances of urban habitat, and thus some are classified as urban exploiters (more abundant in developed areas than in natural areas) and others only as urban adapters (less abundant in developed areas). Cape Town is one of South Africa’s largest and growing cities, situated in the biodiverse fynbos biome. Five nectar-specialist and at least nine nectar-generalist bird species can be found in the suburbs of Cape Town. These two functional groups show different responses to urbanisation in different parts of the world. In order to understand their adaptation to urban settlements and how it is facilitated or constrained, I gathered information on bird traits from literature, and on Cape Town gardens and garden birds through means of a questionnaire. I addressed three specific questions: (1) can nectar-generalist and -specialist birds be classified as urban exploiters or adapters, respectively? (2) Which biological traits of nectarivorous birds most strongly affect the structure of urban bird communities? (3) Which garden traits are the most important predictors of community structure of nectar specialists and generalists?

Chapter 5: After assessing the responses of nectarivorous birds to the fine-scale and community-level distribution of nectar sources, I explored the landscape level distribution of nectar resources and responses of nectarivorous birds. Flowering phenology patterns may respond to a number of environmental factors, and consequently, floral abundances may show large fluctuations in time and space. Highly mobile nectarivorous birds are capable of tracking resources at landscape scale, but the profitability of this depends on the spatial variation of resource availability. The landscape scale resource variability and responses of birds are still understudied due to the difficulties of data collection at large scales. I investigated the landscape spatio-temporal patterns of bird-visited Proteaceae plants across the fynbos biome. Two extensive databases were used from the Protea Atlas Project and the second southern African Bird Atlas Project. I expected to find spatially and temporally explicit patterns in the flowering phenology of this group of plants in response to environmental factors. In addition, I expected birds to respond to these patterns. Specifically, I tested whether floral abundances (1) vary temporally across the biome; (2) differ between genera; (3) differ between rainfall regimes and (4) change with elevation. Furthermore, I tested whether nectar scarcities change proportionally with spatial scale and whether bird abundances can be predicted by protea abundance, floral abundance and protea species richness.

Chapter 2: Pink flower preference in sunbirds does not translate into plant fitness differences in a polymorphic *Erica* species

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Abstract

Bird-pollinated plants typically have reddish flowers, but it is not clear whether this trait can be attributed to selection by birds. Here we experimentally test for the first time the foraging behaviour of sunbirds in relation to flower colour, using the Orange-breasted Sunbird *Anthobaphes violacea* (Nectariniidae) and the colour dimorphic *Erica perspicua* (Ericaceae). Pink and white flower morphotypes co-flower in intermixed populations and have similar nectar volumes and concentrations. Using floral arrays in a field aviary, we found that sunbirds preferred pink flowers; 95% of their first choices were to pink inflorescences and they visited and probed more pink inflorescences and flowers, respectively. We also tested for flower constancy (the tendency to move between same colour rather than different colour morphotypes), but found no evidence for this in the sequence of their foraging choices, indicating that this mechanism did not maintain flower colour differences in sympatry. There was evidence for optimal foraging: 80% of moves were to adjacent inflorescences. Unexpectedly, the preference for pink flowers observed in the aviary did not translate into a female fitness advantage for this morphotype in the field, since no difference is found in natural pollination rate, fruit or seed set. This may be because the minimization of flight distances between plants is the primary factor in sunbird foraging choices, overriding their colour preference. Antagonistic nectar robbers did not act as a selective force on the polymorphism, since nectar-robbing rates were equal between white and pink morphotypes in the field.

Introduction

The foraging choices of animals shape the evolution of the plant species on which they feed. The evolutionary responses include not only the bewildering array of defensive devices used to foil and punish herbivores, but also the dazzling diversity of advertisements and rewards that plants use to attract foraging animals to their flowers. Indeed, much of the diversity in plant life is generated at the interface between animal behaviour and plant traits.

Plant populations with polymorphic traits are ideal for testing how particular traits manipulate animal behaviour and how the choices animals make drive the evolution of plants. Flower colour polymorphism is a very commonly observed polymorphism, which has had a large impact on the development of evolutionary theory (Schemske & Bierzychudek 2007). Polymorphic populations present an evolutionary puzzle: genetic drift or directional selection should weed out one of the morphotypes and the population should march towards monomorphism. Persistent polymorphism requires balancing natural selection: fluctuating selection in space or time, heterozygote selective advantage, or negative frequency-dependent selection (Eckhart *et al.* 2006). In the case of flower colour polymorphism, pollinators are the obvious agents of selection, but antagonistic animals (Irwin *et al.* 2003; Carlson & Holsinger 2013) and the abiotic environment (Schemske & Bierzychudek 2001) can also impose balancing selection, often by acting on traits that are correlated with flower colour.

The response of pollinators to flower colour will depend on their sensory systems as well as innate and learned preferences (Chittka, Thomson & Waser 1999). Pollinators forage optimally by selecting the best nectar sources, which they find through an association between reward size and floral advertisements (Montgomerie *et al.* 1984) or spatial cues (Henderson, Hurly & Healy 2001), and minimizing movement distances (Pyke 1981). In flower colour polymorphic populations, pollinators are often found to impose directional selection on flower colour by preferring one morphotype, leaving the question of what maintains the polymorphism unanswered (Irwin & Strauss 2005). A notable exception is the deceptive, non-rewarding orchid *Dactylorhiza sambucina* in which negative frequency depended selection was detected: pollinators learn to avoid the common flower colour morphotype, thus maintaining the polymorphism (Gigord, Macnair & Smithson 2001). In other flower polymorphic systems, pollinators have fluctuating preferences depending on nectar properties (Jones & Reithel 2001), plant/inflorescence height (Levin & Watkins 1984) and flower abundance (Eckhart *et al.* 2006), which may maintain polymorphisms.

Extreme preference for a particular morphotype results in so-called flower constancy -- pollinator species or individuals develop a strict fidelity to one flower morphotype, skipping over others (Waser 1986). Flower constancy behaviour has been detected in several insect species and can have a large impact on the occurrence of different flower colour morphotypes in polymorphic populations because constancy promotes assortative (intra-morphotype) mating (Jones & Reithel 2001) and thus results in a deficiency of heterozygotes, which may be of intermediate colour. Because flower constancy can result in reproductive isolation between colour morphotypes it is additionally interesting as a potential mechanism for sympatric speciation (Grant 1994).

Here we focus on populations of the shrub, *Erica perspicua* (Ericaceae), in which individuals have either white or pink flowers (Fig. 2.1a) or rarely, intermediates. The long-tubed flowers are pollinated exclusively by birds, mainly the Orange-breasted Sunbird (*Anthobaphes violacea*; Nectariniidae, Fig. 2.1b) (Skead 1967; Rebelo & Siegfried 1985). Surprisingly little is known about the flower colour preference of nectar-feeding birds other than hummingbirds, despite recent advances in understanding their sensory systems (Ödeen & Håstad 2010). Only one study has tested sunbirds' floral colour preferences and found no difference in visit rates between pink and white morphs in the field (Carlson & Holsinger 2013). However, foraging choices should also be investigated in a system without the effect of other factors such as differences in number of flowers, nectar properties, floral spatial distribution or the surrounding floral community. Globally, red colouration is one of the most distinctive characteristics of bird-pollinated flowers, but whether this association results from selection by birds remains highly controversial. While some studies find that hummingbirds prefer red flowers over white (Meléndez-Ackerman, Campbell & Waser 1997) and show a preference for red over pink and white (Dudash *et al.* 2011), others conclude that hummingbirds do not have a preference for reds (Bené 1941; Stiles 1976; McDade 1983; Delph & Lively 1989; Proctor, Yeo & Lack 1996). Recent reviews suggest that instead of birds, antagonistic nectar robbing insects, which have greater difficulty distinguishing red from green, may be the evolutionary driver of red coloration in bird-pollinated flowers (Rodríguez-Gironés & Santamaría 2004; Lunau *et al.*

2011). This study however, does not address this question since the pink *E. perspicua* reflects in the blue and red regions of the light spectrum and is therefore visible to insects.

As with flower colour preference, flower constancy is poorly explored in birds despite its importance for determining patterns of pollen transfer. Hummingbirds are the only nectarivorous birds that have been tested and experiments suggest that they are not constant for flower colour differences alone (Meléndez-Ackerman *et al.* 1997), but may be constant when faced with a choice between hummingbird- and hawkmoth- pollinated plant species that differ in many traits including colour (Aldridge & Campbell 2007). Similar tests have not been conducted on sunbirds (Nectariniidae), the Old World equivalent of the hummingbirds.

We use *E. perspicua* to explore the foraging behaviour of Orange-breasted Sunbirds. We specifically ask whether sunbirds (1) show flower colour preference; (2) show flower colour constancy; (3) minimize movement distances between nectar sources; and (4) affect morphotype type fitness through their choices. In addition (5) we test whether antagonistic nectar robbers act as a selective force on flower colour.

Methods

Plant traits

In the genus *Erica*, about 38% of the species show substantial intraspecific flower colour variation (Rebelo & Siegfried 1985). An even larger proportion (49%) of the more than 66 species conforming to the bird-pollination syndrome has multiple colour morphotypes (Rebelo & Siegfried 1985). Pink and white flower colour morphotypes of the study species, *E. perspicua* subsp. *perspicua* (Oliver & Oliver 2005), co-flower in mixed stands. In the Kogelberg study area (south-western Cape, South Africa, 34° 19' 45" S 18° 50' 30" E) intermediate morphotypes exist, but the two extremes predominate and were used in all experiments. The study area was dominated by large populations of thousands of plants of this reseeding species, with no other co-flowering bird-pollinated plants in the immediate vicinity. All study sites were further than 100 m from road traffic, which is known to impact on the rate of bird-pollination in this species (Geerts & Pauw 2011).

During peak flowering (May) the floral density of each morphotype was estimated in twelve 5 x 5 m plots in three populations approximately 10 km apart (Table S2.1). To compare nectar production between morphs, nectar properties were measured every two hours from 9:00 till 17:00 in the plant population where the behavioural experiments were conducted (Pringle Bay). At each time interval, different plants were used to randomly select ten young, unvisited flowers, identifiable by their unbroken anther rings (Geerts & Pauw 2011), from each morphotype on at least five different inflorescences. Nectar volume (µl) was measured with a capillary tube and nectar concentration (% sugars) with a handheld refractometer (Bellingham & Stanley Ltd.). The nectar of *E. perspicua* consists of 87 % sucrose, 8 % glucose and 5 % fructose (Barnes, Nicolson & Vanwyk 1995). Flowers may last for multiple days, but since only young and unvisited flowers were measured, these represent nectar production of unvisited flowers. These young flowers show no morphological changes within the first three days of opening after which they start wilting. To compare spatial variation of nectar production, the same methods were used to measure flowers in another population (Kleinmond; 34º 20’ 16.35” S 18º 59’ 48.69” E) in the following year, but only at 9:00.

The reflectance spectra of the two types of flowers were measured on five flowers per morphotype with a calibrated Ocean Optics spectrometer (USB4000). Colour distances (chromatic contrast) between the morphotypes were measured in Just Noticeable Differences (JND, the Euclidian distances weighted by the Weber fraction of the photoreceptor cones) (Backhaus & Menzel 1987). To show how the birds likely perceive the colours, the spectra were projected into avian vision colour space using the maximum absorption values for the four photoreceptors of the European starling *Sturnus vulgaris* which is also in the Passerida clade (Hart, Partridge & Cuthill 1998). However, the maximum absorption of the Ultra-violet (UV) sensitive receptor of Nectariniidae is known (Ödeen & Håstad 2010) and therefore this was specified in the model. This modelling was done with the pavo package in R software (R Development Core Team (RDCT) 2006).

Sunbird behaviour experiments

During May and June 2012, experiments were done in a green shade net aviary in the field (2 x 2 m and 1.6 m high) with natural low growing vegetation as ground cover. Inside we erected a square floral array (four rows and columns) of inflorescences in water bottles on 1.1 m high stands. Eight inflorescences of each morphotype were arranged randomly (according to randomly drawn numbers) and spaced 0.4 m apart, the distance that sunbirds most often move between inflorescences (Gill & Wolf 1977). Each inflorescence contained 10 mature, unvisited flowers to equalise attractiveness but also encourage movement between inflorescences. Orange-breasted Sunbirds (21 individuals; 15 males, 5 females and one juvenile of unknown gender) were caught with mist nets at the site between 7:00 and 16:00 and ringed. The birds were caught in the breeding season, but mostly males were caught, who are less involved in the breeding process. Females build the nests and incubate the eggs alone and provide 65% of the chick feeding (Broekhuysen 1963). Females with brood patches were released immediately and not used in the experiment. The mist nets were no more than 200 m from the aviary, thus birds were transported the short distance in bird bags. A single bird at a time was released into the aviary, allowed to settle and forage freely from the floral array while its sequence of movements and number of probes per inflorescence were recorded. Birds were caught in the aviary with a handheld gauze net (30 cm diameter), causing as little stress as possible, to be released outside again. A few sunbirds were reintroduced into the aviary after a rest period or when recaptured on another day, but with an unfamiliar floral arrangement, thus some birds were subjected to more than one experimental trial (32 trials in total). No bird was kept in captivity for longer than 3 hours (ethical clearance permit SU-ACUM12-00026).

Plant female fitness

Plant fitness was measured in one of the pink morph dominated populations. Several fitness proxies for the two morphotypes were quantified and compared, but its ability to self-pollinate was not tested. In one population, 25 inflorescences (1136 flowers) of each morphotype were marked on separate plants and the pollination rate of mature flowers (number of flowers with ruptured anther rings) was recorded. A ruptured anther ring is a proxy for the male component of fitness because it indicates pollen release, and is additionally a good indicator of female reproductive success because it is highly correlated with pollen receipt (Geerts & Pauw 2011). When fruits matured six weeks later we collected the inflorescences and counted the number of fruits. Three to five mature fruits (to a total of 101 of white morphotype & 99 of pink morphotype) were randomly chosen from each inflorescence and its seed set counted.

Nectar robbing

Twenty-one 100m^2 plots were set up in 11 populations across the Kogelberg area (including the sites where plant fitness and nectar was measured). Sixteen plants were randomly selected in each plot and five flowers were inspected for evidence of nectar robbing by carpenter bees (*Xylocopa spp.*) and honeybees (*Apis mellifera* subsp. *capensis*). The proportion of robbed flowers, visible as a slit in the corolla, was scored for 139 white plants and 197 pink plants.

Statistical analyses

Plant traits

The difference in morphotype densities (ratio of pink to white flowers) between the three populations was tested with a Kruskal-Wallis test. Nectar concentration was converted to mg of sugar by multiplying the nectar volume with the mg per ml sugar (Kearns & Inouye 1993). To test for differences in nectar volume and in sugar mass between morphotypes, we used a Linear Mixed Model (LMM) with morphotype as fixed factor and plant identity as random factor. This was done for each population separately. In addition, to test whether nectar volume and sugar mass changed over time, we included time of measurement as a continuous covariable in the fixed model of the Pringle bay population. The Brown-forsythe modified Levene’s test (Brown & Forsyth 1974) was used to compare the variance of nectar volume and sugar mass in each site. We also compared the mean colour distances between all pairs of flowers of the same and different morphotypes with a Mann-Whitney U test.

Sunbird behaviour experiments

During a trial in the aviary, individual birds usually made several foraging bouts, separated by rest periods. Therefore data were first analysed considering all the visits in one trial as one foraging bout, then with only the single longest foraging bout of each individual. The results differed negligibly; therefore the results are given for the first-mentioned method. Furthermore, to avoid the effect of pseudoreplication the data from multiple trials were pooled for individuals tested in more than one trial, so that each individual is represented only once in the dataset. The results were the same as when only the first trial of each individual was tested.

The sunbirds’ preferences and constancy was compared to expectations with one-sample t-tests and one-sample Wilcoxon tests for parametric and non-parametric data, respectively. For each individual bird the proportion of visits to pink inflorescences and the proportion of probes at pink flowers were calculated. To test their preference, the proportion of visits and probes were compared to an expected mean of 50%, which would be the outcome if birds showed no preference. The average number of probes per inflorescence was also compared between morphotypes with a Wilcoxon signed rank test.

Likewise, the birds' proportion of intermorph transitions was determined. We tested for flower constancy by comparing the transitions to an expectation of random foraging (which is a probability of 8/15 to visit another colour, excluding the inflorescence from which the bird departs). We also calculated the Constancy Index according to Gegear & Laverty (2005): CI = (c - e)/(c + e - 2ce), with c as the proportion of moves between the same csoloured flowers and e as the expected proportion of moves between same coloured flowers based on the overall frequency of each colour morphotype. The index varies from -1 to 1, where -1 is complete inconstancy, 0 is complete random foraging and 1 indicates perfect flower constancy. To test whether the birds showed a significant preference for adjacent inflorescences, the proportion of moves to adjacent inflorescences was determined. First, the expected probability of moving to an adjacent inflorescence was calculated for each move (inflorescences on the edges and corners have fewer directly adjacent inflorescences than the interior inflorescences) and then the average probability for each trial was determined. Thus, each trial had its own proportion of expected moves. The matched lists of observed and expected values were compared using a Paired t-test.

Plant female fitness

The pollination rate and fruit set per inflorescence was compared between morphotypes (24 flowers of each morphotype) with Welch two sample t-tests. Seed set was analysed with a Generalized Linear Mixed Model with a Poisson error distribution and plant identity as a random effect. A Mann-Whitney U test was used to compare the total seed output per plant. The number of flowers per inflorescence on these experimental inflorescences was also compared with a Mann-Whitney U test.

Nectar robbing

The effect of flower colour on nectar robbing rates was tested with a Generalized Linear Mixed Model with a binomial error distribution and population as a random effect.

In all cases where Linear and Generalized Linear Mixed Models were used, the significance of the explanatory variable was tested by comparing two models with and without the variable of interest with a log-likelihood ratio test. All analyses were done in the statistical software R version 3.0.0 (R Development Core Team (RDCT) 2006).

Results

Plant traits

Overall, the average density ratio of the two morphotypes was similar (45:10:45 for pink: intermediate: white), but it differed between the three populations (X^2_2 =8.234, N = 12, P = 0.016). In two populations pink morphotypes were dominant by far and in the other the white morphotype was dominant. Nectar characteristics measured in a 100 flowers did not vary significantly throughout the day (volume X^2_1 = 0.630, P = 0.428; sugar mass X^2_1 = 1.939, P = 0.164, Fig. 2.2). The nectar properties (volume, sugar mass and variance of these properties) of the morphotypes did not differ significantly in either of the two sites (Table 2.1). The overall distance between the colour spectra of pink and white morphotypes is 6.46 JND, which is higher than the discrimination threshold of > 1 JND, thus the birds can most likely distinguish the two colours (Fig. 2.3). The mean colour distance between pairs of different coloured flowers was significantly higher than that of pairs of the same morphotype (U = 16, N_1 = 30 N_2 = 36, P < 0.001). The experimental conditions should not influence the birds' discrimination ability since the shade net of the aviary only reduces the reflective intensity of the flowers and not the reflectance spectra.

Behaviour experiments

The birds visited a pink inflorescence first 95% of the time (first trials only, N = 21). Pink inflorescences were visited more frequently (t_{20} = 3.948, P < 0.001, Fig. 2.4a) and overall more pink flowers were probed than expected (U = 228, N = 21, P < 0.001, Fig. 2.4b). The average number of probes per inflorescence, however, did not differ between morphotypes (U = 119, N = 21, P = 0.919). No evidence of flower constancy was found since the proportion of intermorph transitions was similar to the expected (U = 153, N = 21, P = 0.198, Fig. 2.4c). The Constancy Index suggests that the sunbirds tend towards inconstancy (- 0.30312). Eighty percent of the birds' moves were to adjacent inflorescences and the proportion of moves to adjacent inflorescences was significantly more than expected if foraging was random (t_{20} = 16.466, P < 0.001, Fig. 2.4d). The data were also analysed for only the male individuals, since their foraging tactics may differ from females because of their territorial behaviour in the breeding season. However, the results were the same as when all individuals were analysed, suggesting that males and females behaved the same way in these experiments.

Plant female fitness

None of the fitness variables measured differed significantly between the two morphotypes. There was no difference in the pollination rate (t_{46} = -1.568, P = 0.137, 48 flowers), fruit set per inflorescence (t_{46} = -0.492, P = 0.625, 48 flowers) or seed set (X^2_1 = 0.084, N = 200, P = 0.772). Total inflorescence production, the total number of fruits times average seeds per fruit, also showed no difference between morphotypes (U = 265.5, N = 46, P = 0.991). The number of mature flowers per inflorescence does not differ significantly between morphotypes (U = 293, N = 24, P = 0.926).

Nectar robbing

In total, 1680 flowers were checked for evidence of nectar robbing. Analyses showed that flower colour does not affect nectar robbing rates (X^2_1 = 0.011, N = 336, P = 0.916). The average proportion of flowers robbed were 0.166 for the pink morphotype and 0.167 for the white morphotype.

Discussion

Orange-breasted sunbirds show a spontaneous preference for pink flowers above white, but lack flower constancy for it under the controlled conditions of an aviary. The preference for pink flowers by Orange-breasted Sunbirds is consistent with the observation that bird-pollinated flowers throughout the world are typically reddish in colour (Faegri & Van der Pijl 1979). At least a subset of honeyeater-pollinated flowers in Australia seems to have evolved reddish flowers (Shrestha *et al.* 2013). The birds have the visual ability to distinguish the two colours (Fig. 2.3) and it is evident from their initial and sequential choices that they prefer pink flowers over white ones (Fig. 2.4a & b). This preference for pink might be innate, because all four juveniles used in the experiment preferred pink inflorescences and the colour difference is not associated with a reward difference, which would normally be necessary to stimulate a learned preference.

At both sites where nectar properties were investigated, the morphotypes provided a similar reward to pollinators (Table 2.1). The average number of probes per inflorescence indicates the birds' reaction to the nectar reward (Gill & Wolf 1977), thus it is not surprising that the birds' average probes did not differ between the morphotypes. The mean nectar concentration of both morphotypes (12-15 %) is slightly lower than the typical preference of sunbirds (20 – 25 %; (Lotz & Nicolson 1996; Brown, Downs & Johnson 2010b)). Flowers are not arranged developmentally along inflorescences (Fig. 2.1a) and the morphotypes do not differ in their average number of flowers per inflorescence, therefore we do not expect inflorescence architecture to influence visitation rates differentially between morphotypes.

The subspecies of *Erica plukenetii* that are pollinated by sunbirds are mostly pink flowered, while the moth-pollinated subspecies have white flowers (Van der Niet *et al.* 2014). This may also be an indication that Orange-breasted and Malachite Sunbirds prefer pink flowers over white. In contradiction to this and our study, sunbirds and sugarbirds visit pink and white morphotypes of *Protea aurea* equally frequently in the field, suggesting they do not show preference for flower colours (Carlson & Holsinger 2013). The birds did spend more time at white inflorescences at one site, but this is most likely because of the higher number of flowers and nectar volume in this morph. Unfortunately, this study does not specify the behaviour of Orange-breasted sunbirds. Similar to our study, the fecundity of the *Protea aurea* morphs did not differ, perhaps due to the indifference shown by the pollinators.

Unexpectedly, the preference for the pink morphotype, demonstrated in the aviary, did not translate into higher female fitness measures of this morphotype in the field. There was no difference in any of the proxies of fitness (pollination rate, fruit and seed set) between pink and white flowered plants. However, self-pollination was not tested thus the contribution of seeds produced through self fertilization is not known. A possible explanation is that the minimization of flight distances between plants is the overriding factor in foraging choices under field conditions (Gill & Wolf 1977; Pyke 1981; Waser 1982; Krauss *et al.* 2009). In a natural setting, birds will seldom be faced by a perfectly balanced choice between colour morphotypes that are equidistant and of equal size. Most often, one plant will be nearer, and the demonstrated preference for adjacent plants (Fig. 2.4d) will dictate the choice. This conclusion is in accord with several studies that demonstrate that nectar reward distribution predicts the small-scale movements of hummingbirds and honeyeaters (Gill & Wolf 1977; Pyke 1981; Sutherland & Gass 1995; Baum & Grant 2001; Burke & Fulham 2003).

The resulting lack of selection (through female fitness) on flower colour by sunbirds and nectar robbers may in part explain why both morphotypes persist in all studied populations, albeit in varying ratios (Table S2.1). In large populations, selectively neutral polymorphisms may take very long to drift to monomorphism (Kimura 1985). Another possible explanation is that other forms of balancing selection, which we did not investigate, act to maintain the polymorphism. In some pink and white polymorphic proteas, for example, pollinators apparently do not act as selecting agents, as indicated by similar seed set between morphs (Carlson & Holsinger 2010). Neither one of the morphs are dominant, seemingly due to deleterious pleiotropic effects in one morph and higher seed predation in the other morph. Abiotic factors, such as elevation and precipitation, may also act differentially upon morphotypes if they prefer different habitats (Arista *et al.* 2013). While random genetic drift is one explanation for the observed differences in morphotype ratios among populations, selection again seems a more likely mechanism. Interestingly, human flower colour preference may be a factor: in populations dominated by white flowers, the pink morphotype has likely been overharvested for the cut flower trade (Schumann, Kirsten & Oliver 1992).

