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Article

Urban nectarivorous bird communities in Cape Town, South Africa, are structured by ecological generalisation and resource distribution

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Biological communities are increasingly faced with novel urban habitats and their response may depend on a combination of biological and habitat traits. The response of pollinator species to urban habitats are of particular importance because all species involved in the pollination mutualism may be affected. Nectarivorous bird communities worldwide show varying tolerances to urban areas, but studies from Africa are lacking. We investigated nectarivorous bird communities in a medium-sized South African city and asked which biological and garden traits best predict the community assembly of specialist and opportunistic nectarivorous birds. Information was collected on garden traits and the frequency of nine nectarivorous bird species for 193 gardens by means of a questionnaire. Information on biological traits of birds was obtained from published literature. Habitat generalism and tree nesting were identified as the most important biological traits influencing bird occurrence in gardens. A greater diversity of indigenous bird-pollinated plants and the presence of sugar water feeders increased the numbers of nectar specialist birds and species richness of nectarivorous birds. While bird baths increased the species richness of nectar specialist birds, opportunistic birds' urban adjustment was further facilitated by large vegetated areas in gardens and limited by the distance to the nearest natural habitat. In conclusion, though some biological traits and dispersal barriers seem to limit urban adjustment, a combination of natural and artificial nectar resource provisioning could facilitate this adjustment.

Keywords: avian nectarivores, bird feeders, citizen science, fynbos, indigenous garden, Nectariniidae, nectar feeders, occasional nectarivores, Promeropidae, urbanisation, urban green space

Introduction

The urban environment is one of the fastest growing habitats on earth (United Nations 2014). Urban development often transforms and fragments natural habitat and therefore numerous negative effects on native organisms have been recorded



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(Rodewald 2003). However, urban areas can also create novel habitats that are used by species across several taxonomic groups (MacGregor-Fors et al. 2016). Thus, species show a diversity of responses to urbanisation that varies along a continuum, from species that are completely absent in urban areas to species that thrive only in urban areas (Blair 1996, Croci et al. 2008). Humans' activities are expected to play a large role in structuring urban communities (Aronson et al. 2016). Since birds are relatively easy to monitor and their high mobility allows them to track their preferred habitat, they are often used as indicators of how biodiversity is responding to urbanisation (Vandewalle et al. 2010). Furthermore, the response of birds is relevant to the human population because birds have a strong impact, both positive and negative, on people in urban areas (Whelan et al. 2008).

Increasingly, urban landscape planning aims to create ecologically friendly urban areas that support biodiversity and encourages movement of species across urban landscapes in order to prevent isolation of natural habitat fragments (Kormann et al. 2016, MacGregor-Fors et al. 2016). However, in order to achieve this we need to understand which factors enable species to tolerate and adjust to urban environments. Two of the main factors that could explain birds' responses to urbanisation, and their community assembly, are their biological traits and the local habitat traits (Evans et al. 2009, Brown and Graham 2015, Valladares et al. 2015). Numerous biological traits, or species traits, have been identified that determine how birds respond to urban areas. Generalist foragers (omnivores) tend to be more urban tolerant and thus more abundant in urban areas than specialist feeders (Croci et al. 2008, Conole and Kirkpatrick 2011). 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. Furthermore, habitat specialist species may suffer greater physiological stress from intensive anthropogenic land use than habitat generalists (Deikumah et al. 2015). High adult survival rate and high annual fecundity (Møller 2009), as well as nests located high above the ground or in cavities may facilitate urban adaptation (Croci et al. 2008, Conole and Kirkpatrick 2011).

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 (Davis and Wilcox 2013). Garden use may be encouraged by vegetated urban edges (Hodgson et al. 2007), habitat corridors (Wood 1993) and large percentages of vegetated areas (Cristaldi et al. 2017). Contrary to