In contrast to some insect groups (Waser 1986; de Jager, Ellis & Dreyer 2009), differences in flower colour did not elicit constancy behaviour in the sunbirds. Thus, assortative mating mediated by birds is unlikely to influence morphotype ratios. The bird-pollinated subspecies of *Erica plukenetii* differed from the other subspecies in corolla length, nectar volume and scent (Van der Niet *et al.* 2014), therefore morphs with differences in nectar properties or in multiple floral traits, may encourage discriminate foraging in sunbirds. However, sunbirds will even visit a rare bird-pollinated *Erica* species that is new in an *Erica* community (Heystek & Pauw 2014), suggesting that the sunbirds may not even show flower constancy in a multi-species community.

Clearer understanding of the factors that determine morphotype ratios in this species is not currently possible because the genetic system that determines flower colour in *Erica* is unknown. In general, much remains to be learned about the flower traits that influence sunbirds' preferences and foraging, and how this affects flower polymorphisms and plant diversity. Studies of pollinator foraging choices will be useful to provide answers, particularly in conjunction with investigations of natural plant fitness.

Acknowledgements

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Table 2.1 The nectar properties of the two morphotypes of *Erica perspicua* did not differ significantly. For each nectar property the results for the Pringle Bay site is given in the first row and for the Kleinmond site in the second row. The respective number of plants and flowers sampled in Pringle Bay is 59 and 100, and in Kleinmond is 18 and 42.

Nectar property	**Degrees of freedom***	**Test statistic**	**P-value**
Volume	1	X^2 = < 0.001	0.990
	1	X^2 = 1.546	0.214
Sugar mass	1	X^2 = 1.373	0.241
	1	X^2 = 0.198	0.657
Volume variance	1, 98	F = 0.289	0.592
	1, 40	F = 0.902	0.348
Sugar mass variance	1, 98	F = 0.675	0.413
	1, 40	F = 0.140	0.711

* Where two degrees of freedom is given, the first is the numerator and second the denominator degrees of freedom.

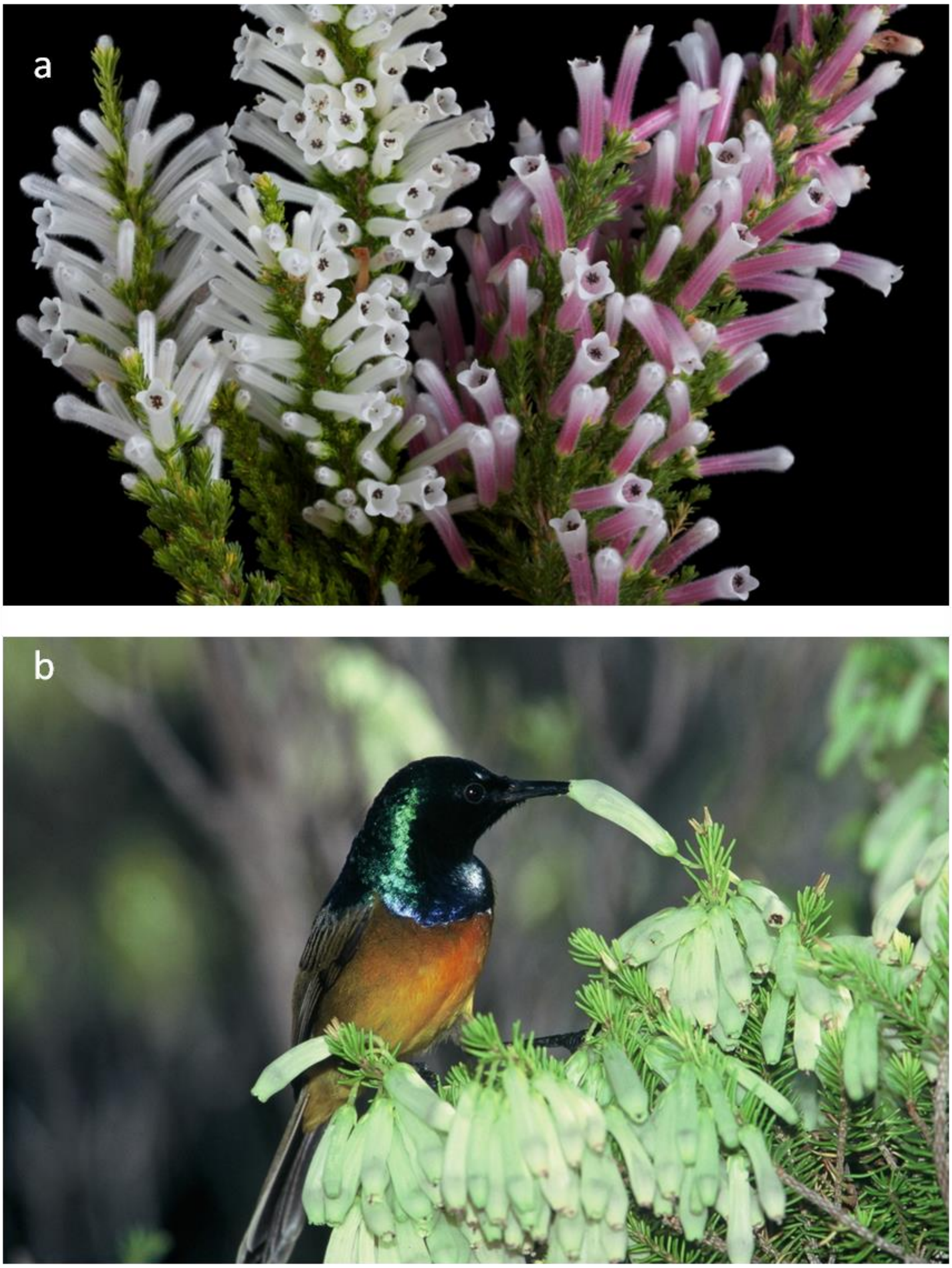

Figure 2.1 (**a**) White and pink flower morphotypes of *Erica perspicua* collected from Pringle Bay in the Cape Floristic Region. Their average corolla length is 22 mm (Oliver & Oliver 2005). (**b**) An Orange-breasted Sunbird drinking from *Erica mammosa*, one of 33 polymorphic bird-pollinated *Erica* species (Images by A. Pauw).

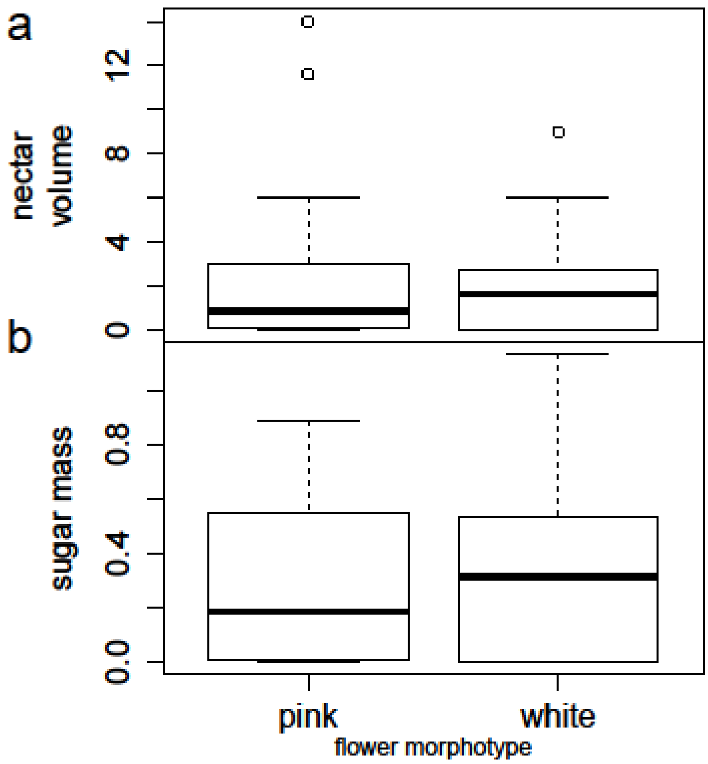

Figure 2.2 Nectar volume (µl) (**a**) and sugar mass (mg) (**b**) of *in situ* pink and white flowers of *Erica perspicua* did not differ significantly (only the results from the Pringle Bay site are displayed here). The bold line indicates the median, the box the interquartile range, whiskers the ranges and points are outliers.

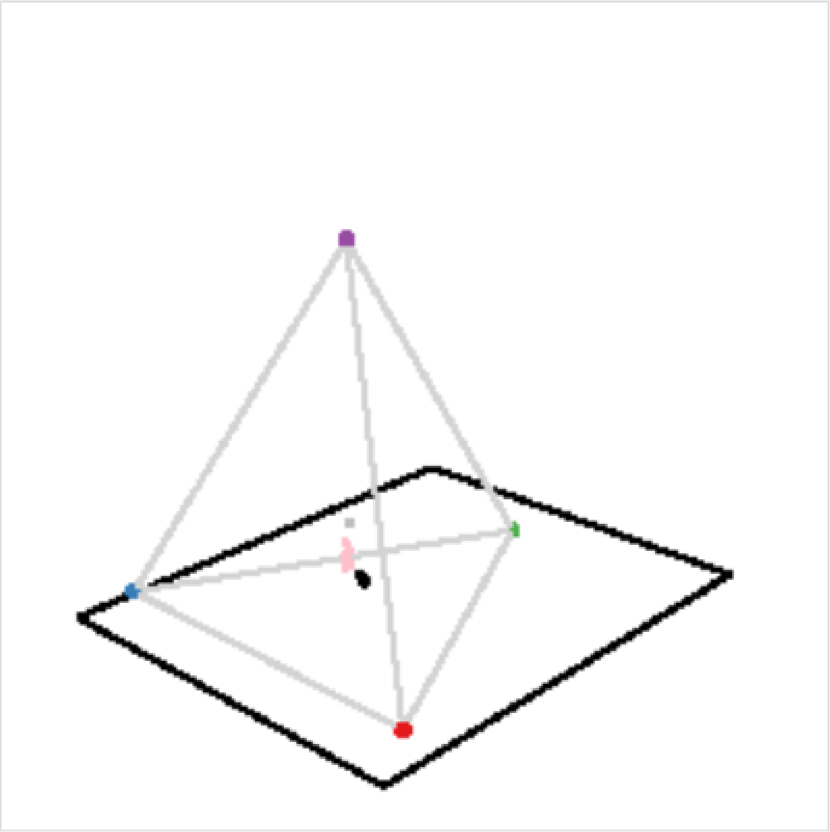

Figure 2.3 Flower colour of the two morphotypes in avian colour space. The green, blue, red and purple dots on the corners of the tetrahedron represent the four light receptors of birds. A colour is plotted based on the relative absorption of each receptor and the grey dot in the centre of the tetrahedron is thus white light. Reflectance spectra of the pink (pink cluster on the left) and white (black cluster on the right) flowers group completely separately, indicating that the apparent colour difference can be perceived by birds.

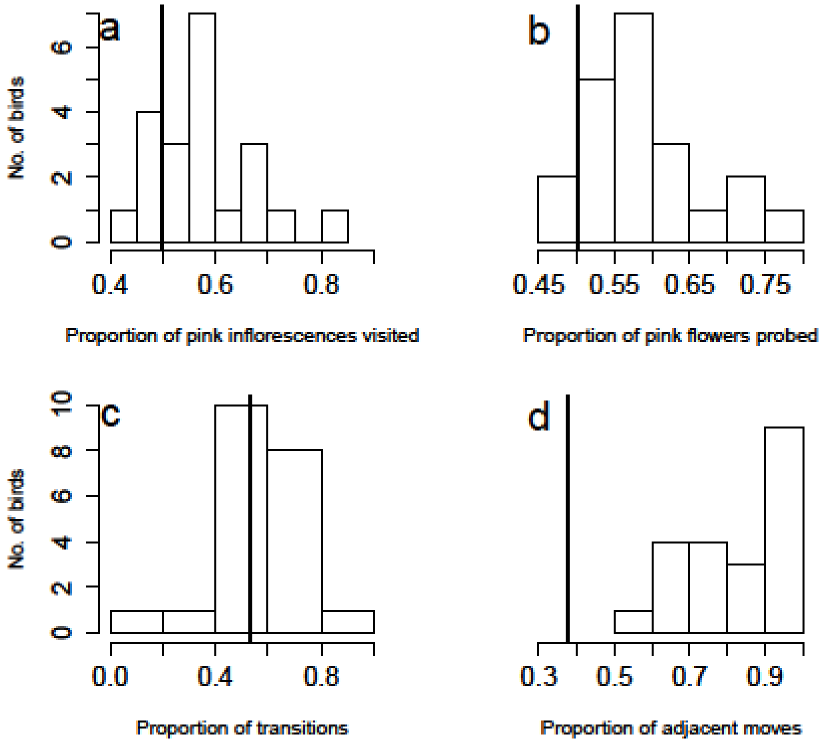

Figure 2.4 During the aviary experiments, sunbirds tended to visit significantly more pink inflorescences (**a**), and overall they probed significantly more pink flowers than white ones (**b**). No flower constancy was detected since bird transitions between different and same coloured inflorescences did not differ from the expectation of random foraging (**c**). They did, however, make more movements to adjacent inflorescences than expected (**d**). In total, 80% of sunbirds' moves were to adjacent inflorescences. The vertical lines show the expected proportions and in (**d**), the average expected proportion is shown, since the expected differed in individual trials and ranged from 0.31 to 0.45.

Chapter 3: Cape Proteaceae communities are structured by competition and facilitation through shared pollinators and interspecific pollen transfer

Abstract

Pollinators may contribute to structuring plant communities through competitive and facilitative interactions between coexisting plants. This can be tested by investigating the distribution patterns of pollination-related traits. We investigate the distribution patterns of pollination syndromes and style lengths in the Proteaceae of the Cape Floristic Region, South Africa, using Protea Atlas Project data. The patterns of co-occurrence within major genera (*Protea*, *Leucadendron* and *Leucospermum*) and pollination syndrome groups (bird-, insect-, non-flying mammal- and wind-pollinated) are also tested separately. Null models were used to determine whether patterns of functional traits are significantly non-randomly distributed. Patterns were analysed in small (500m diameter plots) and large (8 x 8 km grid cells) communities. The dataset with 334 species assembled in 28 479 communities was spatially autocorrelated, necessitating the use of a null model that maintains the spatial structure. Proteaceae species that share pollination syndromes and have similar style lengths tend to co-occur less often than expected by chance. This suggests that pollination competition contributes to structuring these communities. Pollinator sharing is reduced by using different pollen vectors and interspecific pollen transfer may be avoided by differential style lengths, which corresponds to the use of different pollen placement sites. Co-occurring congeneric species often have different pollination syndromes, but have more similar style lengths than expected by chance. Within pollination syndrome groups, patterns of style length often depend on the spatial scale. In conclusion, pollination niches strongly affect Proteaceae communities through both facilitative and competitive interactions. Although the family as a whole appears to be structured mainly by competitive interactions, both facilitation and competition are actually operating on congeneric species. By investigating community assembly of a plant family across

a biome, we show that patterns detected at the family level may be the result of different processes operating at lower taxonomic and functional levels.

Introduction

Plant community composition is the result of a number of filtering processes that determine which species can colonise and persist in a community (Götzenberger *et al.* 2012). Successful coexistence often requires species to utilize different resources or be able to share limited resources through, for example, temporal segregation. Similar to the abiotic niches that co-occurring species compete for, plants must also find a suitable pollination niche to be able to persist in a community (Sargent & Ackerly 2008).

Species that co-occur may affect each other positively or negatively through interspecific interactions. A plant's pollinator attraction can be facilitated by another species and its seed set increased (Ghazoul 2006; Tachiki, Iwasa & Satake 2010). Species with such positive effects on each other are more likely to occur together (Sargent & Ackerly 2008). On the other hand, competition for the services of pollinators can reduce plant species' reproductive fitness (Bell, Karron & Mitchell 2005). For this reason, species with different pollination niches may have a better chance of coexisting successfully than species that have to share these pollinator resources (Pauw 2013).

The pattern of distribution of functional traits within and among communities gives insight into the processes that govern community assembly. Therefore, to understand the effect of pollination on community structuring one can analyse the distribution patterns of pollination-related traits, such as pollination syndrome and pollen placement sites (Sargent & Ackerly 2008). Facilitation among species would result in the clustering of similar traits in the same communities (Callaway 1995). This pattern can also arise when a pollinator acts as a biotic filter and only species adapted for the dominant pollinator can persist in a community (Pellissier *et al.* 2010). In contrast, competition would produce an overdispersed pattern, with low levels of co-occurrence of similar traits.

Null models are often used to detect non-random structure in the trait composition of communities (Gotelli & Ulrich 2012). Over the years of using this technique there has been refinement in how the spatial scale and randomization method should be chosen (Gotelli & Ulrich 2012). However, community assembly tests have mostly been conducted on small datasets due to the challenges of obtaining such data. Large datasets are becoming increasingly available, but also pose new problems. Community data collected over large spatial scales will most likely have some degree of spatial autocorrelation (Gotelli & Ulrich 2012) because of the spatial coherence of species' ranges. In such cases, communities are not independent of each other, as assumed in most null models. Consequently, models that do not consider the spatial coherence of ranges may create fragmented distribution ranges and violate assumptions. As yet, there are a lack of models that can satisfactorily deal with spatial autocorrelation in large datasets containing continuous and categorical variables.

A plant family whose communities are potentially influenced by pollination niches is Proteaceae with its variety of pollination modes. Proteaceae is one of the dominant elements of fynbos vegetation, found in the Cape Floristic Region (CFR, South Africa). We expect pollinators to play a significant part in the community assembly of Proteaceae species due to the variety of distinct pollination modes found in this group; bird-, insect-, non-flying mammal- and wind-pollination. In addition, interactions with pollinators may be particularly important in this group, because most species are non-sprouters that depend on seed set for recruitment after regular fires (Cowling & Lamont 1998). Furthermore, the pollination mechanism of these flowers provides the potential for species to easily diverge in their mode of pollination. Flowers have a much reduced perianth and the tip of the style presents pollen before it matures into a stigma (Rebelo 1995), ensuring accurate pollen placement. Thus, style length indicates very closely where pollen placement will be and therefore any difference in style length between species will likely lead to reduced interspecific pollen transfer (Miyake & Inoue 2003) and pollinator sharing. As a result, the extent of negative effects (competition) between species can be approximated as the difference in their style lengths (Armbruster, Edwards & Debevec 1994). Another benefit of this trait is that style length may be a more accurate measure of pollinator use than pollination syndromes. This is necessary since specialization within a syndrome group may occur, such as species specializing for long-billed bird-pollination (Geerts & Pauw 2007). Some *Aloe* species are able to place pollen on different body parts of sunbirds due to their different style lengths and flower orientations and this reduces interspecific pollen transfer (Botes, Johnson & Cowling 2008). In *Leucospermum* species, style length can be used to some extent to predict which functional pollinator groups would be important to a species (Johnson 2015).

The pollination resource use of Proteaceae species can thus be described in at least two ways: pollination syndromes (the pollinator type it uses) and style length (which determines pollen placement site). An overdispersed pattern of pollination syndromes would indicate spatial niche segregation. On the other hand, clustering of pollination syndromes may be a result of the benefit of collective pollinator attraction. Another possible community pattern is overdispersion of style length differences. This may be an indication of avoidance of interspecific pollen transfer by species sharing a pollinator (Armbruster *et al.* 1994; Muchhala & Potts 2007), or a more subtle subdivision of syndromes into, for example, large and small insects or large and small birds. Clustering of species with similar style lengths is not beneficial, but may occur if interspecific pollen transfer is prevented in other ways.

The Protea Atlas Project database provides the information needed to determine whether Proteaceae communities are structured in terms of pollination niches. The dataset contains 334 species assembled in 28 479 communities which are distributed over an area of 8000 km^2 (Rebelo 1995). Since this dataset suffers from spatial autocorrelation, we use two null models; one that does not maintain the level of spatial autocorrelation in the dataset and one that does. We assess trait distribution patterns at two community sizes and attempt to answer the following questions: (1) is syndrome non-randomly structured, (2) is style length non-randomly structured and (3) do the patterns differ for separate genera and for each syndrome group?

Methods

Study system

The distribution data of Proteaceae species in the Cape Floristic Region were extracted from the Protea Atlas Project database. These data were collected from 1991 – 2002 with the aim of covering all areas within the Cape Floristic Region in which Proteaceae plants occurred (Rebelo 2006). The communities were grouped into 29 fynbos regions (eg. Agulhas, Cederberg, Langeberg) measuring between 168 and 17523 km^2 in size, based on the Centres of

Endemism of the Proteaceae in the Cape Flora (Rebelo & Siegfried 1990), and the models were run on each region separately. These regions are often delimited by dispersal barriers such as deep valleys and areas of non-fynbos vegetation.

All species for which sufficient data are available were included in the analyses. This includes 334 perennial, woody species of the genera *Aulax*, *Brabejum*, *Diastella*, *Leucadendron*, *Leucospermum*, *Mimetes*, *Orothamnus*, *Paranomus*, *Protea*, *Serruria*, *Sorocephalus*, *Spatalla*, and *Vexatorella*. The species were categorised into pollination syndromes (Table 3.1) based on pollinator activity records in the Protea Atlas database (Rebelo 2006), but this was also updated based on recent literature (Steenhuisen et al. 2012; Johnson 2015). The pollination syndrome classifications of Proteaceae have thus far proven to be correct (Hargreaves, Harder & Johnson 2012; Johnson, He & Pauw 2014; Welsford, Midgley & Johnson 2014; Johnson 2015), with some exceptions in non-fynbos proteas (Steenhuisen et al. 2012). The style length of each species was used as an independent measure of pollinator use. The average (of reported minimum and maximum) style length for each species was obtained from field guides (Rebelo 1995), taxonomic revisions (Williams 1972) and measurements of specimens in the Compton herbarium (Cape Town, South Africa).

A methodological constraint is that the analyses uses species-level data of style lengths for population-level analyses, thus ignoring differentiation between populations and possible community-level character displacement. However, most species have a small distribution range and show little variation, thus variation between populations is much smaller than between species. An example of the most extreme variation is presented by the unusually widespread *Protea repens*, with a style length range of 70 – 90 mm. In cases such as this, the use of species-level data will bias the outcome against our expectation of a non-random pattern.

Community size

The community patterns were analysed for two community sizes. Firstly, each 500 m diameter circular plot recorded by the Protea Atlas Project is considered to be a small community containing populations of different species. The average number of species in these small communities was 4.27 (range: 1-20). Secondly, large communities were created by dividing the whole biome into 8 x 8 km grid cells. To ensure that these grid cells were sufficiently represented by plot data, cells that contained < 20 plots were excluded (median no. of plots per grid cell = 26). The list of unique species in a cell was taken to constitute the community. Thus duplicate populations were removed. The average number of species in large communities was 17 (range: 3-51). The Swartland Islands region of endemism was excluded because it contained an insufficient number of large communities. At this larger spatial scale, species may interact via birds that transfer pollen over large distances. Species interactions at the larger spatial scale are rarer, but frequent enough to be relevant in evolutionary time scales. Thus, analyses at this scale test whether communities are structured by reinforcement.

Taxonomic and functional groups

To test for non-random patterns of co-occurrence within genera, we repeated the analyses, this time including only *Protea* species, *Leucadendron* species or only *Leucospermum* species. The datasets for the other genera of Proteaceae were too small to analyse. Furthermore, the behaviour of a particular pollination syndrome group could drive community structure. Therefore, we also analysed the style length patterns of bird-, insect-, non-flying mammal- and wind-pollinated species separately.

Community pattern analyses

Metrics

Firstly, we defined the pollination niche as the pollination syndrome of a species. The test statistic was calculated as the total number of species sharing a niche. Secondly, pollination niche was defined as a species’ style length. We used two widely used and robustly tested metrics: SDNDr (Standard Deviation of Neighbour Distances, corrected for range) and variance (Kraft & Ackerly 2010; Aiba *et al.* 2013). SDNDr is useful for detecting overdispersion in the presence of filtering (Cornwell & Ackerly 2008). It detects a pattern that is created when all species in a community have diverged to avoid competition. The standard deviation of neighbour distances is zero when species are spaced evenly along the niche axis, within the limits set by habitat filtering. In addition, we also developed a metric that measures the degree of niche overlap as the average style length difference between all species pairs. This metric is similar to that used by Muchhala & Potts (2007), but differs in calculating the overlap between all species pairs in a community, rather than only nearest neighbours. In contrast to SDNDr, this metric will detect a pattern when there is only one or a few species that have diverged from other co-occurring species. Style length was logged before calculation of variance and style difference because we expect competition to increase exponentially with trait similarity (Fayle *et al.* 2015).

Null models

Two null models were used, Complete Spatial Randomness Model and Spatial Autocorrelation Model. The plots with single species were included during analyses, since they form part of the pattern.

Complete spatial randomness model

This model is based on Waterman *et al.* (2011) and essentially randomizes the functional traits among communities in the region. This is a very commonly used model. Null communities were created by randomly sampling species from the regional species pool, weighted by their frequency, and assigning them to communities. Co-occurrence of different populations of the same species was prevented. The exact number of species per community and the approximate ubiquity of each species in the region were conserved, such that rare species remain rare. This method, however, changes the spatial structure of species' distributions, resulting in highly fragmented species ranges and consequently a low level of spatial autocorrelation in species composition across the landscape (Fig. 3.1). Thus, while on average 37% (19-63%) of communities in a region are unique in the observed data, the randomized data contain significantly more unique communities.

Spatial autocorrelation model

One of the solutions proposed for preserving spatial autocorrelation is the "random patterns test" (Roxburgh & Chesson 1998). It approximately maintains the spatial pattern of each species, but randomization possibilities are limited when this is applied to species rich datasets and therefore it was insufficient for our purposes.

Our spatial autocorrelation model randomizes the traits among species, maintaining distribution ranges. A list of the species occurring in the region is created and then traits are shuffled among species by sampling without replacement from the trait pool. All populations of a species are then assigned the same "new" randomly selected trait. Thus, the number of species that share a particular trait remains the same, but the frequency of the trait in communities across the region is changed. This model maintains distribution patterns without fragmenting them and maintains community diversity (Fig. 3.1). The same amount of spatial autocorrelation in community composition is present in the original and randomized data.

Note that, in both models, when genera and syndrome groups were analysed separately, the pool of traits to be randomized included only that of the subgroup being analysed.

Statistical analyses

For every community, the observed metric was compared to the frequency distribution of the metrics of 999 null communities. A one-tailed test was used to determine whether observed SDNDr values are significantly higher than the upper 5 percentile. Since the other two metrics can detect overdispersion and clustering, we used two-tailed tests to determine whether the observed metric is significantly lower or higher than the lower or upper 2.5 percentile, respectively. Then, to determine if the Cape as a whole is structured, a Wilcoxon test was applied to the effect size values (observed value minus the mean of expected, divided by the standard deviation of expected) of all communities to establish whether it differs significantly from an expected distribution around zero. If significant, the dominant pattern was taken to indicate the overall Cape pattern. The Wilcoxon test may detect an overall significant pattern even if very few or no communities are significantly structured according to the one- and two-tailed tests.

Vegetative traits

The distribution of traits in a community can be non-random, either because these traits directly influence community membership, or because they are correlated with other traits that determine community membership. Firstly, to test whether style length is independent from the pollination syndrome categories, we tested the relationship between these variables. Secondly, style length may be related to other vegetative traits, which would make it unclear which traits are actually producing the observed patterns. We tested for correlations of style length with plant height, leaf length and resprouting ability. Information on these variables was obtained from the protea field guide (Rebelo 1995). The means of the reported maximum and minimum lengths were used. Data on the resprouting ability were only available for 246 species. In all these analyses the residual variance was not constant and therefore we used a Generalized Least

Squares test with constant variance structure (for categorical variables) or with a fixed variance structure (for continuous variables) (Zuur *et al.* 2009).

Results

Community patterns

There was mostly agreement in the results of the two models and two spatial scales (Table 3.2), therefore only the dominant patterns are described here. The SDNDr metric often could not detect a pattern (Table S3.1) and this is likely because it is only sensitive to competition in the presence of filtering. In the analyses of different taxonomic groups, the Complete Spatial Randomness (CSR) model on small communities often found different results to the other models, suggesting that it is less reliable, or not suited for analyses at small scales.

Pollination syndromes of Proteaceae species are randomly distributed in large communities, but overdispersed in small communities. Style lengths were overdispersed at both community sizes according to all metrics, except the SDNDr metric which was only significant in the CSR model at small scales. The *Protea* communities are overdispersed in terms of pollination syndrome and clustered in terms of style length. Pollination syndromes within *Leucadendron* are clustered according to the Spatial Autocorrelation (SAC) model, while the CSR model gives different results for the two community sizes. Style length of *Leucadendron* species show a clustered pattern. *Leucospermum* communities are overdispersed in terms of pollination syndromes. In all models the SDNDr metric detected an overdispersed pattern of style length in *Leucospermum* species. The other metrics detected either no significant pattern or clustering (with the exception of the CSR model). This suggests that both facilitation/filtering and competition mechanisms are acting simultaneously. The lack of a significant overall pattern is in fact due to an almost balanced number of overdispersed and clustered communities (Table S3.1).

The style lengths of co-occurring bird-pollinated species are clustered according to the SAC model at large scale and the other models suggest that it is random according to the SDNDr and log style difference metrics. The variance metric, however, detected overdispersion in these other three models. The variance metric is more likely to detect a significant difference than the style difference metric when there are large evenly spaced differences in the style lengths of species. Thus, the style lengths of these species are overdispersed in the sense that most of the species differ from each other, and there is not just one species differing greatly from the others.

All the models, except one, suggest that style lengths of co-occurring insect-pollinated species are clustered. Non-flying mammal-pollinated species show clustering of style lengths in small communities, but at large scale it is randomly distributed. Three models find no significant pattern in the style lengths of wind-pollinated species, but the SAC model found overdispersion at small scales. Note that no results could be obtained for SDNDr in the small scale models due to small sample sizes.

Vegetative traits

Style length differed significantly between pollination syndrome groups ($F^3_{334} = 212.467$, $P < 0.001$), but there is overlap between groups (Fig 3.2.a). Bird-pollinated species showed the most variation in style lengths and this overlapped mostly with non-flying mammal-pollinated species (Fig. 3.2.a). In contrast, wind-pollinated species have the least amount of variation and the mean is close to that of insect-pollinated species (Fig. 3.2.a). The style lengths of *Protea* and *Leucospermum* species overlap a lot, while the style lengths of *Leucadendron* species are shorter (Fig. 3.2.b). Style length is significantly positively correlated with plant height ($F^1_{336} = 5.602$, $P = 0.019$, Fig. S3.1A) and leaf length ($F^1_{336} = 115.444$, $P < 0.001$, Fig. S3.1B), but there is clearly still a lot of unexplained variance. Likewise, style length differed significantly between resprouting (N = 45) and non-sprouting species (N = 146) even though there is overlap in style lengths ($F^1_{224} = 6.130$, $P = 0.014$, Fig S3.1C).

Discussion

Across the fynbos biome, co-occurring Proteaceae species tend to have different pollination syndromes (in small communities) and different style lengths. Thus, competition for pollination plays an important role in the assembly of these communities. By using different pollen vectors, fewer plant species are competing for the same pollinator. And those species that do share pollinators, can reduce heterospecific pollen transfer through differential style lengths that enable species to use different pollen placement sites on the same pollinator (Johnson 2015). The random assembly of pollination syndromes in large communities may suggest either that species do not interact at this spatial scale or that differential style lengths are sufficient to avoid negative interactions.

The SAC model is an important tool to analyse large datasets where spatial structure may affect species associations. Spatial autocorrelation can be caused by dispersal limitations and environmental gradients (Fuller & Enquist 2012). We suspect that both play a role in Proteaceae distributions since the fynbos is a particularly heterogeneous habitat (Cowling & Richardson 1995) and dispersal distances (facilitated by wind, rodents or ants) are relatively limited. Rodent dispersers can move seeds up to 5 m from the parent plant (Midgley *et al.* 2002), although long-distance dispersal may be possible (Rusch, Midgley & Anderson 2013). The maximum distance dispersed by wind differs among species from 3 m to 59 km (Schurr *et al.* 2005). In fact, it has been shown that colonization ability partly explains the extent to which Proteaceae species fill their potential range (Schurr *et al.* 2007). Therefore, we focus the interpretation of the results for the taxonomic and functional groups on the SAC model results.

When analysing the three largest genera separately, the SAC model reveals that the genera show different community patterns and are thus perhaps structured by different processes. Co-occurring *Protea* species seem to avoid competition by using different pollinators. The patterns that we observed do not take abundance into account, but the effect of community composition on *Protea* is in fact dependent on plant density. The seed set and lifetime fecundity of the animal-pollinated *Protea repens* initially increases with increasing Proteaceae community density, but then declines at high densities (Nottebrock, Esler & Schurr 2013). Therefore, our study appears to be detecting patterns of high density *Protea* communities. Ninety percent of the *Leucadendron* species included in this study are insect-pollinated (Table 3.1) and it has much less variation in style length compared to the other genera (Fig. 3.2b). The clustering of pollination syndromes within *Leucadendron* may be the result of pollinator facilitation, since several insect pollinators visit multiple *Leucadendron* species (Welsford *et al.* 2014). The *Leucospermum* species also avoid sharing pollinators. The results suggest that these species have diverged their style lengths despite some filtering mechanisms acting upon this trait. Different style lengths cannot only allow species to use different pollinator subgroups (insects with short- and long mouth parts), but can even enable them to place pollen on different body parts of a single pollinator species (body feathers and crown feathers of birds; Johnson 2015).

Bird-pollinated species co-occurring in small communities tend to have different style lengths. This is the spatial scale at which birds are most frequently foraging and since they do not show perfect flower constancy behaviour (Carlson & Holsinger 2013; Heystek *et al.* 2014; Johnson 2015), the plants need a mechanism to prevent heterospecific pollen transport. Different style lengths in *M. fimbriifolius* and *L. conocarpodendron* facilitate placement of pollen on the throats and crowns of birds, respectively (Johnson 2015). The clustered style lengths in large communities may indicate pollinator filtering by the dominant bird pollinator in the landscape (long- or short-billed birds).

The group of insect-pollinated species is the largest functional group and include species from all but one genus of Proteaceae (Table 3.1). The results show that these species tend to have similar style lengths where they co-occur. This is a large categorical group that contains several pollination syndromes; for example beetle, bee and fly pollination (Welsford *et al.* 2014; Johnson 2015). Thus, although co-occurring species may have similar style lengths they are potentially not using the same pollinators. This group also includes species that are nocturnal (Johnson 2015) and some that attract specific pollinators through specialised scents (Steenhuisen et al. 2012).

The non-flying mammal-pollinated species showed distinctly different patterns at the two spatial scales. At large scales, their style lengths are randomly distributed because almost all of them have small non-overlapping ranges, often restricted to specific soil types (Wiens 1983). In the few instances where their ranges do overlap, the species seem to have similar style lengths. However, pollinator competition is prevented by sequential flowering (Wiens 1983).

Style lengths in the wind-pollinated species (9 *Leucadendron* species, Table 3.1) were randomly distributed at large scales, but unexpectedly, locally co-occurring species had different style lengths. These species have very little variation in their style lengths (Fig. 3.2). Yet, there is the possibility that the reproductive structures can create an airflow environment that promotes conspecific pollen receipt (Friedman & Barrett 2008). 80% of pollen found on the stigmas of *Leucadendron rubrum* was its own, even in the presence of other flowering wind-pollinated species (Linder & Midgley 1996).

Several other studies that have used null models to investigate plant community assembly in relation to pollination found traits to be overdispersed among communities (Armbruster *et al.* 1994; Muchhala & Potts 2007; Eaton *et al.* 2012). Most were limited in the number of communities and species analysed, with the number of communities ranging from 18 to 236 and the species from 19 to 116, and most included only the species of one genus. Likewise, a study on Ericaceae, another dominant fynbos family, found that competition for pollination contributed to structuring *Erica* communities (Heystek & Pauw 2014). One of the few studies that have explored pollination niche effects with larger datasets was the study by (Pellissier *et al.* 2010). Their study included 771 species (of several different families) in 870 communities and, in contrast to our study, found clustering of functional types.

Although the style lengths of the protea species were correlated to their plant height, leaf length and resprouting ability, there is a lot of variation left unexplained (Fig. S3.1) and these other traits are thus unlikely to cause the patterns we detected. In fact, Potts et al. (2011) assessed community patterns in relation to leaf traits of *Protea*, *Leucospermum*, *Leucadendron*, *Mimetes* and *Aulax* species in two regions. Using a lottery assembly null model, they found that Proteaceae communities are rarely structured by leaf traits. However, it is possible that other unmeasured traits, such as flowering phenology, may play a role.

Co-occurring Proteaceae species tend to have different pollination syndromes and style lengths. While *Leucadendron* communities appear to be structured by facilitation and *Leucospermum* communities appear to be more influenced by competition, *Protea* communities are affected by both interaction types. Within pollination syndrome groups, patterns of style length often depend on the community size. This study shows that both pollination facilitation and competition strongly influences Cape Proteaceae community assembly.

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Table 3.1 Number of species in each Proteaceae genus belonging to each pollination syndrome. This includes only the 334 species included in this study.

	Pollination syndrome			
Genus	**Bird**	**Insect**	**Non-flying mammal**	**Wind**
Aulax		3		
Brabejum		1		
Diastella		9		
Leucadendron		78		9
Leucospermum	28	17	3	
Mimetes	12			
Orothamnus		1		
Paranomus		19		
Protea	39	8	29	
Serruria		47		
Sorocephalus		9		
Spatalla		18		
Vexatorella		4		
Total	79	214	32	9

Table 3.2 Distribution patterns of pollination syndrome and style length in communities of Cape Proteaceae and of some of its genera and functional groups. Patterns were determined at two community sizes by two null models: CSR (Complete Spatial Randomness model) and SAC (Spatial Autocorrelation model). In each case, the pattern for the whole Cape is indicated as significantly clustered (C), overdispersed (O) or randomly distributed (R). See Table S3.1 for sample sizes and statistics.

Taxonomic/Functional group	**Community size**	**CSR**		**SAC**	
		syndrome	**style**	**syndrome**	**style**
Proteaceae	small	O	O	O	O
	large	R	O	R	O
Protea	small	O	C	O	C
	large	O	C	O	C
Leucadendron	small	O	C	C	C
	large	R	C	C	C
Leucospermum	small	O	O	O	C, O
	large	O	R, O	O	R, O
Bird-pollinated	small		O		O
	large		O		C
Insect-pollinated	small		O		C
	large		C		C
Non-flying mammal-pollinated	small		C		C
	large		R		R
Wind-pollinated	small		R		O
	large		R		R

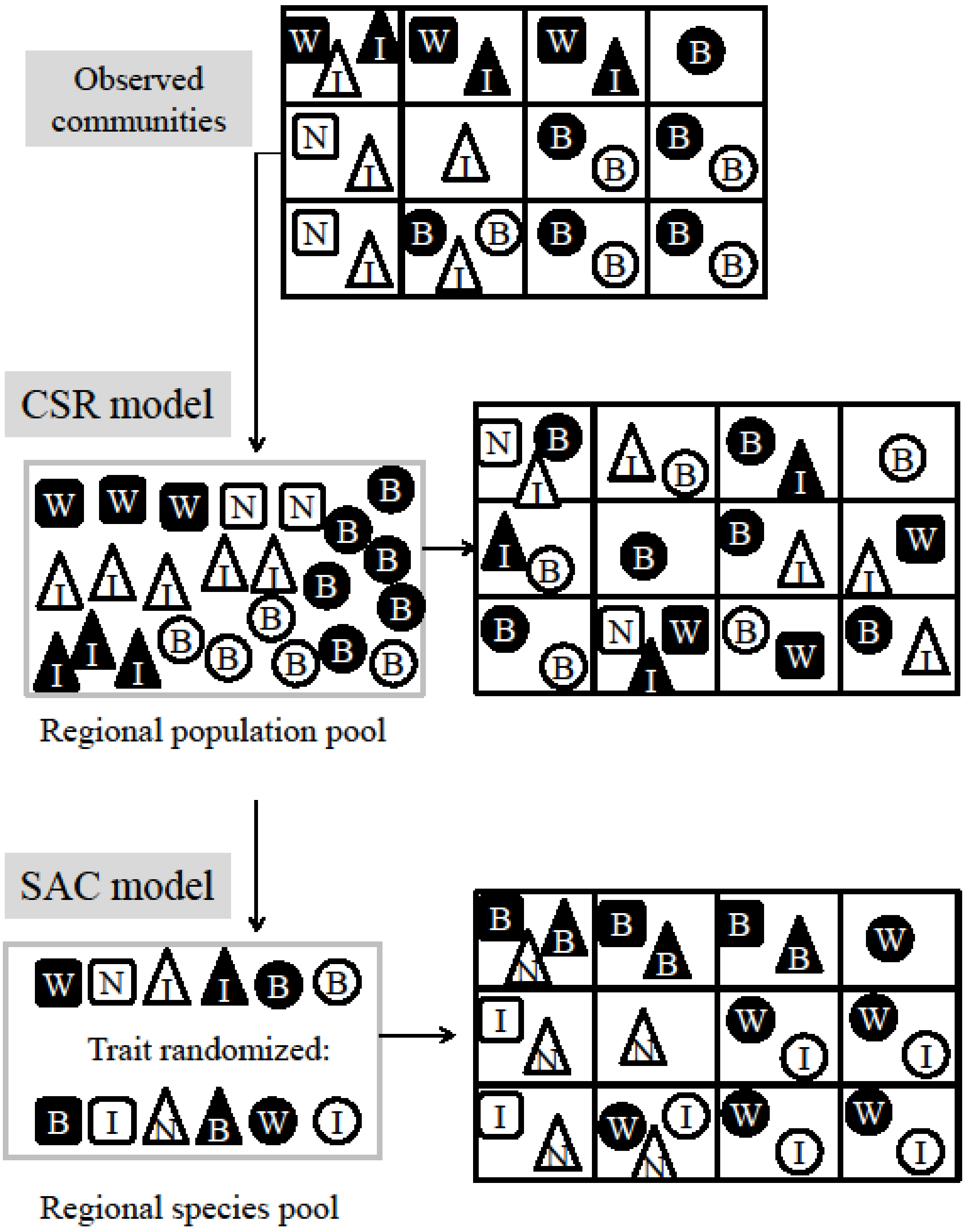

Figure 3.1 An illustration of how the two null models create null communities. Each rectangle is a spatially explicit representation of a region with 12 communities. Different species are represented by different symbols with their pollination syndromes indicated with a B (bird-pollinated), I (insect-pollinated), N (non-flying mammal-pollinated) or W (wind-pollinated). The Complete Spatial Randomness (CSR) model uses the entire regional population pool to randomly assign species to communities. This changes the spatial structure of species' ranges. The Spatial Autocorrelation (SAC) model randomizes traits in the regional species pool, and

then assigns each species its new trait. This maintains the original spatial cohesion and maintains the degree of spatial autocorrelation in the observed data.

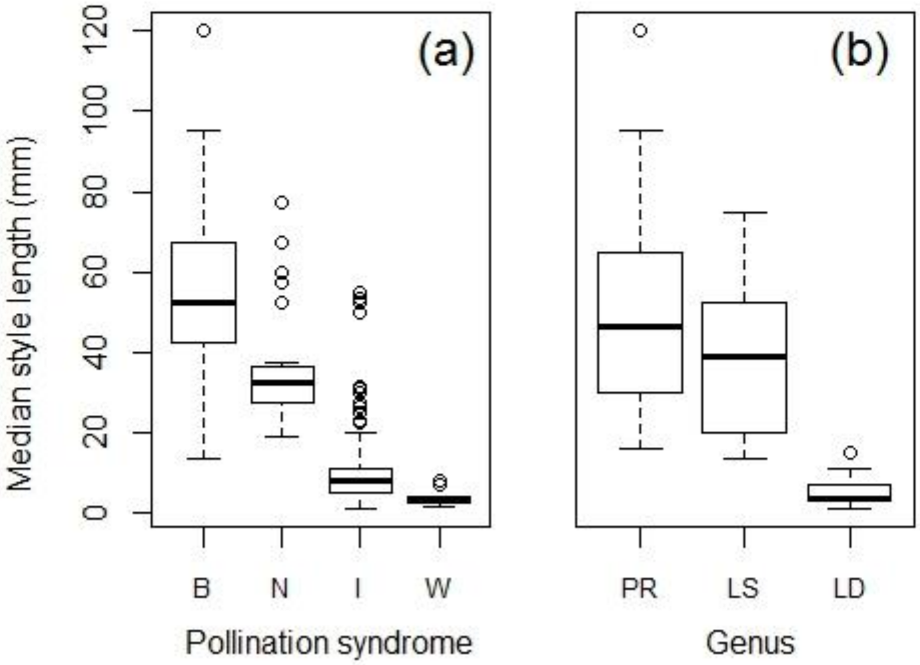

Figure 3.2 Median style length (mm) for Proteaceae species with different pollination syndromes (a): bird (B), non-flying mammal (N), insect (I) and wind (W). Median values are also shown for the three largest genera (b): *Protea* (PR), *Leucospermum* (LS) and *Leucadendron* (LD). See Table 3.1 for sample sizes of each group. The bold line indicates the median, the box the interquartile range, whiskers the ranges and points are outliers.

Chapter 4: The importance of nectar dependence, food availability and dispersal barriers in structuring urban nectarivorous bird communities in Cape Town, South Africa

Abstract

It is recognised that both species and habitat traits may influence the assembly of biotic communities. Determining which traits most strongly affect community assembly will help us understand how communities may change with land-use change, such as urbanisation. Many nectarivorous birds worldwide show a tolerance of urban areas. It is important to determine which factors influence their urban adaptation because this may affect their behaviour and survival and, eventually, the plant species that depend on their pollination services. The degree of urban tolerance of nectarivorous species varies and, thus, some species are classified as urban exploiters (more abundant in developed areas than natural areas), and others only as urban adapters (less abundant in developed areas). We investigated this in the Cape Town metropolitan area of South Africa, a medium city situated within one of the world's biodiversity hotspots that contains a disproportionately large number of bird-pollinated plant species relative to the number of nectarivorous bird species. Information was collected on nectarivorous bird abundances and garden traits for 191 gardens throughout Cape Town through means of a questionnaire, and biological traits of birds were obtained from published literature. We predicted that community assemblages would be best predicted by versatility in habitat use and in diet (biological traits) and food sources and distance to natural habitat (garden traits). A comparison of bird abundances in gardens and in the nearest protected area suggests that nectar-generalist birds were urban exploiters, while nectar-specialist birds were urban adapters. This is likely due to the generalist birds' low dependence on nectar, since nectar dependence was identified as the most important biological trait influencing bird abundances. Their urban adjustment is further facilitated by large vegetated areas in gardens as well as by bird baths. The urban adjustment of nectar-specialist species was facilitated by sugar water feeders and indigenous plant abundances. Abundances of all nectarivorous bird species, but not their richness, were negatively related to the distance to nearest natural habitat. In conclusion, nectar-generalist species dominated South African urban nectarivorous bird communities. Though some biological traits and dispersal barriers seem to limit urban adaptation by nectar specialists, certain garden traits could facilitate this adaptation.

Introduction

Community assembly can be influenced by species traits as well as habitat traits. When habitat patches have different abiotic and biotic conditions, they may favour different species that have biological traits adapted to different habitat conditions (Cornwell & Ackerly 2008; Barnagaud *et al.* 2014). Land-use change is removing certain habitats, but also creating new habitats and thus generating new ecological communities (Pautasso 2007). One of the rapid and widespread land-use changes currently occurring is urbanisation and it is evident that this dramatic change affects biotic communities (Tryjanowski *et al.* 2015b; Verma & Murmu 2015). Some species adjust to the new urban environment and are not negatively affected by it. This adjustment is a process involving, at least, the ability to exploit the resources in urban areas (Blair 1996) and to breed in these areas (Møller 2009). In order to understand how urbanisation will affect biotic communities, we must first determine which species and habitat traits facilitate and prevent urban adjustment.

Many bird species have adjusted to urban environments (Evans, Newson & Gaston 2009; Conole & Kirkpatrick 2011) and because of birds' size and conspicuousness, as well as their popularity with humans, the responses of birds to land-use change can be followed more easily than many other smaller organisms. However, African urban bird ecology requires investigation, since there have only been four studies on this subject on this continent (Ortega-Álvarez & MacGregor-Fors 2011). In particular, attention needs to be paid to birds involved in important mutualistic relationships, since impacts on them may have cascading effects on ecosystems.

Avian nectarivores are a guild involved in pollination mutualisms with plants. It is thus important to determine what affects their urban adjustment. Pollinator foraging and dispersal behaviour and the vulnerability of mutualisms will determine how pollination systems are affected by land-use changes (Phillips *et al.* 2010). The most sensitive species may undergo population declines or extinction, while other species may experience profound ecological and evolutionary changes resulting from adaptation to urban environments. A first step in understanding these dynamics is to determine what biological traits, as well as the traits of anthropogenic habitats such as gardens, affect urban bird community assembly.

Bird species' responses to urbanisation differ greatly. Bird species have been classified as urban avoiders, adapters and exploiters based on their relative abundances along an urbanisation/disturbance gradient (Blair 1996). Species that are most abundant in the most natural areas, moderately developed areas and the most developed areas are classified as urban avoiders, adapters and exploiters, respectively (Blair 1996). Likewise, if birds are not particularly attracted to or averse to urban areas, then we expect their abundances in urban areas to reflect those in natural habitat around cities (Kremen *et al.* 2007; Dale, Lifjeld & Rowe 2015). Several studies have shown that different foraging guilds fall into different urbanisation response categories, and nectarivorous birds appear well capable of adapting to and exploiting urban areas. It has been found in Australian urban areas that these birds are more likely than birds in other guilds to move from natural habitats into high density housing areas (Hodgson, French & Major 2007). In fact, the most abundant native species in Australian urban areas are nectarivorous birds (Parsons, French & Major 2003).

Nectarivorous birds can be classified as nectar specialists (primarily dependent on nectar) and nectar generalists (occasionally feeding on nectar) (Johnson & Nicolson 2008; Brown, Downs & Johnson 2009). These groups have shown differential responses to urbanisation in some regions. Evidence from North America suggests that both nectarivorous specialists (e.g. Anna's Hummingbird *Calypte anna*) and generalists (e.g. European Starling *Sturnus vulgaris* and Hooded Oriole *Icterus cucullatus*) are urban adapters (Blair 1996). Similarly, nectarivorous specialist species in Argentina appear to be urban adapters, since they were found at highest abundances in suburban areas and less densely human-populated peri-urban areas (Leveau 2013). In Australia, most of the nectar-specialist and -generalist species are urban avoiders, although some are exploiters (Conole & Kirkpatrick 2011). Nectar-specialist sunbirds in India show no significant differences in abundance in wildlands, suburbia and urban areas, suggesting that they are urban adapters (Verma & Murmu 2015). On the other hand, some of the nectar generalists in India are urban exploiters while others are adapters (Verma & Murmu 2015). Thus, it appears as if nectar-specialist birds are most often urban adapters, while nectar-generalist species show a range of responses.

Besides foraging specialisation, which other biological traits are important in predicting the composition of urban bird communities? Firstly, the degree of habitat specialisation tends to allow different levels of tolerances. Habitat specialist species may suffer greater physiological stress from intensive anthropogenic land use than habitat generalists (Deikumah, Mcalpine & Maron 2015). Furthermore, habitat generalists are more likely to be behaviourally innovative, having the ability to invent new behaviours (Overington *et al.* 2011), which may enable them to survive in novel habitats such as human settlements. High adult survival rate and high annual fecundity have been found to characterise urban birds of the Western Palearctic (Møller 2009). Nests located high above the ground or in cavities appear to facilitate urban adaptation (Croci *et al.* 2008; Conole & Kirkpatrick 2011). Lastly, diet may also affect birds' adaptability: omnivores may easily adapt to highly urbanized areas and nectarivores could adapt to suburban areas, whereas granivores might only adapt to agricultural areas (Leveau 2013).

Variability in habitat traits may also influence urban bird community assembly due to particular functional groups responding to different habitat traits and, in particular, garden traits. Most evidence of garden trait influences on nectarivorous birds come from studies in Australia. The proximity to remnant natural habitats did not influence bird community composition in urban areas (Parsons *et al.* 2003). However, habitat corridors and vegetated areas may facilitate birds' movement through an urban landscape (Wood 1993). A less favourable matrix around gardens, such as high building densities, may limit the dispersal of birds into urban landscapes (Evans *et al.* 2009).

On the other hand, greater shrub and canopy cover at the urban edge encourage the movement of birds into urbanised areas (Hodgson *et al.* 2007). The increase in abundance of honeyeaters in an urban Australian nature reserve was associated with abundant flowering plants (Wood 1993). White *et al.* (2005) found nectarivores mainly in parks and in streets that are dominated by native vegetation, whereas alien vegetation supported lower bird species richness and abundances. In particular, nectarivorous birds in urban areas visit both native and exotic garden plants, but they prefer the former (French, Major & Hely 2005). Likewise, urban birds in Israel (Paker *et al.* 2013) and Tasmania (Daniels & Kirkpatrick 2006) prefer native plants.

Urban landscapes offer novel combinations of risks and benefits. Novel predators such as cats and dogs may deter birds from gardens, while supplementary resources may attract them. A study in gardens in Israel found that human-associated predators such as dogs reduce bird abundances but that cats had no effect (Paker *et al.* 2013), while an Australian study found that neither cats nor dogs affect bird abundances (Parsons *et al.* 2006). Free-ranging domestic cats in Cape Town, South Africa, were reported to prey on birds (Morling 2014) and cats close to urban edges show higher predation rates than cats closer to the centre of the urban area (George 2010). One may expect bird baths to be attractive, but water availability was found to be of little importance in Tasmanian gardens (Daniels & Kirkpatrick 2006). On the other hand, supplementary feeding can increase bird abundances in urban areas (Evans *et al.* 2009), since the feeders contribute to reducing birds' sensitivity to human disturbance (Møller *et al.* 2015). Experimental feeding of bread and seed to birds in New Zealand changed the community structure and caused large increases in granivores (Galbraith *et al.* 2015). As for nectarivores specifically, hummingbirds are attracted to suburbs with sugar water feeders (Inouye *et al.* 1991; Arizmendi *et al.* 2007).

Cape Town is one of South Africa's largest cities and is situated in the Cape Floristic Region, one of the world's smallest biodiversity hotspots (Myers *et al.* 2000). The fynbos biome surrounding this city contains more than 200 plant species that rely on birds for pollination (Rebelo *et al.* 1984). The lowlands in this area have been extensively urbanised, but most of the mountains are currently protected and conserved (Rebelo & Siegfried 1990). Five nectar-specialist bird species and at least nine nectar-generalist species occur in the larger Cape Town area. This group of nectarivorous birds shows some functional trait variability: their longevity varies from 6-20 years, they all nest above the ground (in shrubs, trees or any high substrate) and some species use only one habitat type, while others may use up to eight types (Hockey *et al.* 2005). The direct effects of urbanisation in this region have only been investigated for nectar-specialist species. These species showed differential responses to the proximity of natural habitat (Pauw & Louw 2012). The causes of the negative impacts of urbanisation identified in the fynbos-endemic nectarivore Cape Sugarbird *Promerops cafer* are still uncertain. Sugarbirds living closer to urban areas or occurring in large urbanised sites show signs of low body condition and greater incidences of fluctuating asymmetry, tarsal disease and stress bars on feathers (Mackay 2014). These indices of stress, however, did not appear significantly linked to adjacent human population density (Mackay 2014). There is thus a need to determine the important factors facilitating urban adaptation of these birds.

In this study, we assess garden bird assemblages in Cape Town to address three questions: (1) Can specialist and generalist nectarivorous birds be classified as urban exploiters or urban adapters? (2) Which biological traits of nectarivorous birds most affect the assembly of urban bird communities? (3) Which garden traits are the most important predictors of specialist and generalist nectarivore community assembly?

Firstly, we expect nectar-generalist birds to be classified as urban exploiters and nectar specialists as urban adapters. Secondly, we predict that versatility in habitat use and diet will be the most important biological traits, while longevity and nest site will be less important. Thirdly, we predict that indigenous garden plants, sugar water feeders and distance to natural habitat will be the most important predictors of nectar specialist bird communities, but that introduced plants, vegetated area size, other bird feeders, bird baths, carnivorous pets and the surrounding landscape will be less important. Lastly, we expect that the communities of nectar-generalist species will be best predicted by the presence of sugar water feeders and other bird feeders, and that the other factors will be of little importance.

Methods

Data collection

The study was focused on the Cape Town metropolitan and adjacent Drakenstein Municipal areas, located in the southwest of South Africa (Fig. 4.1). The study area spans 11027 km^2. To gain information on garden characteristics and bird assemblages, hard copy and online questionnaires (Supplementary Information B) were distributed to members of two urban bird clubs and other garden owners in the study area. The questionnaire was aimed at citizens knowledgeable about bird and plant identification, but pictures were also provided to avoid confusion of names. A total of 193 complete responses were returned. No information was gathered about the age of the garden or the intensity of respondents' observations.

We listed 10 nectarivorous bird species in the questionnaire, and respondents reported the maximum number of each seen at one time drinking from sugar water feeders or flowers (applicable all year round). This included five nectar-specialist species (*Promerops cafer*, *Anthobaphes violacea*, *Cinnyris chalybeus*, *Nectarinia famosa* and *Chalcomitra amethystina*) and five nectar-generalist species (*Zosterops virens*, *Pycnonotus capensis*, *Ploceus capensis*, *Sturnus vulgaris* and *Onychognathus morio*) (Table S4.1). Only *S. vulgaris* is an introduced species. Birds were classified as specialist nectarivores if nectar was their main food source (Hockey *et al.* 2005), and the rest were classified as generalists.

Response variables

To test whether birds are urban adaptors or exploiters, we compared their abundances in gardens with their abundances in the nearest natural protected area. We used data from the Birds in Reserves Project, coordinated by the Animal Demography Unit (University of Cape Town, http://birp.adu.org.za/site_list.php?prov=WC). These data provide reporting rates for species (an estimation of species abundance) in nature reserves/national parks (Underhill, Oatley & Harrison 1991). Sufficient data were only available for the Table Mountain National Park (31 data collection days). Reporting rates for the study species, an index of abundance relative to other species in the bird community (Underhill *et al.* 1991), were extracted and related to their total abundances in the gardens for which this park was the nearest protected area (95 gardens, Table S4.2). The abundance in gardens was log-transformed (base 10) due to non-normality and a linear regression was used to determine whether abundances in the national park predict abundances in gardens. The Amethyst Sunbird *Chalcomitra amethystina* was excluded from this analysis, since it is a recent immigrant to the study area and thus its abundances were judged not comparable to the other resident species.

In order to test the effect of biological traits of birds on garden bird communities, we calculated the average abundance per garden for each species separately. This was log-transformed due to non-normality. Again, *Chalcomitra amethystina* was excluded from this analysis. A problem with comparing abundances between species in gardens (estimated as the maximum number of individuals of a species seen by a respondent at any one time) is that the abundances of group-foraging species may be inflated. However, the log average abundance is not significantly higher in species that are group foragers (Mann-Whitney U test, U = 13, p = 0.381). Nonetheless, the effect of foraging group size was included in the analysis.

Lastly, to test the effect of garden traits on bird communities, the bird abundances reported in the questionnaires were summarised into four response variables: nectar-specialist bird abundance per garden; nectar-generalist bird abundance per garden; nectar-specialist species richness per garden and nectar-generalist species richness per garden (Table 4.1).

Predictor variables

For the aim of testing biological trait effect, trait data for the nine bird species were extracted from Robert's Birds of Southern Africa (Hockey *et al.* 2005). The following traits were selected based on evidence from literature that they are associated with urban tolerance (Table 4.1, Table S4.2): mean body mass, maximum adult longevity, number of habitats used by a species, nectar rank (the importance of nectar in their diet: 3 = main food, 2 = secondary food or 1 = occasional food), diet diversity (number of food types used), mean annual clutch size and nest site (tree, shrub or adaptable).

To test the effects of garden traits, I used information gathered through questionnaires (Table 4.1). The reported garden locations were used to obtain the distance to, and the type of matrix in between, the nearest protected area for each garden. The locations of gardens were mapped in Google Earth Maps and then combined with maps of the City of Cape Town Biodiversity Network and Drakenstein Critical Biodiversity Areas, compiled by the South African National Biodiversity Institute (http://bgis.sanbi.org/projectsearch.asp?prov=WC). These maps indicate which areas are natural and which are non-natural. The shortest straight line distance (in km) from each garden to the nearest proclaimed protected area of more than 500 hectares, was measured using ArcGIS 10 (ESRI ArcMap 2010). The matrix between each garden and the nearest protected area was also scored as predominantly natural or non-natural based on which land use type covered the most area along the straight line. Respondents also reported the shortest distance (km) from their garden to the nearest vegetated park, greenbelt, river or dam (henceforth referred to as distance to park).

The estimated garden size (in square meters) and percentage of garden comprised of plants (including trees, shrubs and herbs and excluding lawn and hard surfaces) were also reported and multiplied to obtain the size of planted area of a garden. In the questionnaire, we listed 17 locally common garden bird-pollinated plant genera, for which respondents had to report the number of plants in their gardens. This included 13 native genera (*Protea*, *Mimetes*, *Leucospermum*, *Erica*, *Watsonia*, *Chasmanthe*, *Tecoma*, *Strelizia*, *Aloe*, *Kniphofia*, *Leonotus*, *Schotia* and *Erythrina*) and four introduced genera (*Eucalyptus*, *Hibiscus*, *Callistemon* and *Phormium*). For each garden, the total numbers of indigenous plants and introduced plants were then calculated. Respondents also reported the number of cats and dogs in their gardens, as well as the presence of bird baths, supplementary sugar water feeders and other bird feeders (providing seed, fruit or insects).

Data exploration

Response variables were tested for normality with the Shapiro-Wilks test and checked for overdispersed variance to determine the most appropriate regression analyses for each response. Collinearity was tested between explanatory variables (Zuur, Ieno & Elphick 2010) that were concerned with the same question using Spearman rank correlations, Kruskal-Wallis rank sum tests and Pearson's Chi-square tests. Nectar rank and diet diversity were related to each other and to body mass and clutch size (with correlation coefficients > |0.8|). Since this study focusses on nectarivorous birds, it is biologically more meaningful to include nectar rank in analyses. Regarding garden traits, several variables were related (Table S4.3), but these were all weak relationships (correlation coefficients < 0.5) and thus all variables were included in the analyses. All data exploration and analyses were conducted in R software (R Development Core Team (RDCT) 2006).

Biological traits of birds

In order to determine the best predicting biological traits of bird communities, a model set of ten models was created with different combinations of the four selected biological traits. Each model was tested with a linear mixed-effects model that included the largest foraging group size of each species (pairs or groups (Hockey *et al.* 2005)) as a random factor . Model performance was assessed with second order bias correction of Akaike Information Criterion (AICc) and models were compared with AICc differences and Akaike weights (Burnham, Anderson & Huyvaert 2011).

Garden traits

The prediction strength of eleven garden traits was tested on the four response variables. A model set with a total of 29 models was created. Models predicting the numbers of birds were tested with negative binomial Generalised Linear Models, because of the overdispersed variance of the count data. Models assessing predictions of the number of bird species were tested with Generalised Linear Models fitted with Poisson error structures due to the non-normality of the count data. Again, models were compared with AICc differences and Akaike weights.

Results

Natural bird abundance

The abundance of species in gardens closest to Table Mountain National Park was not predicted by their abundance in this national park ($t = -0.682$, $p = 0.517$, degrees of freedom = 7). Instead, species abundances in the park seemed to be associated with the degree of nectar specialisation. All but one of the nectar-generalist species had very low abundances in the park, while the specialist species had relatively high abundances (Fig. 4.2).

Biological traits

The model predicting nectar rank effect on the abundance of the nine different species in gardens received the strongest support ($w_i = 0.75$) (Table 4.2). The negative trend ($X^2_1 = 3.220$, $p = 0.072$) shows that species with lower dependence on nectar (*Zosterops virens*, *Pycnonotus capensis*, *Ploceus capensis*, *Sturnus vulgaris* and *Onychognathus morio*) were more abundant in gardens (Fig. 4.3, Table S4.2). Models including nest site were the weakest (Table S4.4).

Garden traits

The effect of garden traits could be analysed for 172 gardens. Numbers of specialist birds are seemingly most influenced by the distance to protected area and presence of sugar water feeders (Table 4.3). The abundance of specialist birds were negatively related to the distance to protected area (Fig. 4.4.a, $z = -3.73$, $p < 0.001$) and positively affected by sugar water feeders (Fig. 4.4.c, $z = 3.684$, $p < 0.001$). The abundance of nectar-generalist birds were best predicted by a model with distance to protected area and the planted area in a garden (Table 4.3). The two best models included the sum of and the interaction between these two predictor variables and had a collective Akaike weight of 0.79. The abundance of generalist birds were also negatively related to the distance to protected area (Fig. 4.4.b, z = 2.986, p = 0.003) and positively related to the size of planted area (Fig. 4.4.d, z = 2.604, p = 0.009). As for species diversity, the top models predicting the number of specialist species barely differed, but the two best models contain the number of indigenous plants (Table 4.3, Fig. 4.4.e). This predictor variable is marginally significantly related to specialist bird species richness (z = 1.845, p = 0.065). The best model predicting generalist species richness was weakly supported, but the top five models all contained bird bath (Table 4.3, Fig. 4.4.f), indicating the importance of this variable which has a positive effect on the species richness (z = 3.23, p = 0.001). In most cases, models which included the number of introduced plants, cats or dogs were not well supported (Table S4.5).

Discussion

This study shows that nectar specialisation, dispersal barriers and food sources in gardens most strongly affect the guild of urban nectarivorous birds. Urban communities were dominated by nectar-generalist birds, since low nectar dependence seems to facilitate urban adjustment. Almost all generalist species were rare in Table Mountain National Park and relatively more abundant in gardens, suggesting that they are urban exploiters (Blair 1996). The only exception was *Onychognathus morio* (Red-winged Starling), but this species was still more abundant in gardens than all the nectar-specialist species (Fig. 4.2). Furthermore, we found that nectar rank was the most important biological trait predicting bird abundances in gardens, which shows that it is in fact the generalist species' low dependence on nectar that allows them to exploit gardens better.

The distance to the nearest protected area affected all nectarivorous birds, but limited only the number of birds and not species richness. This shows that the urban environment does pose a barrier, even though it is penetrable. All species are capable of crossing this barrier, but birds are less likely to reach the gardens furthest from protected areas. Importantly, this is not an artefact of several garden traits differing consistently with distance from protected area. This distance was only directly related to the presence of sugar water feeders (Table S4.1), thus the shortage of this luxurious resource in the inner urban gardens may make them less attractive. Likewise, in Venezuela, the higher bird diversity in traditional towns relative to recent suburbs is thought to be partly due their proximity to protected areas (Sanz & Caula 2015).

The successful urban adjustment of nectar-generalist birds is further facilitated by large vegetated areas and the presence of bird baths. Large planted areas provide shelter as well as a diversity of food types and nest sites, which may be exploited by more adaptable generalist species. In contrast, nectar specialists were not sensitive to the size of planted area, despite sunbirds showing a preference for dense vegetation in natural habitat (Larsson & Hemborg 1995). Secondly, the presence of bird baths increased generalist species richness. This may be both for the benefit of drinking and bathing. Sunbirds are known to drink water to maintain water and energy balances (Nicolson & Fleming 2003), and generalists may also show this behaviour (Symes *et al.* 2011), considering their preference for low nectar concentrations (Brown, Downs & Johnson 2012). Experimental studies on *Sturnus vulgaris* show that recent bathing affects feather structure so that it slows a bird's flight down, but allows more accurate escape flight (Brilot, Asher & Bateson 2009).

Natural and artificial nectar resources, in the form of indigenous bird-pollinated plants and sugar water feeders, seem to facilitate nectar specialists' urban adjustment. The numbers of these birds are increased by the presence of sugar water feeders, likely because these provide a superabundant food source. Species richness is increased by a larger number of individual indigenous plants. This may be due to the preferences of different bird species: *Promerops cafer* feed largely from Proteaceae plants, while *Anthobaphes violacea* feed predominantly on *Erica* (Rebelo *et al.* 1984) and *Nectarinia famosa* forages mostly from very long-tubed flowers (Geerts & Pauw 2009). At the landscape scale, abundances of nectarivorous birds are also strongly related to the species richness of Proteaceae plants in the Cape Floristic Region (Chapter 4).

It is uncertain what the implications are of abundant supplementary food provided by artificial feeders for nectarivorous birds and their pollination mutualisms. On the one hand, anthropogenic subsidies of garden nectar resources may replace natural resources destroyed during urbanisation and could provide stepping stones connecting patches of protected areas. On the other hand, there are three possible negative effects. Firstly, birds' attraction to bird baths and bird feeders may increase the contact rate between individuals and species and thus increase disease transmission rates (Bradley & Altizer 2007). Secondly, birds may be overconsuming sugars at feeders and cause imbalances in their diet, which would require them to consume more water and arthropods (their protein source) (Nicolson & Fleming 2003b; Schaefer, Schmidt & Bairlein 2003). Thirdly, these superabundant, easily accessible nectar sources may attract birds away from natural plants (Arizmendi *et al.* 2007) which rely on their pollination services. However, the latter does not seem to occur yet, since these birds are still more abundant in protected areas than in gardens (Fig. 4.2). In fact, in accordance with a previous finding of a lack of endemics in the urban assemblages (González-Oreja 2011), the two fynbos-endemic species *Promerops cafer* and *Anthobaphes violacea* were among the three least abundant species in gardens. However, the seasonal patterns of nectarivorous birds' use of urban nectar resources require detailed investigation.

Although fynbos nectarivores have been recorded visiting introduced plant species, the abundance of introduced plants was not an important factor influencing community assembly. It may be that introduced plants are less preferred resources. Alternatively, this result may also reflect our decision to include only a few introduced plant species in the questionnaire. Likewise, the presence of carnivorous domestic animals was not an important influence on bird abundances in gardens. The same result was found in a study of Australian garden birds (Daniels & Kirkpatrick 2006; Parsons et al. 2006). Although cats in Cape Town are known to prey on birds (Morling 2014), birds may tolerate the presence of these potential predators by adopting more cautious behaviour. Tryjanowski & Morelli et al. (2015) showed that birds take longer to use feeders the more cats there are present.

In conclusion, South African urban nectarivorous bird communities are dominated by nectar-generalist species, seemingly due to their lower dependence on nectar and ability to use other resources. Nectar-specialist birds are more abundant when indigenous and/or artificial nectar sources are available in gardens. Distances between gardens and protected areas limit bird abundances, but not species richness, in gardens. Thus, although a biological trait (nectar dependency) limits bird species' ability to adjust to urban environments, garden traits, such as indigenous and artificial nectar resources, can facilitate this adaptation.

Acknowledgements

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Table 4.1 List of response and predictor variables for testing the effects of bird traits and garden traits on urban bird community composition in Cape Town, South Africa

Variable	data type	Range	units
Effect of bird traits			
Response variable[a]			
average species abundance across all gardens	numerical (log-transformed)	-0.17-1	per species
Predictor variables[b]			
longevity	numerical	6-20	years
number of habitats used	numerical	1-8	
nectar rank	integer	1-3	
nest site	categorical	shrub/tree/adaptable	
Effect of garden traits			
Response variables[a]			
number of nectar-specialist birds	numerical	0-53	per garden
number of nectar-generalist birds	numerical	0-118	per garden
number of nectar-specialist bird species	integer	0-5	per garden
number of nectar-generalist bird species	integer	0-5	per garden
Predictor variables[a]			
distance to nearest protected area	numerical	0.001-20.887	km
distance to nearest park	numerical	0-5	km
matrix	categorical	natural/non-natural	
planted area	numerical	80-534600	square meters
number of indigenous plants	numerical	0-201	per garden
number of introduced plants	numerical	0-106	per garden
number of cats	numerical	0-6	per garden
number of dogs	numerical	0-12	per garden
bird bath	binary	Yes/No	
sugar water feeder	binary	Yes/No	
other feeders	binary	Yes/No	

[a] Information obtained from questionnaires

[b] Information obtained from Hockey et al. (2005)

Table 4.2 The set of five best models testing which biological traits of nine nectarivorous birds predict their abundances in gardens. Models were tested with linear mixed-effect models that included the largest foraging group size as random factor. For each model the number of parameters (K), log likelihood (L), Akaike Information Criterion (AICc), difference in AICc from the best model and Akaike weight (w_i) is presented.

Model[a]	K	L	AICc	ΔAICc	w_i
nectar rank	4	-4.07	26.13	0	0.754
habitats	4	-5.89	29.78	3.648	0.122
longevity	4	-5.98	29.97	3.837	0.111
nest site	5	-2.16	34.31	8.182	0.013
habitats + nectar rank	5	-5.88	41.75	15.621	0

[a] nectar rank = importance of nectar in diet; habitats = number of habitats used; nest site = location of nest

Table 4.3 A summary of the five best models of nectarivorous bird abundances in gardens as predicted by garden traits. Predictions were made for the number of birds and numbers of generalist and specialist species separately. For each model the number of parameters (K), log likelihood (L), Akaike Information Criterion (AICc), difference in AICc from the best model and the Akaike weight (w_i) is presented.

Model[a]	K	L	AICc	ΔAICc	w_i
Generalist nectarivorous birds					
distance PA + planted area	4	-704.85	1417.94	0	0.544
planted area * distance PA	5	-704.59	1419.53	1.594	0.245
distance PA	3	-708.01	1422.17	4.225	0.066
distance PA + sugar water feeder	4	-707.07	1422.38	4.436	0.059
distance PA + matrix	4	-707.75	1423.74	5.8	0.03
Specialist nectarivorous birds					
distance PA + sugar water feeder	4	-493.34	994.92	0	0.558
matrix * distance PA	5	-493.58	997.53	2.606	0.152
distance PA + matrix	4	-495.29	998.81	3.891	0.08
sugar water feeder + matrix	4	-495.4	999.03	4.106	0.072
planted area * distance PA	5	-494.92	1000.19	5.269	0.04
Generalist nectarivorous species					
planted area + bird bath	3	-313.16	632.47	0	0.41
bird bath	2	-314.77	633.6	1.133	0.233
intro. plants + bird bath	3	-314.42	634.99	2.516	0.116
indig. plants + bird bath	3	-314.59	635.32	2.849	0.099
other feeders + bird bath	3	-314.75	635.64	3.169	0.084
Specialist nectarivorous species					
indig. plants + bird bath	3	-278.58	563.31	0	0.292
indig. plants + sugar water feeder	3	-278.64	563.42	0.11	0.276
sugar water feeder * indig. plants	4	-278.56	565.36	2.055	0.104
sugar water feeder + matrix	3	-279.77	565.67	2.366	0.089
indig. plants	2	-281.14	566.34	3.036	0.064

[a] distance PA = distance to nearest protected area; planted area = size of planted area in garden; matrix = predominant landscape between garden and protected area (natural/non-natural); other feeders = seed, fruit & mealworm bird feeders; indig. plants = number of indigenous plants

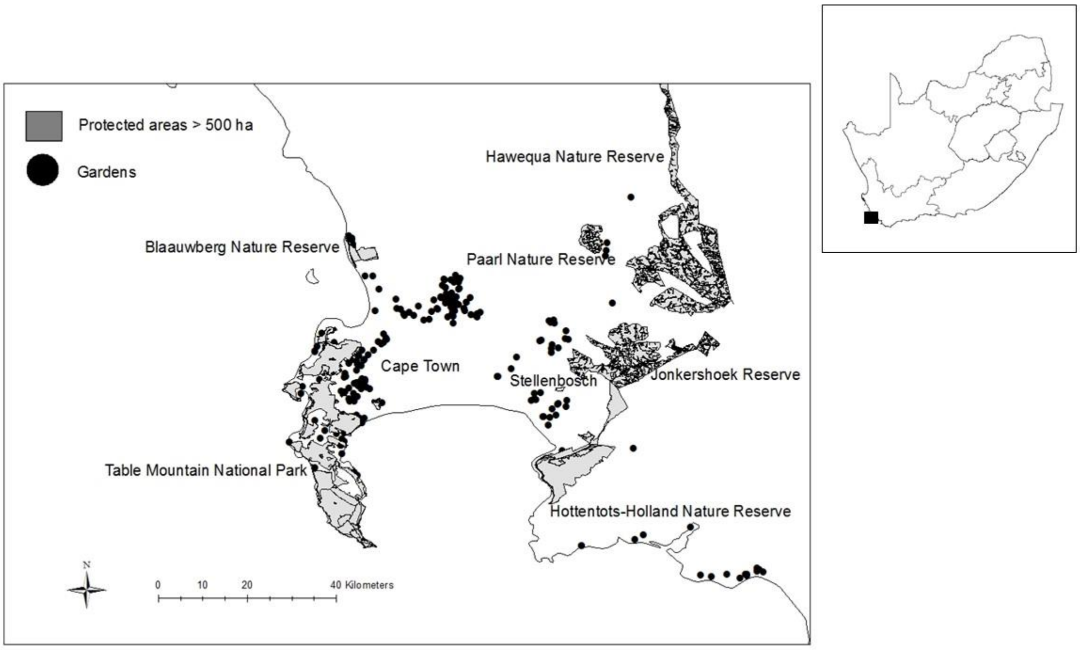

Figure 4.1 Location of study area and gardens. The insert on the right shows South Africa and indicates the location of the study area (enlarged map) with a black square. On the enlarged map, the black dots surrounding Cape Town City and the town of Stellenbosch shows the 193 gardens included in this study. The grey areas represent protected areas and the white terrestrial areas include other natural as well as non-natural areas.

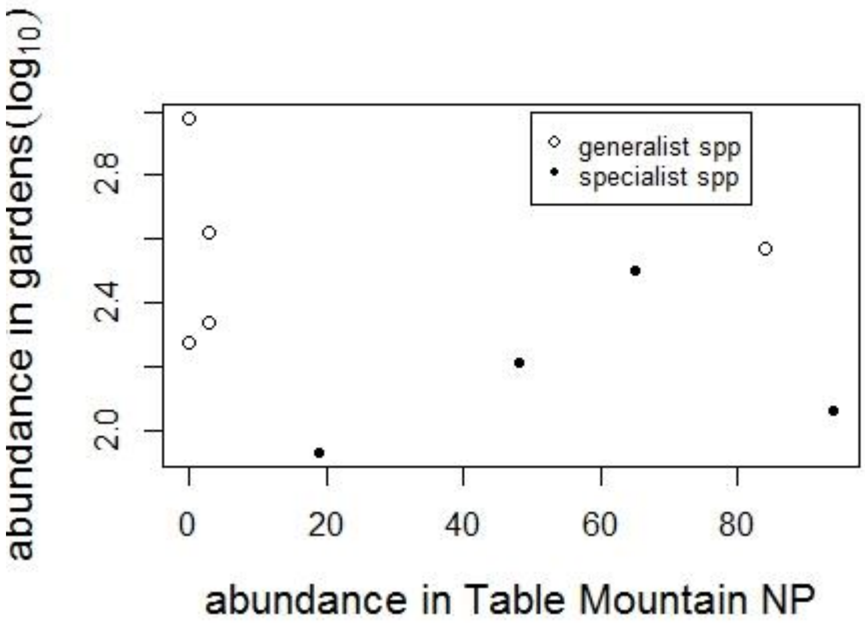

Figure 4.2 The abundance (reporting rates) of nine nectarivorous species in Table Mountain National Park, Cape Town, and in gardens closest to this park (reports from questionnaires, n = 95 gardens). All nectar-generalist species have low abundances in the park, except for *Onychognathus morio*, which has similar abundances to nectar-specialist species.

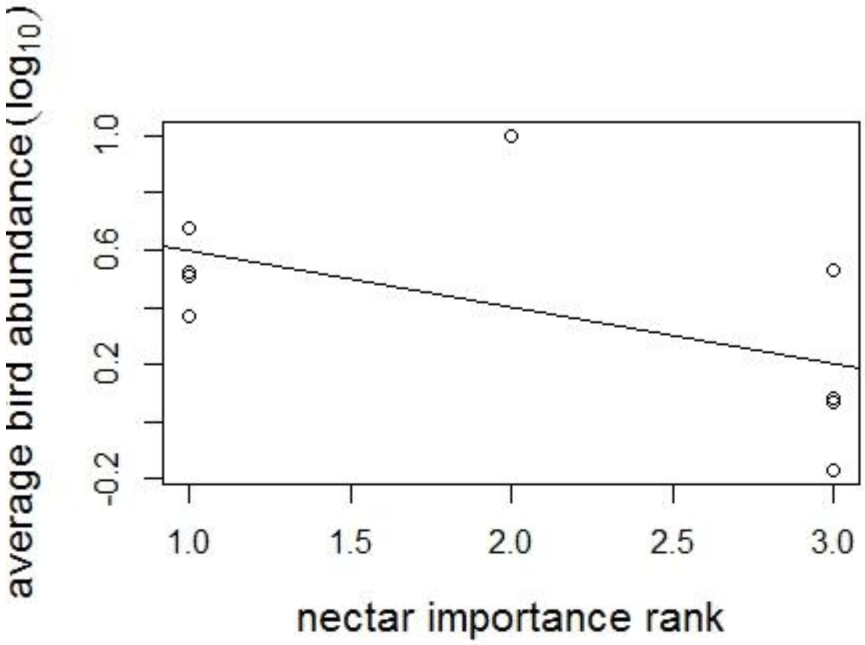

Figure 4.3 The importance of nectar in birds' diets was found to be the biological trait that most strongly predicts nectarivorous bird abundances in gardens. Each point shows the average abundance of a species across all sampled Cape Town gardens ($X^2_1 = 3.220$, $p = 0.072$).

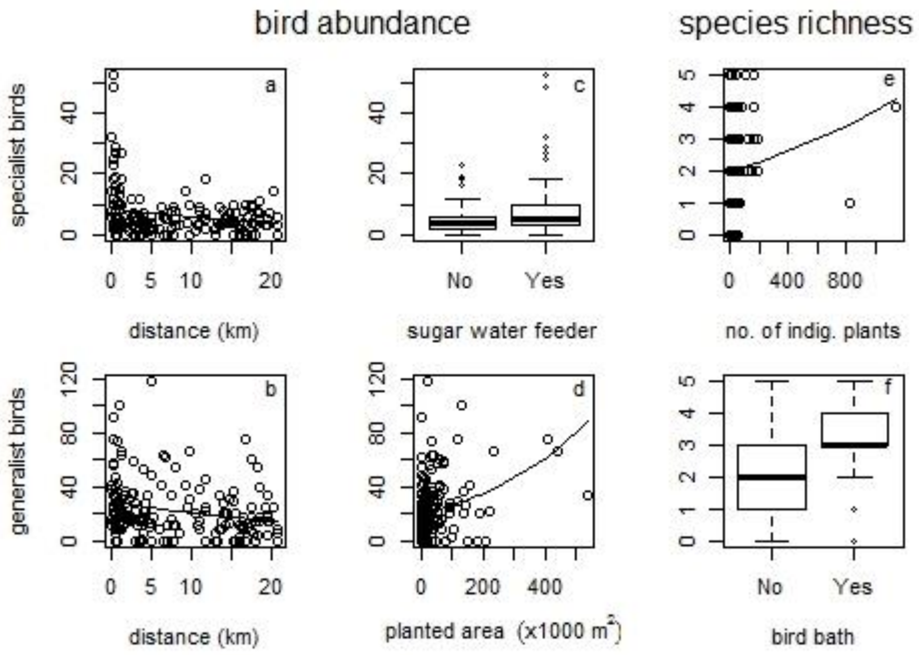

Figure 4.4 Garden traits identified as the most important predictors of the abundance (a-d) and species richness (e-f) of nectarivorous birds in gardens in Cape Town, South Africa. All relationships were significant. In the box and whisker plots, the solid line indicates the mean, the box indicates the interquartile range, whiskers show the range and dots are outliers.

Chapter 5: Phenology of Proteaceae nectar resources for birds at landscape scale: the importance of species richness

This project was initiated by A.G. Rebelo and data analyses and manuscript writing was done by Anina Coetzee.

Abstract

Many animals depend on resources that can vary greatly in time and space, which may require them to track these resources. Availability of plant resources often depends on phenological changes in abundance that are affected by a number of environmental factors, and thus may show strong fluctuations across time and space. The landscape scale patterns, and consequences of this variability are still understudied due to the difficulties of data collection at large scales. Nectar-feeding birds, which depend on floral resources, are highly mobile organisms and capable of tracking resources at landscape scale. However, the profitability of resource tracking depends on the spatial variation of resource availability. This study investigates the spatio-temporal patterns of bird-visited plants of the Proteaceae in the Cape Floristic Region, South Africa, and determines whether resource abundance or diversity is most important to nectar-feeding birds. Two extensive databases were used from the Protea Atlas Project and the second Southern African Bird Atlas Project. Very similar temporal patterns were found throughout the region, with a winter floral abundance peak. However, the floral abundance of *Leucospermum* and *Mimetes* species peak in the dry summer months when *Protea* resources are low. Nectar scarcity decreased with increasing spatial scale, but birds must increase their foraging area more than four-fold to double the floral abundance to which they have access. Nectar-feeding bird abundances were most strongly related to species richness of Proteaceae. This is perhaps due to the complementary flowering of species of the different genera and an indication that Proteaceae diversity may be very important in sustaining nectarivorous bird populations throughout the year. Since floral abundances are low across the biome at the same time of year, migration across mountain ranges may not be profitable to these birds, but direct evidence of their movements is needed.

Introduction

The abundance of different resource types varies in space and time. While a low degree of resource variation may allow resource users to maintain a sedentary life style, predictable seasonal variation may necessitate resource users to adopt migratory behaviour (Mueller & Fagan 2008). Animals can switch between local foraging and searching over large distances (Nabe-Nielsen *et al.* 2013) and recent movement ecology theory suggests that these movement decisions are determined by the external environment, internal state and navigation capacity (Nathan *et al.* 2008). Highly mobile organisms, such as birds, have the ability and capacity to search for available resources during seasonal resource depletion (Thomas, Hockey & Cumming 2015). However, seasonal resource tracking is only feasible if there is sufficient spatial variation in resource availability in the greater landscape (Beerens *et al.* 2015).

Specialist nectar-feeding birds depend primarily on nectar resources provided by flowers, which may vary dramatically in time and space (Collins & Briffa 1982; Feinsinger & Swarm 1982). Flowering phenology may change with seasons, rainfall or elevation gradients (Hart *et al.* 2011). Current evidence suggests that these birds seem to deal with this variability by tracking resource abundance and moving accordingly. Hummingbirds (Trochiliformes, nectar-feeding birds in the Americas) tend to move to where nectar resources are most abundant (Feinsinger 1976, 1978; Cotton 2007; Hart *et al.* 2011). There is evidence of honeyeaters (Meliphagidae, nectar-feeding birds in Australasia) moving between habitat types in different seasons to follow flower resources (Collins & Briffa 1982). In South Africa, sugarbirds (Promeropidae) and sunbirds (Nectarinidae) are likely to move around seasonally within a mountain range as flowering abundance changes (Rebelo *et al.* 1984), or even between parallel mountain ranges (ATK Lee and M Brown, unpubl. data). The local movement of Gurney's Sugarbird *Promerops gurneyi* can be predicted by the seasonal change in nectar producing protea plant abundances (De Swardt 1991).

To fully understand the implications of temporal and spatial variation in resource availability for the movements of these birds, we need to investigate landscape-wide patterns of flowering phenology of bird-pollinated plants (Woinarski et al., 2000). Very few studies have looked at the patterns of resource availability at landscape scales, due to the lack of extensive datasets, especially in African ecosystems. The fynbos biome, situated in the Cape Floristic Region

(CFR) of South Africa, provides a perfect opportunity to investigate this. One of the dominant elements of this vegetation is the Proteaceae, a widespread and abundant resource for nectar-feeding birds. One sugarbird and three sunbird species are resident and widespread in the CFR. There is still uncertainty about the extent to which each of these species shows landscape scale movements.

Investigating the distribution patterns of resources at landscape scales will also shed light on whether large scale movements benefit birds. The Protea Atlas Project and South African Bird Atlas Project databases provide biome-wide spatial records of Proteaceae and bird species, as well as temporal (phenological) records which can be used to explore patterns and relationships between these two groups.

Geerts (2011) showed that the abundance and species richness of nectar-feeding birds increases with the abundance and richness of bird-visited Proteaceae species. This study neatly showed the strong relationship between birds and proteas at small and large scales, which supports the hypothesis that proteas are important resources in this system. Yet it has not been clear how nectar availability in time, as well as space, corresponds to bird abundance and richness. Furthermore, since Geerts (2011) identified protea diversity as an important variable, it is worthwhile to explore the patterns of protea genera separately.

In the western part of the fynbos biome, distinct winter rainfall seasonality occurs with very low precipitation in the summer months. Consequently, most plants flower during winter and spring and very few in the summer (Johnson 1993). Rainfall is less seasonal in the southern Cape (east of the 12° 3’ E longitude) and there, more plants show peak flowering in early summer (Cowling 1992; Johnson 1993) (Fig. 5.1). Furthermore, species occurring only in the eastern region are responsible for a relatively long period of flower abundance because of the high number of species showing peak flowering during October–January (Johnson 1993). We will determine whether this general pattern also holds for the group of bird-visited Proteaceae.

Elevation gradients have also been shown to influence flowering phenology greatly. Large elevation ranges provide a moisture gradient that changes seasonally. The majority of species flower at low elevations during winter due to high rainfall and low temperatures at high elevations (Johnson 1993). During summer, however, conditions are dry at low elevations, limiting flower abundance, but plants at high elevations may flower where mist provides moisture (Johnson 1993; Pauw & Johnson 1999). These patterns have been recorded in some of the Proteaceae and *Erica* species in Jonkershoek, a well-studied site in the west of the biome (Rebelo *et al.* 1984).

Perhaps a more important aspect of resource patterns is not where and when they are abundant, but rather where and when they are least abundant and potentially limiting. One can investigate the change in floral abundance minima at different spatial scales to estimate the spatial extent of nectar scarcity (Woinarski *et al.* 2000). This would provide insight into the range size needed for birds to persist in an area.

The aim of this study is therefore to determine whether nectar-feeding birds respond to the spatio-temporal flowering patterns of bird-visited Proteaceae in the CFR. Specifically, we test the hypotheses that floral abundances (1) vary temporally across the biome, (2) differ between genera, (3) differ between rainfall regimes and (4) change with elevation. Furthermore, we test whether nectar scarcities, estimated as the lowest floral abundance maxima in each month, change proportionally with spatial scale. Finally, we hypothesise that bird abundances can be predicted by protea abundance, floral abundance and protea species richness.

Methods

Study area

The study was restricted to the CFR, where the greatest Proteaceae diversity occurs in Africa and also where the greatest data coverage is. Thus, all datasets were clipped with the Cape boundary GIS layer derived from the Cape Action for People and Environment project (CAPE), obtained from the South African National Biodiversity Institute. The CFR can be divided into 29 subregions based on the clustering of Proteaceae species, which are generally centred on mountain ranges or contained within lowland basins (Rebelo & Siegfried 1990). Spatial data were projected to the WGS 1984 geographic coordinate system. Spatial analyses were conducted in ArcMap 10.3 (ESRI ArcMap 2010).

Study species

The four nectar-specialist bird species resident in the CFR are the Cape Sugarbird *Promerops cafer*, Orange-breasted Sunbird *Anthobaphes violacea*, Malachite Sunbird *Nectarinia famosa* and Southern Double-collared Sunbird *Cinnyris chalybeus*. The first two species are endemic to the CFR (Hockey *et al.* 2005). They all have long curved bills adapted to drink from tubular flowers (Skead 1967).

The Proteaceae is one of the characteristic families of fynbos vegetation, and 80 species are visited by birds [see Table S5.1, as updated by S. Geerts from (Geerts 2011)]. These include 41 *Protea*, 26 *Leucospermum* and 13 *Mimetes* species. These species have brush-type inflorescences with morphological adaptations for bird-pollination described in detail in Rebelo et al. (1984). Bird-visited species of *Protea* and *Leucospermum* have predominantly hexose nectars (Nicolson & Van Wyk 1998).

Cape Sugarbirds are most closely associated with Proteaceae (Rebelo *et al.* 1984). Sunbirds also feed from Proteaceae (Carlson & Holsinger 2013), although the Orange-breasted Sunbird and Southern Double-collared Sunbird often rob nectar from *Leucospermum* and *Mimetes* inflorescences (Johnson 2015). Since Proteaceae are used as a food source by all the nectar-feeding birds and are a widespread and common group in the fynbos, their numbers can provide a good estimate of the resources available to birds in this biome.

Floral abundance patterns

The Protea Atlas Project (http://protea.worldonline.co.za) collected distribution data on southern African Proteaceae in 500 m diameter plots during 1991 – 2002 (Rebelo 2006) as well as ecological data such as plant abundance, flowering status and elevation. Population codes recorded during the project give an estimate of population abundances (Table S5.2). Details of the distribution and flowering patterns of bird-visited Proteaceae species were extracted from the atlas project database. This data subset of 101047 plots also includes 2472 well-distributed control plots in fynbos vegetation with no Proteaceae, which serve as accurate absence data.

During sampling, the flowering status of each species in a plot was recorded based on the condition of the majority of inflorescences on all plants. Since most plots were only sampled once there is not complete phenological data available for every location. Thus, all the flowering data for a species were combined and the calculation of floral abundance per month was extrapolated to all the plants of a species, which assumes relative uniformity of flowering patterns across the biome. Most species have a small distribution range and thus likely show little spatial phenological variation. The proportional floral abundance per month was calculated as a proportion of all records:

$$\frac{\frac{\mathrm{BUD}}{4} + \mathrm{PEAK} + \mathrm{FLOWER} + \frac{\mathrm{OVER}}{2}}{\mathrm{BUD} + \mathrm{PEAK} + \mathrm{FLOWER} + \mathrm{OVER} + \mathrm{CONE} + \mathrm{NONE}}$$

The abbreviations indicate the proportion of individuals in bud (BUD), in peak flowering (PEAK), flowering (FLOWER), mostly finished flowering (OVER), bearing cones (CONE) or that have no buds, flowers or cones (NONE). BUD was divided by four since only about a quarter of plants were in flower. Likewise, when a population was classified as OVER, only half of the plants were bearing open flowers. In some cases, no flowers may have been recorded because of a recent fire and plants were not mature enough to flower yet. However, most data were collected in mature veld. Nevertheless, it is better to regard the data as restricted to the period 1991-2002.

The locational floral abundance of a species was calculated by multiplying the proportional floral abundance for a given month with the population abundance of the given location. Then, for each plot sampled, the total floral abundance was estimated by adding up the floral abundance of all species in the plot for a particular month.

Spatio-temporal patterns

Firstly, temporal patterns were investigated by looking at the mean species floral abundance in each month across the whole biome. Patterns for each genus were also investigated separately. Secondly, we tested whether the floral abundances vary temporally across the biome, by comparing mean floral abundance (across all species) for each month across all subregions. We used a multiple comparison test after a Kruskal-Wallis test (R package *pgirmess*), due to the non-parametric distribution of the data. Thirdly, we determined differences in floral abundance between the subregions, using a Friedman ANOVA with a post hoc test.

To test whether phenology patterns differ with rainfall regime, the biome was divided into eastern (n = 10) and western subregions (n = 19) at the 21° 3' East longitudinal line, where a pronounced change in rainfall patterns occurs due to the convergence of frontal systems (Johnson 1993). The annual maximum and minimum floral abundances were averaged and compared between subregions with a Mann-Whitney U test. Elevation was recorded in every Protea Atlas plot. To test if this affects overall flowering phenology, the relationship between elevation and annual floral abundance per plot was tested with a Spearman rank correlation test.

Nectar scarcity

To test whether nectar resource scarcities change proportionally with spatial scale, the lowest maxima for the monthly floral abundances were determined at a range of spatial scales: 2 x 2 km, 4 x 4 km, 8 x 8 km and 16 x 16 km (roughly 1.25', 2.5', 5' and 10', respectively). The Protea Atlas point data were converted to grid data with the Point to Raster tool in ArcGIS. Each cell value was assigned the value of the point with the highest floral abundance value of all the points within the cell. This conversion was done separately for each month, so that the maximum abundance per grid cell was obtained for each month, and the smallest of these monthly values was considered to be the nectar scarcity. This was repeated at all four spatial scales (1.25', 2.5', 5' and 10'). The mean nectar scarcity across the region was compared at the different spatial scales with a Kruskal-Wallis ANOVA test and Tukey's post hoc test. Analyses were conducted in the statistical software R version 3.2.0 (R Development Core Team (RDCT), 2006).

Protea and bird relationships

Bird distribution data were obtained from the second South African Bird Atlas Project (SABAP2) database, provided by the Animal Demography Unit (University of Cape Town, Cape Town, www.sabap2.adu.org.za). Bird occurrences were recorded by volunteers since July 2007, and data collected to 7 September 2015 were used in this study. Records of species occurrences were collected as checklists in grids with a pentad resolution: 5' x 5' (approximately 8 x 8 km). We used only grid cells with at least four checklists (n = 788 cells). The number of checklists per cell ranged from 5 to 1134 (average 26). Reporting rates (number of times a species was recorded in a grid cell as a proportion of the total checklists for the cell) from repeated visits to sites can be used as an estimate of the abundance of a species at the location (Underhill *et al.* 1991).

Atlas data have been shown to be reliable for the assessment of species abundances (Szabo, Fuller & Possingham 2012; Tulloch & Szabo 2012; Bird *et al.* 2014). SABAP data should be interpreted with caution because reporting rates are not always directly proportional to bird abundance and also due to observer bias (Harrison *et al.* 1997). Factors that bear on the reliability of SABAP data in our study are that mountaintops are not well sampled, grid cells with a small fraction of fynbos habitat might have biased reporting rates (Huntley *et al.* 2012), and females, juveniles and individuals in eclipse plumage can be more difficult to identify (Harrison *et al.* 1997). On the other hand, the reliability of abundance estimates is increased due to sunbirds being quite conspicuous all year round, which decreases the chances of inaccurate representation in the data (Harrison *et al.* 1997). We will not compare relative abundances between different species in this study (Huntley *et al.* 2012).

Grid cell data were extracted for the four nectar-feeding bird species. The Protea Atlas point data were converted to grid data of the same resolution so that each grid cell represents the mean floral abundance of all plots in the cell. Mean floral abundances and bird reporting rates are thus comparable estimates of abundances. Mean Proteaceae plant abundance and total Proteaceae species richness were also determined for each grid cell. Floral abundances are, as predicted, significantly spatially clustered (Moran's spatial autocorrelation test: I = 0.100561, z-score = 38.748232, p = 0), therefore the plant-bird relationships were tested with linear geographically weighted regressions, which take spatial structure into account (Nakaya 2001). These analyses were implemented in ArcMap 10.3 using fixed Gaussian kernels and corrected AICs to select the appropriate bandwidths. To test if bird abundances can be predicted by Proteaceae traits, we tested the relationship between bird reporting rates and Proteaceae abundance, Proteaceae floral abundance and Proteaceae species richness for each of the four nectar-feeding bird species separately. A model set was created and Akaike Information Criterion (AIC) scores were used to compare the ability of Proteaceae abundance, floral abundance and richness to predict bird reporting rates. As expected, the three Proteaceae variables were correlated. Unfortunately, the sample sizes of the temporal and altitudinal SABAP2 data are currently not yet sufficient to test relationships with bird abundances in different seasons.

Results

Floral abundance patterns

Annual floral abundance across all Proteaceae species shows a unimodal peak in the winter (Jul.-Aug.), while lowest abundance is in the end of summer (Feb.-Mar.; Fig. 5.2). A multiple comparisons test after a Kruskal-Wallis test showed that mean floral abundance per plot in both December and February differed significantly from that in June and July (Chi-squared = 44.025, $p < 0.0001$).

This winter peak in floral abundance is largely due to the hyper-abundant *Protea* genus (which peaks during May-Jul.), since the flowering of *Leucospermum* and *Mimetes* species peaks later in the year (Fig. 5.2). The two last-mentioned genera also have relatively high floral abundances in the months of lowest *Protea* nectar availability (Nov.–Jan.). The species with the highest total floral abundances are four of the most widespread: *Protea repens, P. neriifolia, P. laurifolia* and *P. nitida. Protea repens* produce 20.6% of the total floral abundance in the CFR, and *P. neriifolia* produces 12.2%. Species differ little in the number of inflorescences produced per plant, since floral abundances and population abundances are highly correlated (Spearman Rank correlation: S = 1496, $p < 0.0001$).

Spatio-temporal floral abundance patterns

All subregions of the fynbos show the same broad phenological pattern, only with different total abundances (Fig. 5.3). A Friedman ANOVA with a post-hoc test showed that the subregions' mean annual floral abundances differ significantly (Chi-squared = 324.8713, degrees of freedom = 28, $p < 0.0001$).

Annual floral abundance patterns are the same in the western and eastern subregions, but the mean abundance is much higher in the west. The annual maximum mean of the 19 western subregions is almost double (4 453 461) that of the 10 eastern subregions (2 615 391), but not statistically significantly different (W = 121, p = 0.247). The mean annual minimum is also lower in the east than in the west, though again not significantly so (W = 106, p = 0.636). Floral abundance per plot decreases at higher elevations, although the slope of the correlation is not steep ($S = 1.8 \times 10^{14}$, $p < 0.0001$, Rho = -0.05, Fig. 5.4).

Nectar scarcity

The lowest of the monthly maximum floral abundances per grid cell was significantly higher with every increase in spatial scale (Fig. 5.5, Chi-squared = 622.58, $p < 0.0001$). However, floral abundance does not increase proportionally with spatial scale. The median abundance for the grid cell areas of 4 km^2, 16 km^2, 64 km^2 and 256 km^2 (1.25’, 2.5’, 5’ and 10’, respectively) were 700, 980, 1400 and 2240, respectively. With each spatial scale increase, the grid cell area is increased by 400%, but floral abundance only increased by 40-43% with the first two scale increases and by 60% with the last scale increase (Fig. 5.5). Thus, a four-fold increase in area does not even double the median amount of available floral abundances. The percentage of grid cells with no floral resources in at least one month of the year changes from 1.3% at the smallest spatial scale to 0.3% in the largest spatial scale.

Protea and bird relationships

The abundance of all four nectar-feeding species was best predicted by Proteaceae species richness (Table 5.1). Of all bird species, the Cape Sugarbird and Orange-breasted Sunbird seem to show the strongest relationships with Proteaceae richness (Fig. 5.6).

Discussion

There is a strong relationship between the abundance and richness of bird-visited Proteaceae and nectar-feeding birds. At the same time, there is little spatio-temporal variation in floral abundances at the landscape scale. Broadly similar phenological patterns in Proteaceae flowering are found throughout the biome, with a winter floral abundance peak. Unfortunately, data on geographical variation of phenology patterns within species was not available. However, most Proteaceae species have relatively small distribution ranges and thus it is unlikely that phenology patterns of populations would differ at the coarse scale that we measured it at (monthly abundances). As for the wide-spread species, their floral abundances are likely overestimated and yet we still see a clear pattern of low floral abundances in summer across the biome.

Since abundances will likely be low in all subregions at the same time it may not always be profitable for birds to disperse across mountain ranges to search for nectar resources. However, finer-scale differences in nectar availability may influence birds' decisions of whether to stay or go (Dean, Barnard & Anderson 2009). Studies on the flowering phenology of bird-visited *Eucalyptus* species in Australia propose that reliable and concordant flowering (flowering at the same time across sites and species) discourage movements between sites by nectarivorous birds (Keatley & Hudson 2007). On the other hand, seasonal migrations between forest types are driven by complementary flowering in the different habitats (Keatley & Hudson 2007). Thus, birds may sometimes be permanently clustered in subregions with relatively higher abundances. This may also explain why human settlements in lowlands around fynbos habitat are increasingly occupied by nectar-feeding birds in summer months (unpublished data). Due to this lack of distinct spatio-temporal phenological patterns, we proceeded to test for a permanent, rather than seasonal, association between nectar-feeding birds and Proteaceae.

Unlike the general pattern in a large group of the Cape Flora (Johnson 1993), our results do not show distinctly different flowering patterns among the bird-visited Proteaceae species in the seasonal west and aseasonal east of the biome. Several Northern Hemisphere studies have found evidence that more closely related species tend to flower at the same time of year (Kochmer & Handel 1986; Du *et al.* 2015) and show similar flowering flexibility (Davies *et al.* 2013). In the Cape flora, evolutionary shifts in flowering time among sister species were not frequent (Van der Niet & Johnson 2009). Floral abundances were much higher in the west, but since this trend holds throughout the year, it is more likely that the western subregions sustains larger populations of birds overall, than that birds move westwards in dry months. Although there are different Proteaceae species assemblages in the west and east, the result is confounded by the fact that the dataset did not allow us to consider geographic variation in flowering times of widespread species.

Floral abundance decreases slightly at higher elevations. The highest abundances are found below 500 m above sea level. A great deal of variability is found between 500 and 1500 m, where after abundances start decreasing. In contrast, elevation did not affect flower abundances in a Hawaiian study, although it did affect bird abundances (Hart *et al.* 2011). As the pressures of land-use change increase at lower elevations, birds are increasingly likely to be forced to higher elevations and may in future suffer greater nectar shortages. The compounding effects of climate change increase the vulnerability of mountain species, such as Orange-breasted Sunbird (Simmons *et al.* 2004).

The overall temporal floral abundance patterns of Proteaceae are mainly due to the patterns of the species rich and abundant *Protea* genus. This is the largest group of species and makes up the bulk of floral resources for birds. *Leucospermum* and *Mimetes* species contribute less to total abundances, but produce a substantial amount in the dry months, when *Protea* flowering is at its lowest, and are thus important resources for nectar-feeding birds at times of predicted seasonal energy bottlenecks or nectar scarcity. Co-occurring Proteaceae species that share pollinators often experience competition for pollination services (Chapter 2). These phenological differences in the genera may therefore result from pressures to avoid pollinator sharing. The flowering of *Leucospermum* and *Mimetes* species in the dry months suggests that their conservation is important to the future persistence of nectar-feeding birds and other pollinators in the landscape. These genera are important resources, and already under greater threat than *Protea* species. Of the 41 bird-visited *Protea* species, 22 have a Red List status of conservation concern, whereas 12 of the 13 *Mimetes* species and 20 of the 26 *Leucospermum* species are of conservation concern (www.redlist.sanbi.org).

The complementary flowering of species of different genera may be the reason that bird reporting rates are most strongly related to Proteaceae species richness. If birds are unable to escape nectar scarcity by moving across mountain ranges, then they must remain in areas where there is a diversity of Proteaceae or similar nectar-bearing plants that can sustain them throughout the year. In Costa Rica, sequential flowering of the dominant bird-visited plant species, *Hamelia*, *Inga* and *Lobelia* provides abundant nectar for hummingbirds throughout the year in one mountain range (Feinsinger 1976; Waser & Real 1979). Likewise, the Australasian honeyeaters rely on a diversity of plant species for nectar (Collins & Briffa 1982). Previous studies have shown that Cape Sugarbirds show a strong association with Proteaceae at community scale (Rebelo *et al.* 1984), so our results are not surprising. Even stronger relationships might be found if bird and floral abundances could be compared within seasons.

Our investigation into nectar scarcities at different spatial scales revealed that local scarcities would affect birds most severely if birds remained in small patches of less than 4 km^2. Although birds can significantly increase their access to nectar resources by searching larger areas, the increase in floral abundance is not directly proportional to the increase in area. Not even a four-fold increase in area doubles the median available floral abundance. In comparison, a study on nectar resources for honeyeaters in the Northern Territory of Australia found even smaller increases in floral abundances with four-fold increases in area (Woinarski *et al.* 2000). This proposes that birds will suffer disproportionally high travelling costs to access more Proteaceae nectar sources if they depend primarily on this plant family.

In conclusion, this study shows that the landscape abundance patterns of fynbos nectar-specialist birds are strongly predicted by Proteaceae species richness. This may be due to the flowering phenology differences in the bird-visited genera, but other floral traits may also be important. Most noticeably, there is substantial variation in the nectar volumes and concentrations of bird-visited *Leucospermum*, *Mimetes* (Johnson *et al.* 2014; Johnson 2015) and *Protea* species (Schmid *et al.* 2015). Birds can overcome nectar scarcities by increasing their foraging ranges, but this may have disproportionately high energy costs. Many other plant families in the fynbos provide additional nectar resources for birds, but their relative importance in sustaining birds needs study. Furthermore, there are a number of factors that could constrain resource tracking by birds, such as demographic factors and diet switching, and these may differ between bird species (Hart *et al.* 2011). Nonetheless, this study proposes that diversity in nectar resources is more important in determining bird abundance patterns than the spatial variation in resource abundances, and this makes a strong case for the conservation of plant diversity.

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Table 5.1 Strength of relationships between the abundance of fynbos nectar-feeding birds and traits of bird-visited Proteaceae as tested by geographically weighted regressions at a spatial resolution of 5’ x 5’ (n = 788). Floral abundances represent the total annual floral abundance (proportion of flowering inflorescences).

Proteaceae trait	Bandwidth	R2	R^2 Adj.	AICc	diffAICc
Promerops cafer					
species richness	0.254	0.667	0.600	6750.161	0
floral abundance + species richness	0.301	0.667	0.598	6757.009	6.848
plant abundance + species richness	0.301	0.6678	0.599	6757.763	7.602
plant abundance + floral abundance + species richness	0.877	0.5630	0.544	6798.725	48.563
plant abundance	0.254	0.5022	0.401	7069.813	319.6517
floral abundance	0.254	0.497	0.396	7075.922	325.760
plant abundance + floral abundance	0.712	0.317	0.286	7151.244	401.083
Anthobaphes violacea					
species richness	0.254	0.6154	0.538	6626.411	0
floral abundance + species richness	0.331	0.585	0.514	6656.855	30.444
plant abundance + species richness	0.331	0.5848	0.512	6660.455	34.04367
plant abundance + floral abundance + species richness	0.877	0.491	0.468	6681.997	55.586
plant abundance	0.254	0.431	0.315	6938.443	312.032
floral abundance	0.254	0.427	0.312	6941.110	314.699
plant abundance + floral abundance	0.712	0.2300	0.194	7009.046	382.634
Nectarinia famosa					
species richness	0.254	0.4899	0.387	7058.389	0
plant abundance + species richness	0.256	0.536	0.405	7071.843	13.454
floral abundance + species richness	0.256	0.5318	0.401	7075.487	17.098
plant abundance	0.254	0.4667	0.358	7096.330	37.942
floral abundance	0.254	0.463	0.354	7100.569	42.180
plant abundance + floral abundance + species richness	0.877	0.290	0.259	7153.012	94.623
plant abundance + floral abundance	0.712	0.239	0.204	7208.721	150.333
Cinnyris chalybeus					
species richness	0.254	0.5092	0.410	7133.953	0
floral abundance	0.254	0.501	0.400	7147.831	13.878
plant abundance	0.254	0.4999	0.398	7151.637	17.68372
floral abundance + species richness	0.275	0.512	0.394	7175.268	41.315
plant abundance + species richness	0.275	0.512	0.393	7178.020	44.067
plant abundance + floral abundance	0.712	0.2439	0.209	7310.033	176.080
plant abundance + floral abundance + species richness	0.877	0.215	0.180	7338.802	204.849

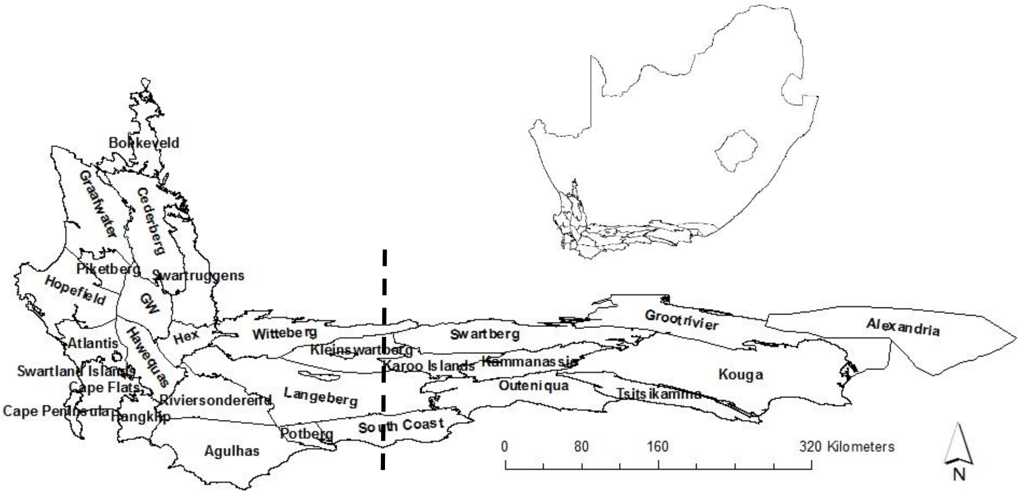

Figure 5.1 Geographical locations of the 29 subregions of the Cape Floristic Region (CFR) as delineated by mountain ranges and lowland basins (Rebelo & Siegfried 1990). The vertical dashed line indicates the 12° 13’ E longitude. The inset shows the location of the CFR within South Africa.

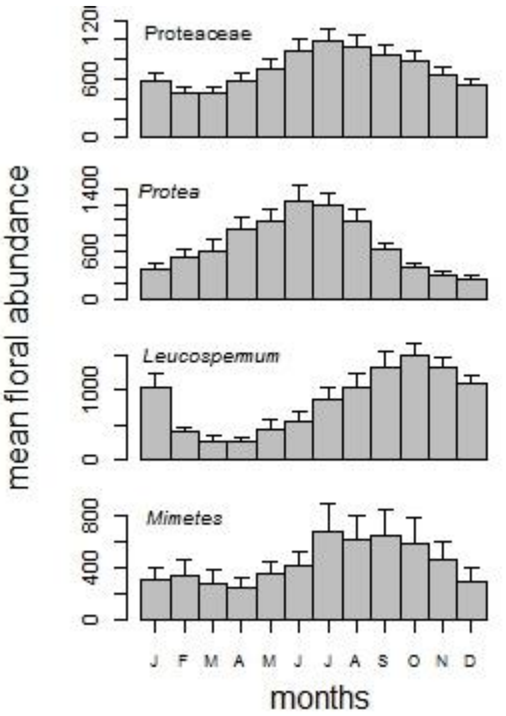

Figure 5.2 Mean species floral abundance per month across the whole Cape Floristic Region, from the Protea Atlas Project (n = 98575 plots). Floral abundances (proportion of flowering inflorescences) are shown for all bird-visited Proteaceae species together (n = 80), as well as for each genus separately (*Protea*, *Leucospermum* and *Mimetes* have 41, 26 and 13 species, respectively). Error bars indicate standard error.

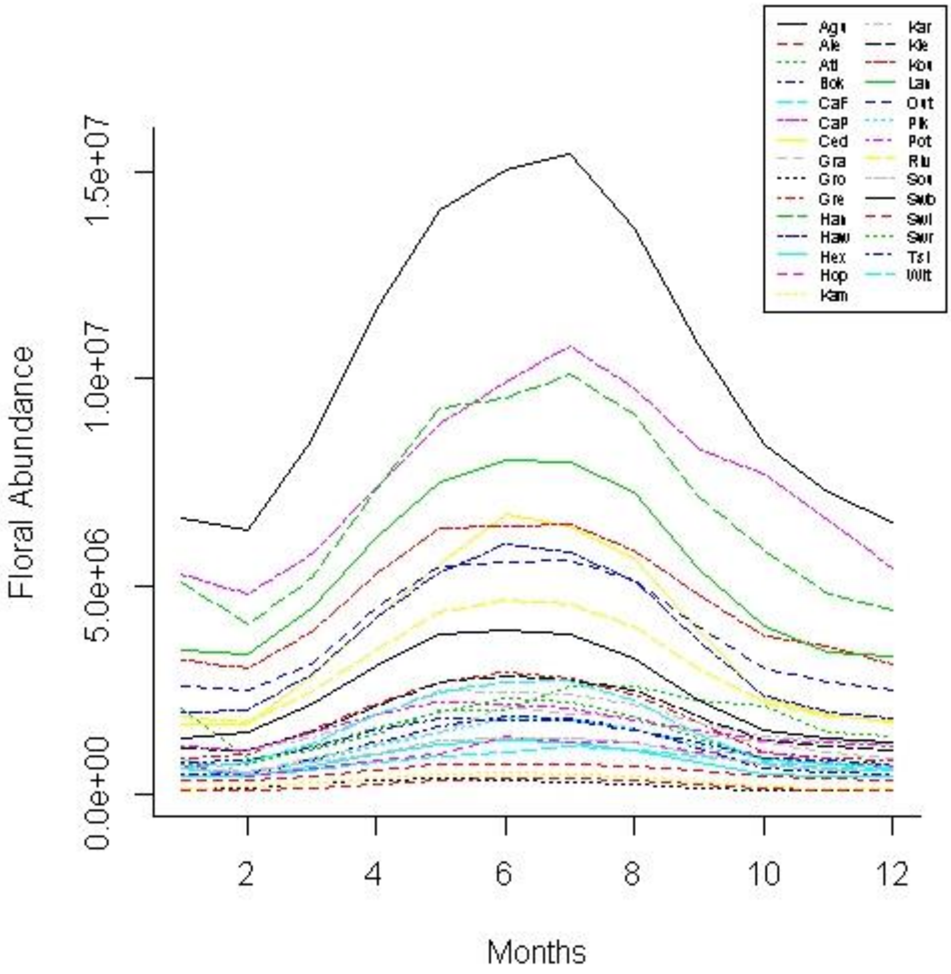

Figure 5.3 Total floral abundances (proportion of flowering inflorescences) per month of bird-visited Proteaceae species in the 29 fynbos subregions (see Fig. 5.1). All subregions show the same pattern with a peak in winter months.

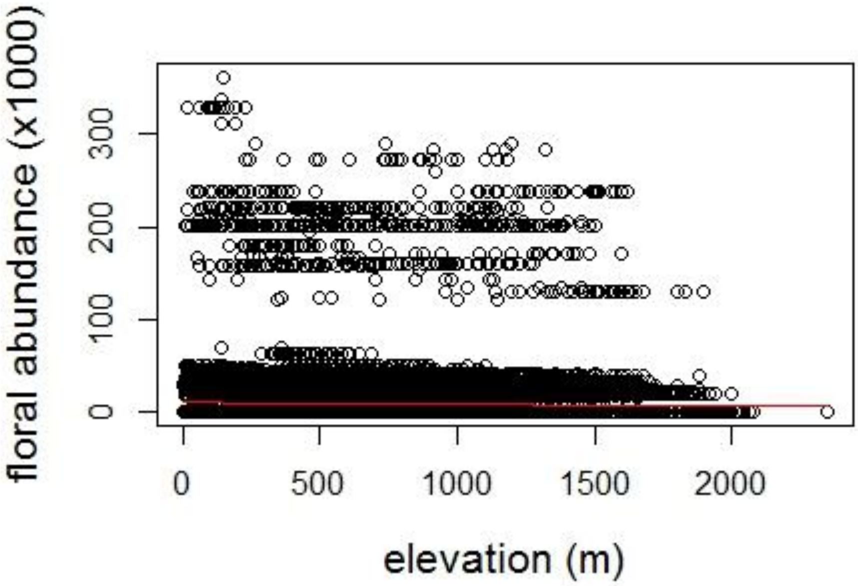

Figure 5.4 Bird-visited Proteaceae floral abundance (proportion of flowering inflorescences) per plot is negatively related to elevation in the Cape Floristic Region ($p < 0.0001$, Rho = -0.05, n = 101047 plots).

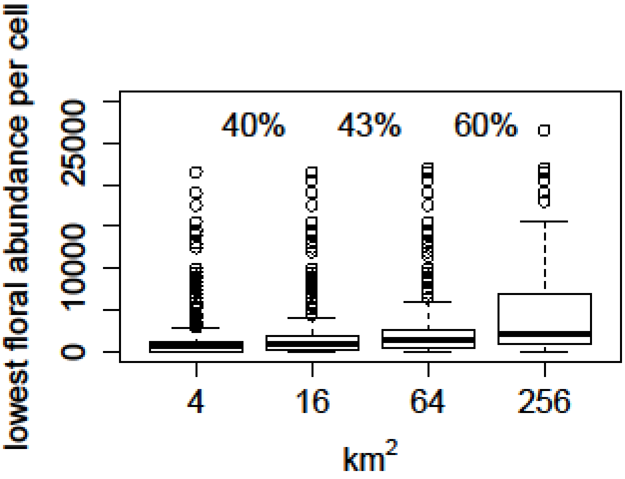

Figure 5.5 Lowest monthly maximum Proteaceae floral abundance values per grid cell for a range of different grid cell sizes (in km^2). Means and standard deviations are shown by the thick horizontal line and whiskers, respectively, and dots indicate outliers. The percentage increase in median floral abundance from the lower cell size to the next larger size is indicated between the boxes. Sample sizes of cells for the smallest to largest cell sizes are 6363, 2666, 996 and 339.

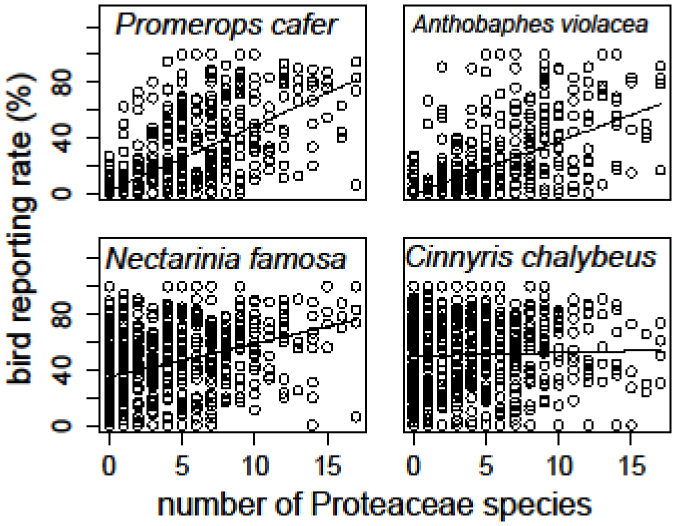

Figure 5.6 Abundance of nectar-feeding birds (reporting rate) in relation to species richness of bird-visited Proteaceae per grid cell (5’ x 5’ spatial resolution) in the Cape Floristic Region (n = 788 grid cells). See Table 5.1 for R^2 values.

Chapter 6: General conclusions

Within the bird-pollination systems of the fynbos biome, the distribution of nectar resources affects the foraging behaviour, community assembly and landscape movements of nectarivorous birds. Although I found evidence of these pollinators influencing the assembly of plant communities, I did not find evidence of pollinators directly affecting flower evolution.

At the flower patch level, visual signals by flowers were important influences on sunbird foraging behaviour (Chapter 2). Sunbirds showed a preference for pink *Erica perspicua* flowers over white ones. This preference appears to be an innate preference, since the nectar rewards of the two morphotypes did not differ significantly. Sunbirds showed no flower constancy and a strong tendency to try to reduce travelling distances during a typical foraging bout. The similarity in the pollination rate, fruit set and seed set of the two morphotypes indicated that the sunbirds' flower colour preferences did not translate directly into plant fitness differences, as expected. This highlights the complexity of the effects of pollinator behaviour on plant evolution. Although the birds showed selectivity, their lack of constancy suggests that they may cause heterospecific pollen transfer among co-occurring species. This in turn suggests that co-occurring sunbird-pollinated plants should have a mechanism to avoid pollen mixing.

Since pollinators are selective about what they feed on, plant species are more likely to occur with species that facilitate their flower visitation, and less likely to occur with species that reduce their flower visitation or pollination success. I showed in Chapter 3 that Proteaceae communities are often structured non-randomly, in such a way that species sharing pollination syndromes or style lengths co-occur less frequently than expected. Thereby, in assemblages of species with different pollination syndromes, fewer species are competing for the same pollen vectors. Species with different style lengths may be able to use different pollen placement sites on the same pollinator and effectively reduce heterospecific pollen transfer. However, at the congeneric level and within functional groups, clustering of similar species suggests that facilitative interactions also play a role. The effect of pollinating birds' limited flower constancy is evident in the communities of bird-pollinated Proteaceae: co-occurring species have different style lengths, presumably to avoid heterospecific pollen transfer. This is only true for small communities in 500 m diameter study plots. This is the spatial scale at which birds forage most frequently and thus where pollen mixing is most likely. At larger spatial scales (8 x 8 km), the style lengths of co-occurring species are similar. This suggests that the resources for long- and short-billed birds are clustered spatially into different areas. The distribution of nectar resources at larger spatial scales was investigated in more detail in Chapter 5.

The distribution of nectar resources in urban areas of Cape Town influenced nectar-specialist bird communities more than nectar-generalist birds. More specialist bird species could be found in gardens with sugar water feeders, while the abundances of these birds were increased by the number of indigenous bird-pollinated plants in gardens. At the landscape scale, abundances of nectarivorous birds are also strongly related to the species richness of Proteaceae plants in the Cape Floristic Region (Chapter 5). Nectar-generalist birds, on the other hand, were mostly affected by other resources, such as bird baths, other bird feeders and the size of vegetated areas in gardens. As also shown in Chapter 2, the travelling distance to a resource affects the chance that birds would visit that resource. All birds were less abundant in gardens further away from large protected areas, where natural resources occur.

It appears that nectar-specialist birds’ high dependence on nectar limits their adjustment to urbanisation, since overall they were less abundant than nectar-generalist birds. They can best be classified as urban adapters. This may be worrying, because the increase in land transformation in and around urban settlements causes greater habitat loss and habitat fragmentation. However, if these nectar-specialist birds become urban exploiters, their numbers may decrease in the natural habitats, where many plant species depend on their pollination services. Currently, the nectar-specialist birds are not abandoning natural habitat, but appear to be capable of using gardens with nectar resources as stepping stones to move between remaining natural habitats.

In the final chapter, I showed that Proteaceae nectar resource availability varies spatially in the fynbos biome, but the same temporal pattern is found throughout the biome. Thus, nectar resources are low in all the subregions at the same time of year. Consequently, the high energetic costs of seasonal long distance migrations between mountain ranges may often not be profitable. Population sizes of nectarivorous birds, and particularly of Cape Sugarbirds, may thus be limited by the seasonal resource bottlenecks. However, some long-distance movements between mountain ranges have been recorded for ringed Cape Sugarbirds (ATK Lee and M Brown, unpublished data), which shows that the movements of nectarivorous birds do require more detailed investigation.

The landscape level bird abundances were not primarily determined by floral abundances, but by Proteaceae species richness. I propose that birds are sustained within resource rich mountain ranges throughout the year by Proteaceae species from different genera, since the flowering peaks of the three bird-visited genera were complementary. Flowering of *Leucospermum* and *Mimetes* species peaked during the dry months when *Protea* floral abundances were at their lowest. The results of Chapter 3 suggest that co-occurring bird-pollinated Proteaceae species experience competition for pollination, thus the differences in flowering times of *Protea*, *Leucospermum* and *Mimetes* species might also be a mechanism to avoid pollinator sharing.

Although complementary flowering patterns may help to sustain bird populations, unavoidable nectar scarcities still occur in February and March across the whole biome. Birds can overcome nectar scarcity by increasing their foraging range, for example, from 4 to 16 km^2. However, this may be challenging, since floral abundance is not directly related to area size, and therefore, the increased costs are much higher relative to the increase in the rewards. In contrast, urban areas may have high rewards in small areas. Sugar water feeders commonly provide more than 500 ml of sugar water. This can feed at least 10 sunbirds, which require on average only 47 ml of nectar per day (Nicolson & Fleming 2003). A bird can therefore, acquire most of or all the nectar it needs in a day from a single location. Thus, nectarivorous birds are expected to be most abundant in urban areas during nectar-scarce times, when foraging in gardens may be more profitable than foraging in natural habitat. If this is the case, then urban gardens with nectar resources may help to sustain nectarivorous bird populations throughout the year. On the other hand, urban nectar resources may also modify birds' seasonal movement patterns and this may have unexpected ecological consequences, including increased risks of predation and disease spread.

Nectarivorous birds show specific foraging behaviour related to optimal foraging and their innate preferences. This may affect flower evolution and community assembly, but the subject needs testing under ecologically relevant conditions. Landscape scale patterns of Proteaceae nectar distribution predict the dispersal of nectarivorous birds to some degree, but we need to evaluate the nectar availability of a wider variety of plant families. In contrast to the nectar shortages found in natural habitat, urban environments provide superabundant artificial resources that are exploited by birds. More information on the seasonal patterns of urban resource use is required to understand the factors that drive urban adjustment in this system. The ecological, behavioural, conservation and epidemiological consequences of birds' adjustment to artificial resources needs urgent attention, since this is likely already affecting natural ecosystems. Overall, there is still much to explore about how birds' foraging decisions affect flower evolution and how nectar distribution determines birds' dispersal.

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Supplementary Information A

Table S2.1 The percentage density of the three flower colour morphotypes of *Erica perspicua* in different populations, as estimated in June 2012. Mean percentage and standard deviation is given.

Population	**Location**	**Sample size**	**Pink**	**Intermediate**	**White**
Kleinmond	34° 20’ 16.35” S 18° 59’ 48.69” E	6	55.15+11.24	14.29+5.52	30.55+13.90
Betty's Bay	34° 21’ 31.50” S 18° 53’ 9.27” E	2	72+0	12+0	16+0
Pringle Bay	34° 19' 45" S 18° 50' 30" E	4	17.529+3.80	1.04+2.08	81.43+4.05

Table S3.1 Distribution patterns of pollination-related traits in Cape Proteaceae communities as tested by two null models: Complete Spatial Randomness and Spatial Autocorrelation models. Patterns were analysed for small communities (500 m diameter plots) and large communities (8 x 8 km quadrats). Results are also presented for the three largest genera and functional groups. The patterns of style length was analysed with three metrics. For each dataset, the number of overdispersed (O), clustered (C) and random (R) communities are given, as well as the total number. The overall pattern for the Cape, as determined by a Wilcoxon test across all communities, is indicated with the same symbols (or NA when sample sizes were too low to analyse).

		Complete Spatial Randomness model						Spatial Autocorrelation model					
Community size	**Metric**	**O**	**C**	**R**	**Total**	**V-value**	**Pattern**	**O**	**C**	**R**	**Total**	**V-value**	**Pattern**
Proteaceae													
small	syndrome	354	1	47237	47592	618074321***	O	377	0	47378	47755	711022997***	O
	style difference	6834	2559	38199	47592	737789999***	O	1848	622	45285	47755	904695866***	O
	style variance	5556	2822	39214	47592	697555629***	O	3227	1001	43527	47755	905221858***	O
	style SDNDr	6547	-	26206	32753	279790487***	O	1447	-	35472	36919	315249666	R
large	syndrome	4	0	613	617	95287	R	4	0	613	617	98348	R
	style difference	22	4	591	617	130263***	O	62	2	553	617	166687***	O
	style variance	24	3	590	617	128850***	O	70	0	547	617	169014***	O
	style SDNDr	24	-	592	616	72133	R	31	-	585	616	59224	R
Protea													
small	syndrome	110	0	27410	27520	225103301***	O	1	0	27542	27543	305616419***	O
	style difference	413	472	26685	27570	166064097***	C	275	589	26706	27570	113590034***	C
	style variance	408	463	26699	27570	148779410***	C	347	750	26473	27570	101308205***	C
	style SDNDr	380	-	11149	11529	29659435	R	196	-	8677	8873	15941756	R
large	syndrome	2	0	586	588	97052*	O	7	0	581	588	100357***	O
	style difference	8	13	569	590	76020**	C	4	29	557	590	51413***	C
	style variance	6	14	570	590	72103***	C	3	27	560	590	48763***	C
	style SDNDr	14	-	523	537	63828	R	16	-	512	528	55368	R
Leucadendron													

		Complete Spatial Randomness model						Spatial Autocorrelation model					
Community size	**Metric**	**O**	**C**	**R**	**Total**	**V-value**	**Pattern**	**O**	**C**	**R**	**Total**	**V-value**	**Pattern**
small	syndrome	31	1	23914	23946	157203466.5***	O	0	0	23972	23972	158727936***	C
	style difference	308	387	23350	24045	123630233***	C	174	1044	22827	24045	65024958***	C
	style variance	285	392	23368	24045	103661452***	C	159	1328	22558	24045	53160834***	C
	style SDNDr	183	-	5456	5639	7497587	R	159	-	4609	4768	5111517	R
large	syndrome	1	0	549	550	74217	R	0	0	550	550	61408***	C
	style difference	2	15	578	595	68538***	C	0	33	562	595	39185***	C
	style variance	4	13	578	595	62160***	C	1	34	560	595	34831***	C
	style SDNDr	20	-	497	517	55330	R	20	-	490	510	44898	R
Leucospermum													
small	syndrome	0	0	1462	1462	298451***	O	0	0	1462	1462	271490.5***	O
	style difference	27	4	1434	1465	465446***	O	23	96	1346	1465	465858***	C
	style variance	27	5	1433	1465	484484**	O	23	72	1370	1465	469532***	C
	style SDNDr	1	-	28	29	364***	O	1	-	28	29	401***	O
large	syndrome	0	0	263	263	14252*	O	0	0	263	263	10473.5***	O
	style difference	1	1	261	263	18813	R	1	3	259	263	16889	R
	style variance	1	1	261	263	17850	R	2	3	258	263	15654	R
	style SDNDr	9	-	88	97	3337***	O	9	-	86	95	3298***	O
Bird-pollinated													
small	style difference	676	325	28937	29938	224774807	R	843	501	28648	29992	225864399	R
	style variance	661	317	28960	29938	202378091***	O	909	506	28577	29992	194036144***	O
	style SDNDr	354	-	11522	11876	28337238	R	112	-	8781	8893	12417068	R
large	style difference	7	5	581	593	84264	R	6	25	569	600	71568***	C
	style variance	7	5	581	593	77140**	O	10	20	570	600	63805***	C
	style SDNDr	18	-	531	549	66456	R	22	-	527	549	57818	R
Insect-pollinated													
small	style difference	586	563	30050	31199	214350978.5***	O	488	920	29791	31199	188772516***	C
	style variance	594	553	30052	31199	191473469.5***	O	487	915	29797	31199	171911611***	C

		Complete Spatial Randomness model						Spatial Autocorrelation model					
Community size	**Metric**	**O**	**C**	**R**	**Total**	**V-value**	**Pattern**	**O**	**C**	**R**	**Total**	**V-value**	**Pattern**
	style SDNDr	500	-	13750	14250	46919522	R	631	-	11191	11822	35053049	R
large	style difference	13	20	565	598	80592*	C	15	27	556	598	79284*	C
	style variance	15	19	564	598	78195**	C	18	28	552	598	79193*	C
	style SDNDr	22	-	522	544	61999	R	27	-	514	541	71968	R
Non-flying mammal-pollinated													
small	style difference	68	68	2782	2918	1873689***	C	2	32	3008	3042	1410021***	C
	style variance	119	151	2648	2918	1503211***	C	3	32	3007	3042	1358504***	C
	style SDNDr	6	-	518	524	72292	R	34	-	518	552	74631	R
large	style difference	3	3	259	265	17465	R	1	1	263	265	15757	R
	style variance	3	4	258	265	16712	R	0	0	265	265	15912	R
	style SDNDr	1	-	135	136	3943	R	0	-	129	129	3403	R
Wind-polllinated													
small	style difference	0	0	98	98	2963	R	0	0	152	152	8378***	O
	style variance	0	0	98	98	2947	R	0	0	152	152	8198***	O
	style SDNDr	0	-	0	0	NA	NA	0	-	0	0	NA	NA
large	style difference	0	0	82	82	2038	R	0	0	82	82	2031	R
	style variance	0	0	82	82	1930	R	0	0	82	82	1973	R
	style SDNDr	1	-	7	8	24	R	0	-	8	8	25	R

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

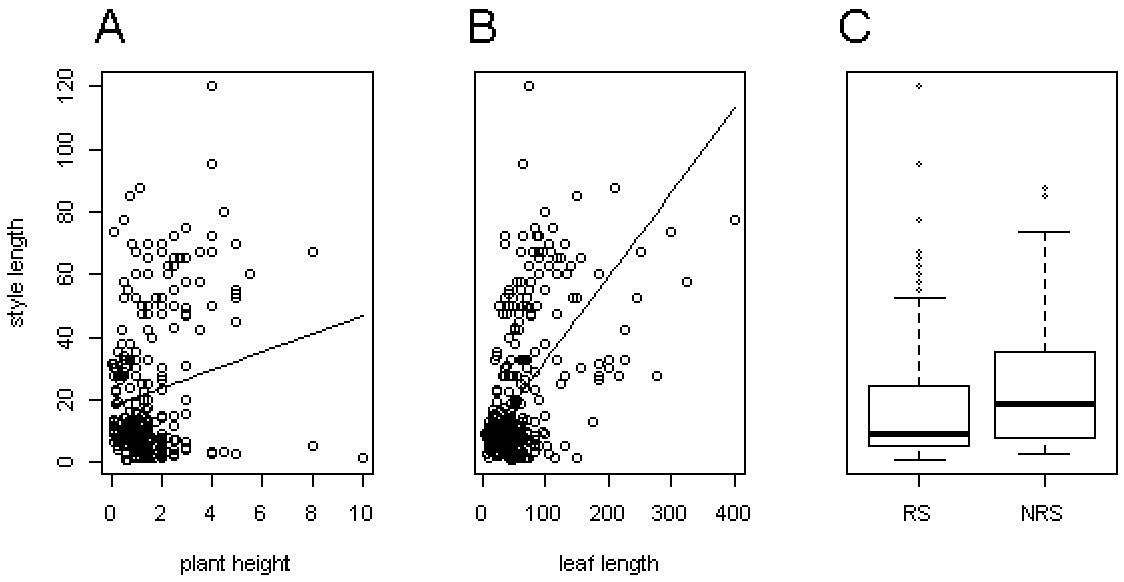

Figure S3.1 In Cape Proteaceae, mean style length (mm) is significantly related to mean plant height (A) and leaf length (B) (334 species). (C) It also differs significantly between species with and without the ability to resprout (RS and NRS, respectively, 246 species).

Table S4.1 Reporting rate, a proxy for relative abundance, of nectarivorous species in Table Mountain National Park (TMNP) and in 95 gardens closest to this park, as reported from questionnaires.

Taxonomic family	Species	English name	garden abundance	TMNP abundance
Promeropidae	*Promerops cafer*	Cape Sugarbird	2.215	48
Nectariniidae	*Anthobaphes violacea*	Orange-breasted Sunbird	2.061	94
	Cinnyris chalybeus	Southern Double-collared Sunbird	2.501	65
	Nectarinia famosa	Malachite Sunbird	1.929	19
Zosteropidae	*Zosterops virens*	Cape White-eye	2.980	0
Pycnonotidae	*Pycnonotus capensis*	Cape Bulbul	2.340	3
Ploceidae	*Ploceus capensis*	Cape Weaver	2.272	0
Sturnidae	*Sturnus vulgaris*	Common Starling	2.622	3
	Onychognathus morio	Red-winged Starling	2.573	84

Table S4.2 Biological traits of the nectarivorous birds of Cape Town. Total and average abundance are across all gardens. Body mass is in grams, longevity in years.

Species	Total abun.	Log average abun.	Body mass	Longevity	Habitats used	Nectar rank	Diet diversity	Clutch size	Nest site	Foraging group
Promerops cafer	217	0.081203239	34.5	12.2	2	3	2	2	shrub	pairs
Anthobaphes violacea	128	-0.169283051	9	6	3	3	2	1.69	shrub	pairs
Cinnyris chalybeus	620	0.532321142	8	8.5	7	3	2	2.2	shrub	pairs
Nectarinia famosa	209	0.064869625	17.5	10	7	3	2	2	shrub	group
Zosterops virens	1791	1.000243137	13.5	12.66	7	2	4	3	tree	group
Pycnonotus capensis	410	0.372230583	39	8	6	1	5	2.74	shrub	group
Ploceus capensis	570	0.510357312	46	7.58	4	1	5	2.6	tree	group
Sturnus vulgaris	841	0.674374238	75	20	1	1	6	4.4	adaptable	group
Onychognathus morio	617	0.52310886	135	7.5	8	1	7	3	adaptable	group

Table S4.3 Relationships between garden trait predictor variables were tested during data exploration. Spearman rank correlations, Kruskal-Wallis rank sum tests and Pearson's Chi-square tests were used and the p-values are indicated here. Significant relationships ($p < 0.05$) are highlighted in bold.

Predictor variables	1	2	3	4	5	6	7	8	9	10
1. distance to PA										
2. distance to park	0.09									
3. matrix	0.078	**0.002**								
4. planted area	0.684	0.077	**0.005**							
5. cats	0.385	0.256	0.522							
6. dogs	0.817	0.63	0.368	**0.004**						
7. indigenous plants	0.725	**0.008**	**0.029**	**<0.0001**	0.375	0.154				
8. introduced plants	0.17	0.34	0.98	**0.000**	0.92	0.45	**0.000**			
9. sugar water feeder	**0.013**	0.763	1	0.3232	0.418	0.850	0.403	0.345		
10. other feeders	0.728	0.939	0.657	0.9937	**0.035**	0.957	0.525	0.073	**<0.0001**	
11. bird bath	0.740	0.72	0.410	0.0556	0.232	0.930	0.097	**0.009**	**<0.0001**	**<0.0001**

Table S4.4 The complete model set testing which biological traits of nine nectarivorous bird species predict their abundances in gardens. Models were tested with linear mixed-effect models that included the largest foraging group size as random factor. For each model the number of parameters (K), log likelihood (L), Akaike Information Criterion (AICc), difference in AICc from the best model and Akaike weight (w_i) are presented.

Model	K	L	AICc	ΔAICc	w_i
nectar rank	4	-4.07	26.13	0	0.754
habitats	4	-5.89	29.78	3.648	0.122
longevity	4	-5.98	29.97	3.837	0.111
nest site	5	-2.16	34.31	8.182	0.013
habitats + nectar rank	5	-5.88	41.75	15.621	0
longevity + nectar rank	5	-6.22	42.43	16.301	0
longevity + habitats	5	-6.52	43.04	16.914	0
nectar rank + nest site	6	-3.12	60.25	34.115	0
habitats + nest site	6	-4.04	62.09	35.957	0
longevity + nest site	6	-4.54	63.08	36.954	0

Table S4.5 The complete model set of nectarivorous bird abundances in gardens as predicted by garden traits. Predictions were made for number of birds and the number of species for generalist and specialist species separately. For each model the number of parameters (K), log likelihood (L), Akaike Information Criterion (AICc), difference in AICc from the best model and Akaike weight (w_i) are presented.

Model[a]	K	L	AICc	ΔAICc	w_i
Generalist nectarivorous birds					
distance PA + planted area	4	-704.85	1417.94	0	0.544
planted area * distance PA	5	-704.59	1419.53	1.594	0.245
distance PA	3	-708.01	1422.17	4.225	0.066
distance PA + sugar water feeder	4	-707.07	1422.38	4.436	0.059
distance PA + matrix	4	-707.75	1423.74	5.8	0.03
matrix * distance PA	5	-707.7	1425.75	7.812	0.011
indig. plants + sugar water feeder	4	-708.84	1425.91	7.971	0.01
planted area + sugar water feeder	4	-709.23	1426.69	8.751	0.007
sugar water feeder * indig. plants	5	-708.39	1427.14	9.196	0.005
other feeders + sugar water feeder	4	-709.76	1427.75	9.812	0.004
intro. plants + sugar water feeder	4	-710.17	1428.58	10.636	0.003
planted area	3	-711.4	1428.94	10.998	0.002
indig. plants	3	-711.55	1429.25	11.307	0.002
sugar water feeder	3	-711.56	1429.26	11.319	0.002
dogs	3	-711.75	1429.64	11.695	0.002
sugar water feeder * intro. plants	5	-710.07	1430.5	12.556	0.001
sugar water feeder + matrix	4	-711.17	1430.59	12.646	0.001

Model[a]	K	L	AICc	ΔAICc	w_i
intro. plants	3	-712.28	1430.71	12.769	0.001
distance park + planted area	4	-711.25	1430.73	12.795	0.001
planted area + bird bath	4	-711.32	1430.89	12.946	0.001
indig. plants + bird bath	4	-711.48	1431.2	13.258	0.001
cats + dogs	4	-711.73	1431.7	13.758	0.001
other feeders	3	-713.2	1432.53	14.594	0
intro. plants + bird bath	4	-712.19	1432.62	14.683	0
matrix	3	-713.41	1432.96	15.017	0
distance park	3	-713.56	1433.27	15.327	0
bird bath	3	-713.61	1433.36	15.415	0
other feeders + bird bath	4	-712.73	1433.69	15.754	0
cats	3	-713.83	1433.8	15.858	0
Specialist nectarivorous birds					
distance PA + sugar water feeder	4	-493.34	994.92	0	0.558
matrix * distance PA	5	-493.58	997.53	2.606	0.152
distance PA + matrix	4	-495.29	998.81	3.891	0.08
sugar water feeder + matrix	4	-495.4	999.03	4.106	0.072
planted area * distance PA	5	-494.92	1000.19	5.269	0.04
indig. plants + sugar water feeder	4	-496.34	1000.92	5.994	0.028
distance PA + planted area	4	-496.55	1001.33	6.41	0.023
distance PA	3	-498.02	1002.18	7.258	0.015
sugar water feeder * indig. plants	5	-495.98	1002.33	7.403	0.014
sugar water feeder	3	-498.93	1004	9.079	0.006
planted area + sugar water feeder	4	-497.95	1004.14	9.216	0.006
other feeders + sugar water feeder	4	-498.22	1004.69	9.765	0.004
intro. plants + sugar water feeder	4	-498.89	1006.02	11.098	0.002
sugar water feeder * intro. plants	5	-498.55	1007.47	12.543	0.001
matrix	3	-501.86	1009.87	14.945	0
indig. plants + bird bath	4	-501.76	1011.77	16.846	0
distance park + planted area	4	-501.88	1012.01	17.086	0
distance park	3	-502.96	1012.06	17.134	0
bird bath	3	-503.29	1012.72	17.797	0
planted area + bird bath	4	-502.42	1013.07	18.148	0
indig. plants	3	-504.08	1014.31	19.384	0
other feeders + bird bath	4	-503.21	1014.66	19.737	0
intro. plants + bird bath	4	-503.23	1014.71	19.785	0
planted area	3	-504.66	1015.46	20.533	0
dogs	3	-504.91	1015.97	21.042	0
other feeders	3	-505.87	1017.88	22.96	0
cats + dogs	4	-504.85	1017.95	23.022	0
cats	3	-506.03	1018.2	23.275	0
intro. plants	3	-506.04	1018.23	23.306	0
Generalist nectarivorous species					
planted area + bird bath	3	-313.16	632.47	0	0.41
bird bath	2	-314.77	633.6	1.133	0.233

Model[a]	K	L	AICc	ΔAICc	w_i
intro. plants + bird bath	3	-314.42	634.99	2.516	0.116
indig. plants + bird bath	3	-314.59	635.32	2.849	0.099
other feeders + bird bath	3	-314.75	635.64	3.169	0.084
planted area + sugar water feeder	3	-316.52	639.18	6.714	0.014
planted area	2	-318.09	640.25	7.782	0.008
distance PA + planted area	3	-317.36	640.86	8.395	0.006
sugar water feeder	2	-318.95	641.97	9.5	0.004
distance park + planted area	3	-318.08	642.3	9.83	0.003
planted area*distance PA	4	-317.12	642.48	10.012	0.003
intro. plants + sugar water feeder	3	-318.23	642.6	10.132	0.003
indig. plants + sugar water feeder	3	-318.57	643.29	10.82	0.002
other feeders	2	-319.65	643.36	10.896	0.002
intro. Plants	2	-319.75	643.57	11.105	0.002
other feeders + sugar water feeder	3	-318.72	643.59	11.116	0.002
sugar water feeder + matrix	3	-318.78	643.69	11.224	0.001
distance PA + sugar water feeder	3	-318.8	643.74	11.269	0.001
distance PA	2	-320.09	644.24	11.773	0.001
indig. plants	2	-320.13	644.33	11.858	0.001
sugar water feeder*intro. plants	4	-318.22	644.68	12.209	0.001
dogs	2	-320.31	644.69	12.22	0.001
matrix	2	-320.37	644.8	12.332	0.001
sugar water feeder*indig. Plants	4	-318.32	644.88	12.408	0.001
cats	2	-320.44	644.96	12.489	0.001
distance park	2	-320.53	645.12	12.652	0.001
distance PA + matrix	3	-319.98	646.09	13.625	0
cats + dogs	3	-320.22	646.59	14.118	0
matrix*distance PA	4	-319.57	647.37	14.902	0
Specialist nectarivorous species					
indig. plants + bird bath	3	-278.58	563.31	0	0.292
indig. plants + sugar water feeder	3	-278.64	563.42	0.11	0.276
sugar water feeder * indig. plants	4	-278.56	565.36	2.055	0.104
sugar water feeder + matrix	3	-279.77	565.67	2.366	0.089
indig. plants	2	-281.14	566.34	3.036	0.064
planted area + bird bath	3	-280.42	566.99	3.681	0.046
planted area + sugar water feeder	3	-281.02	568.19	4.879	0.025
matrix	2	-282.34	568.75	5.446	0.019
distance PA + matrix	3	-281.7	569.54	6.227	0.013
planted area * distance PA	4	-280.69	569.61	6.306	0.012
distance PA + planted area	3	-281.85	569.85	6.542	0.011
distance park + planted area	3	-282.03	570.2	6.896	0.009
bird bath	2	-283.1	570.28	6.967	0.009
planted area	2	-283.32	570.72	7.409	0.007
matrix * distance PA	4	-281.64	571.52	8.211	0.005
intro. plants + bird bath	3	-283.02	572.18	8.868	0.003
other feeders + bird bath	3	-283.09	572.33	9.018	0.003

Model[a]	K	L	AICc	ΔAICc	w_i
sugar water feeder	2	-284.35	572.76	9.453	0.003
distance PA + sugar water feeder	3	-283.86	573.87	10.561	0.001
distance park	2	-285.13	574.34	11.031	0.001
other feeders + sugar water feeder	3	-284.31	574.76	11.45	0.001
intro. plants + sugar water feeder	3	-284.33	574.8	11.488	0.001
distance PA	2	-285.77	575.61	12.302	0.001
other feeders	2	-286.21	576.49	13.186	0
sugar water feeder * intro. plants	4	-284.18	576.6	13.295	0
dogs	2	-286.61	577.29	13.977	0
cats	2	-286.8	577.67	14.362	0
intro. plants	2	-286.81	577.7	14.39	0
cats + dogs	3	-286.59	579.33	16.02	0

[a] distance PA = distance to nearest protected area; distance park = distance to nearest vegetated greenbelt; planted area = size of planted area in garden; matrix = predominant landscape between garden and protected area (natural/non-natural); other feeders = seed, fruit & worm bird feeders; indig. Plants = number of indigenous plants; intro. plants = number of introduced plants.

Table S5.1 Phenological patterns of all the bird-visited Proteaceae species of the Cape Floristic Region, shown as the proportion of records with plants in flower, from Protea Atlas Project data.

Species name	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	n
Leucospermum													
catherinae	0.5	0.17	0	0	0.25	0	0.25	0.27	0.89	0.78	1	0.8	102
cordifolium	0.56	0.21	0.11	0.04	0.12	0.21	0.23	0.31	0.54	0.84	0.91	0.86	954
conocarpodendron conocarpodendron	0.38	0.18	0.12	0.02	0	0.07	0.2	0.14	0.21	0.73	0.83	0.53	213
conocarpodendron viridum	0.24	0.07	0.04	0.03	0.04	0.08	0.2	0.23	0.49	0.78	0.71	0.48	3285
cuneiforme	0.65	0.32	0.25	0.13	0.16	0.28	0.36	0.48	0.64	0.86	0.93	0.74	3596
erubescens	0.93	0.76	0.06	0.42	0.35	0.29	0.3	0.56	0.85	1	0.83	0.83	121
formosum	0.4	0.3	0.2	0.11	0	0.1	0.25	1	1	1	0.5	0.5	30
fulgens	0.1	0.03	0	0.25	0.4	0.6	0.8	1	1	1	1	0.56	53
glabrum	0.2	0	0.13	0.18	0.25	0.17	1	0.35	1	0.86	0.4	0	30
grandiflorum	0.5	0.19	0.05	0.1	0.25	0.17	0.81	0.63	0.25	0.92	1	0.88	96
gueinzii	0	0	0	0.13	0.11	0.22	0.25	0.52	0.88	0.83	0.83	1	99
lineare	0.91	0.8	0.28	0.17	0.2	0.3	0.33	0.64	0.82	0.85	0.94	0.96	250
muirii	0.67	0	0.02	0	0.15	0.2	0.63	0.53	0.67	0.75	0.72	0.67	110
mundii	0.41	0.5	0.14	0.13	0.25	0.44	0.85	0.75	0.8	0.97	0.82	0.5	141
oleifolium	0.36	0.29	0.17	0.22	0.27	0.3	0.3	0.49	0.74	0.84	0.67	0.53	712
patersonii	0.7	0.5	0.04	0.05	0.06	0.2	0.25	0.69	0.66	1	0.17	0.86	122
pluridens	0.63	0.57	0.03	0.1	0.35	0.56	0.52	0.32	1	1	1	1	125
praecox	0.9	0.09	0.12	0.15	0.5	0.35	0.73	0.91	0.88	0.87	0.57	0.5	563
praecox (cf truncatum)	0.76	0	0.5	0.3	0.13	0.62	0.63	0.8	1	0.72	0.42	0.33	135
profugem	0.5	0.3	0.2	0.1	0.06	0.18	0.5	0.13	0.25	0.66	0.6	0.55	27
praemorsum	1	0.6	0.4	0.25	1	0.38	0.73	0.82	0.97	0.96	0.98	0.98	233
reflexum	0.68	0.13	0.07	0	0.15	0.42	0.4	0.45	0.92	0.95	0.92	0.75	57
spathulatum	0.67	0.08	0	0.03	0	0.25	0.13	0.25	0.5	0.81	1	0.88	85
truncatum	0.62	0.11	0.23	0.1	0.12	0.39	0.15	0.42	0.81	0.91	0.85	0.61	625
vestitum	0.58	0.44	0.11	0.21	0.13	0.21	0.65	0.36	0.77	0.82	0.98	0.95	271
wittebergense	0.44	0.23	0.11	0.26	0.23	0.37	0.35	0.5	0.81	0.9	0.88	0.6	2174
Mimetes													
arboreus	0	0.03	0.17	0	0	0.38	0.2	0.1	0	0	0	0	42
argenteus	0.02	0.08	0.61	0.42	0.41	0.75	0.75	0.5	0.3	0.06	0	0	63
capitulatus	0.15	0.71	0.13	0.15	1	0.56	1	0.75	0.38	0.5	0.5	0.5	39
chrysanthus	0.4	0.5	0.63	0.67	0.88	1	0.5	0	0.2	0.4	0.5	0	43
cucullatus	0.58	0.31	0.29	0.23	0.22	0.17	0.22	0.28	0.4	0.56	0.48	0.58	6867
fimbriifolius	0.14	0.13	0.06	0.04	0.08	0.12	0.24	0.44	0.58	0.5	0.43	0.28	1608
hirtus	0.19	0.56	0.58	0.34	0.61	0.63	0.85	0.84	0.95	0.85	0.5	0.33	147
hottentoticus	0.4	0.77	0.43	0.13	0.05	0	0.1	0.25	0	0	0	0	41
palustris	0.5	0	0.1	0.19	0.13	0.5	1	1	1	1	1	0.7	20
pauciflorus	0.39	0	0.08	0.21	0.21	0.37	0.64	0.97	0.93	1	0.79	0.22	244
saxatilis	0.3	0.25	0	0.17	0.25	0.21	1	0.68	0.86	0.7	0.5	0.4	58
splendidus	0	0	0	0	0.2	0.46	0.63	0.83	0.9	0.7	0.5	0.2	32

Species name	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	n
stokoei	0	0	0	0	0	0	0	0	0	0	0	0	5
Protea													
angustata	0.16	0	0.04	0	0.1	0.13	0.17	0.45	0.38	0.4	0	0	101
aristata	0.42	0.5	0.2	0	0.17	0	0.04	0	0.15	0.28	0.56	0.45	79
aurea aurea	0.38	0.46	0.44	0.62	0.57	0.49	0.35	0.31	0.19	0.12	0.07	0.11	611
aurea potbergensis	0	0.25	0.21	0.25	0.7	1	0.7	0.5	0.2	0.1	0	0	32
burchellii	0.03	0.07	0.14	0.23	0.28	0.37	0.77	0.78	0.53	0.18	0.04	0	631
convexa	0	0.03	0.15	0	0	0	0.03	0.06	0.25	0.66	0.2	0.18	129
coronata	0.03	0.13	0.19	0.43	0.49	0.52	0.81	0.54	0.2	0.1	0.13	0.02	991
compacta	0.08	0.07	0.14	0.32	0.50	0.76	0.67	0.87	0.67	0.38	0.18	0.12	936
cynaroides	0.17	0.23	0.22	0.27	0.24	0.21	0.18	0.21	0.19	0.17	0.15	0.17	8519
denticulata	0	0	0.04	0.13	0.13	0.14	0.4	0.25	0.04	0.23	0	0	301
eximia	0.38	0.19	0.19	0.29	0.37	0.39	0.39	0.35	0.46	0.58	0.66	0.51	2393
glabra	0.09	0	0.07	0.09	0.16	0.36	0.48	0.73	0.48	0.21	0.27	0	1092
grandiceps	0.29	0.16	0.09	0.15	0.14	0.24	0.23	0.17	0.2	0.24	0.46	0.32	655
holosericea	0	0.1	0.25	0.5	0.7	0.9	1	0.28	0.63	0.38	0.2	0.04	33
inopina	0.25	0	0	0.1	0.25	0.3	0.4	0.5	0	0.05	0.07	0.11	19
lacticolor	0.33	0.53	0.61	0.75	0.34	0.61	0.32	0.05	0.28	0.13	0	0.06	78
lanceolata	0.08	0.25	0.25	0.29	0.53	0.89	0.66	0.71	0.23	0.04	0.16	0.13	354
laurifolia	0.07	0.05	0.17	0.27	0.42	0.57	0.53	0.49	0.32	0.14	0.11	0.07	10978
lepidocarpodendron	0.1	0.12	0.17	0.21	0.31	0.58	0.64	0.55	0.25	0.12	0.09	0.03	2060
longifolia	0.05	0.11	0.17	0.21	0.33	0.78	0.65	0.53	0.29	0.13	0.05	0.02	1594
longifolia minor	0	0	0.06	0.18	0.3	0.4	0.5	0.81	0.29	0	0	0	41
lorea	0.18	0.69	0	0	0	0.25	0.13	0.21	0.05	0.11	0.19	0	91
lorifolia	0.04	0.09	0.21	0.33	0.65	0.71	0.58	0.39	0.18	0.07	0.09	0.09	5275
magnifica	0.17	0.07	0.06	0.12	0.26	0.24	0.28	0.29	0.31	0.37	0.45	0.46	981
mundii	0.43	0.53	0.74	0.86	0.71	0.46	0.51	0.43	0.21	0.17	0.21	0.21	813
neriifolia	0.14	0.2	0.34	0.52	0.69	0.65	0.61	0.56	0.41	0.15	0.08	0.07	6380
nitida	0.13	0.13	0.15	0.26	0.31	0.42	0.44	0.34	0.25	0.13	0.15	0.14	9441
nitida dwarf	0.02	0.02	0.03	0.18	0.27	0.42	0.49	0.33	0.3	0.31	0.1	0	565
obtusifolia	0.13	0.07	0.18	0.22	0.32	0.8	0.84	0.88	0.26	0.28	0.04	0.15	1338
pendula	0.01	0.07	0.17	0.44	0.33	0.52	0.39	0.38	0.06	0.11	0.02	0.04	536
pityphylla	0	0	0	0.17	0.38	0.35	0.32	0.3	0.1	0	0.4	0.04	53
pudens	0	0.08	0	0.17	0.25	1	0.71	0.71	0.55	0	0	0	68
punctata	0.15	0.25	0.56	0.51	0.35	0.27	0.16	0.06	0.11	0.03	0.07	0.09	2313
repens	0.2	0.28	0.37	0.53	0.61	0.46	0.47	0.36	0.25	0.18	0.14	0.19	15295
rupicola	0.92	0.17	0.03	0.19	0.34	0	0.42	0.02	0.29	0.58	0.83	0.3	113
speciosa	0.18	0.12	0.09	0.16	0.22	0.22	0.2	0.28	0.31	0.31	0.34	0.23	1300
stokoei	0	0.06	0.04	0.38	0.5	0.46	0.2	0.13	0.32	0.4	0	0	75
subvestita	0.62	0.66	0.59	0.33	0.01	0.04	0.29	0.1	0.04	0.05	0.01	0.25	402
susannae	0.18	0.26	0.36	0.72	0.68	0.74	0.64	0.35	0.19	0.12	0.06	0.07	959
venusta	0.2	0.84	0.13	0.3	0.5	0.13	0.25	0	0	0	0.15	0.5	74
witzenbergiana	0.16	0.11	0.13	0.54	0.58	0.64	0.19	0.14	0.18	0.07	0.04	0.04	359

Table S5.2 Population conversion factors for Protea Atlas Project plant population data used in calculating floral abundance. Population abundances were recorded as codes (population code = number of plants seen) and converted to population estimates.

Population code	Population estimate
Blank (not	0
X (not relocated)	0
1	1
2	2
3	3
4	4
5	5
6	6
7	7
8	8
9	9
F (10-100)	70
C (100-10 000)	7 000
A (> 10 000)	50 000

Supplementary Information B

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Questionnaire on nectar-feeding birds in gardens

Vraelys oor nektarvretende voëls in tuine

This questionnaire is for the purpose of research on nectar-feeding birds in suburban gardens in the Western Cape Province and fynbos biome (from Cape Town North to Niewoudtville and East to Port Elizabeth). We encourage people with any type of suburban garden to participate. Please answer the following questions as accurately as possible, particularly the species identities. Any information supplied will remain confidential and results will be reported anonymously. This questionnaire should take approximately 20 min to complete. Please complete the questionnaire before **31 October 2014.**

Hierdie vraelys is vir die doel van navorsing oor nektaretende voëls in voorstedelike tuine in die Wes-Kaap Provinsie en fynbos bioom (vanaf Kaapstad Noord na Niewoudtville en Oos na Port Elizabeth). Ons moedig mense aan met enige tipe voorstedelike tuin om deel te neem. Beantwoord asseblief die volgende vrae so akkuraat moontlik, veral die spesies identiteite. Alle inligting wat verskaf word sal vertroulik bly en deelnemers sal anoniem bly. Hierdie vraelys behoort ongeveer 20 min te neem om voltooi. Voltooi asb die vraelys voor ***31 Oktober 2014****.*

Please return the completed questionnaire by e-mail or postage:
Stuur asb voltooide vraelyste terug per e-pos of pos:
gardensunbirds@gmail.com
A Heystek
Department of Botany and Zoology
Private bag X1
Matieland
7602

The questionnaire can also be accessed through this website/ *Die vraelys kan ook bekom word deur die webtuiste:*
http://academic.sun.ac.za/botzoo/heystek/Sunbirds-questionnaire.htm
or through the direct link/ *of deur die direkte skakel:* **https://surveys.sun.ac.za/Survey.aspx?s=f9d36c88ba834b83a5e4453ea846f283**

1. Please provide your physical address (where your garden is located).
Verskaf asb u fisiese adres (waar u tuin geleë is).
Street/ *Straat*____

Suburban area/ *Woongebied*____

City/ *Stad*____

Postal code/ *Poskode*________________________

2. How big is your garden approximately? (m^2). *Ongeveer hoe groot is u tuin? (m^2).*

____

3. How close is your garden to the following? *Hoe naby is u tuin aan die volgende?*

	Distance in km/ *Afstand in km*
Park, green belt, river or dam (with shrubs and/or trees) *Park, groenbelt, rivier of dam (met struike en/of bome)*	
Nature reserve or national park *Natuurreservaat of nasionale park*	

4. How much of your garden (in percentage) is made up of the following:
Watter persentasie van u tuin bestaan uit die volgende:

	Percentage of this in your garden *Persentasie hiervan in u tuin*
Plants (trees, shrubs, herbs)/ Plante (*bome, struike, kruie)*	
Lawn/ *Grasperk*	
Hard surfaces (eg. pavement)/ *Harde oppervlaktes (bv. plaveisel)*	

5. Which of the following do you provide in your garden? *Watter van die volgende items is in u tuin?*

	Yes/ *Ja*	No/ *Nee*
Bird bath/ *Voëlbad*		
Sugar water feeder/ *Suikerwatervoerder*		
Other bird feeders (seed, fruit, mealworms)/ *Ander voedsel vir voëls (saad, vrugte, meelwurms)*		

6. How many cats and dogs do you keep in your garden? *Hoeveel katte en honde hou u aan in u tuin?*

	Amount/*Aantal*
Cats/ *Katte*	
Dogs/ *Honde*	

7. Do you regularly have stray cats in your garden? *Het u dikwels rondloper katte in u tuin?*

Yes/ *Ja*		No/ *Nee*	

8. How many, of the following bird-attracting flowering plants are in your garden? Pictures are provided of examples of the flowers, but some flowers may have different colours and sizes. / *Hoeveel van die volgende voël-lokkende plante is in u tuin? Prentjies is verskaf om voorbeelde van die blomme te wys, maar sommige blomme kan ander kleure of groottes wees.*

Plant name ***Plantnaam***	**Example** ***Voorbeeld***	**No. of plants** ***Aantal plante***
Protea		
Pincushions/ *Speldekussings* (*Leucospermum*)		
Watsonia		
Cape Honey Suckle/ *Handskoentjie* (*Tecoma*)		
Aloe/ *Aalwyn* (large flowers/ *groot blomme*)		
Wild dagga/ *Wilde dagga* (*Leonotus*)		
Gum tree/ *Bloekomboom* (*Eucalyptus*)		
New Zealand Flax/ *Vlas* *(Phormium)*		
Bottle brush/ *Bottelborsel* (*Callistemon*)		

Plant name ***Plantnaam***	**Example** ***Voorbeeld***	**No. of plants** ***Aantal plante***
Pagoda bush *(Mimetes)*		
Erica (tube shaped flowers/ *buisvormige blomme*)		
Cobra lily/ Piempiempie *(Chasmanthe)*		
Strelizia		
Red hot poker/ *Vuurpyl (Kniphofia)*		
Coral tree/ *Koraalboom (Erythrina)*		
Hibiscus (large flowers/ *groot blomme*)		
Weeping Boer-bean/ *Huilboerboon (Schotia)*		
Others (specify) *Ander (spesifiseer)*		

9. For how long have you been providing sugar water feeders in your garden? *Ongeveer hoe lank voorsien u al suikerwatervoerders in u tuin?*

Years/ *Jare*		Months/ *Maande*	

10. How many sugar water feeders do you have in your garden (one bottle counts as an entity, no matter how many perches or feeding holes there are)? *Hoeveel suikerwatervoerders is in u tuin (een bottle tel as 'n entiteit ongeag hoeveel sitplekke of openings dit het)?*

____

11. Is your sugar water feeder specific for sunbirds and sugarbirds (opening about 3mm in diameter) so that other birds or insects cannot drink from it? *Is u suikerwatervoerder spesifiek vir suikerbekkies en suikervoëls (opening van 3mm diameter) sodat ander voëls en insekte nie daaruit kan drink nie?*

Yes/ *Ja*		No/ *Nee*	

12. What is the sugar concentration of your sugar water solution? (How much sugar do you add to how much water?) *Wat is die suiker konsentrasie van u suikerwateroplossing? (Hoeveel suiker voeg u by hoeveel water?)*

____

13. What other substances do you add to the sugar water and how much of it? *Voeg u enige ander bestandele by die suikerwater en hoeveel van dit?*

____

14. What is the total volume of sugar water that you provide each time? *Wat is die totale volume suikerwater wat u elke keer voorsien?*

____

15. How often do you provide sugar water in your garden? (tick one box please)
Hoe gereeld voorsien u suikerwater in u tuin? (merk een blokkie asb)

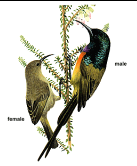
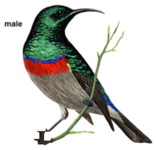
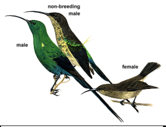
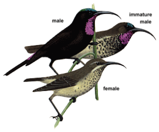
Irregularly/ *Ongereeld*	
Once a month/ *Een keer 'n maand*	
Once a week/ *Een keer 'n week*	
Once a day/ *Een keer 'n dag*	
Twice a day/ *Twee keer 'n dag*	
Other (please specify)/ *Ander (spesifiseer asb)*	

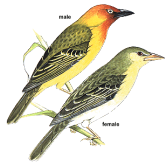
16. Are you aware of any sunbirds or sugarbirds breeding in your garden in the past five years? If so, which species? *Is u bewus van enige suikerbekkies of suikervoëls wat in u tuin gebroei het in die afgelope vyf jaar? Indien wel, watter spesies?*

____

17. Which bird species have you seen feeding **at your sugar water feeder and garden flowers**? Please indicate whether they fed at your sugar water feeder or garden flowers, or both. What is the **maximum number** of individuals you have seen at one point in time?

Watter voëlspesies het u al sien drink ***by u suikerwatervoerder en tuinblomme****? Dui asb aan of hulle gedrink het by die suikerwatervoerder of tuinblomme, of albei. Wat is die* ***maksimum aantal*** *individue wat u al op een slag gesien het?*

Bird species ***Voël spesie***		**Once** ***Een keer***	**Rarely** ***Skaars***	**Frequently** ***Gereeld***	**Sugar water feeder** ***Suikerwater-voerder***	**Garden flowers** ***Tuin-blomme***	**Maximum at one time** ***Maksimum op een slag***
		Tick one column *Merk een kolom*			Tick column(s) *Merk kolom(me)*		Estimate numbers *Skat getalle*
Cape Sugarbird *Kaapse Suikervoël*							
Orange-breasted Sunbird *Oranjebors-suikerbekkie*							
Southern Double-collared Sunbird *Klein-rooiband-suikerbekkie*							
Greater Double-collared Sunbird *Groot-rooiband-suikerbekkie*							
Malachite Sunbird *Jangroentjie*							
Amethyst Sunbird *Swart-suikerbekkie*							
Cape White-eye *Kaapse Glasogie*							
Cape Bulbul *Kaapse Tiptol*							

Bird species ***Voël spesie***		**Once** ***Een keer***	**Rarely** ***Skaars***	**Frequently** ***Gereeld***	**Sugar water feeder** ***Suikerwater-voerder***	**Garden flowers** ***Tuin-blomme***	**Maximum at one time** ***Maksimum op een slag***
		Tick one column *Merk een kolom*			Tick column(s) *Merk kolom(me)*		Estimate numbers *Skat getalle*
Common Starling *Europese Spreeu*							
Cape Weaver *Kaapse Wewer*							
Red-winged Starling *Rooivlerkspreeu*							

18. Have you seen sugarbirds or sunbirds in your garden with infected feet? An example of an affected sugarbird is shown (thickened legs and feet and/or lesions). *Het u al suikervoëls of suikerbekkies in u tuin gesien met geïnfekteerde pote? 'n Voorbeeld van 'n geaffekteerde suikervoël word gewys in die foto (verdikte pote en/of letsels).*

____

Please provide your name and contact details (this is optional)/ *Verskaf asb u naam en kontakbesonderhede (hierdie is opsioneel)*

Name & surname/ *Naam & van*: ____

Phone number/ *Telefoonnommer*: ____

E-mail address/ *E-pos adres*:____

Thank you very much for participating in this survey.

This will provide valuable information towards our study. We aim to determine what, where and how many food sources are available in suburban areas for birds that feed on nectar. It is also important to find out which bird species use these resources. For more information or to provide comments, contact Anina Heystek at gardensunbirds@gmail.com or 021 808 2604.
If you have seen birds with coloured rings on their legs or birds with infected legs, please contact Dr. Phoebe Barnard at p.barnard@sanbi.org.za or 021 799 8722.

Baie dankie vir u deelname in die opname.

Hierdie sal waardevolle inligting bydra tot ons studie. Ons probeer bepaal watter, waar en hoeveel voedselbronne beskikbaar is in bewoonde areas vir voëls wat nektar eet. Dit is ook belangrik om uit te vind watter voëls die bronne gebruik. *Vir meer inligting of om kommentaar te lewer, kontak Anina Heystek by gardensunbirds@gmail.com of 021 808 2604.*
Indien u voëls gesien het met gekleurde ringe aan hul pote of met geïnfekteerde pote, kontak asb vir Dr. Phoebe Barnard by p.barnard@sanbi.org.za of 021 799 8722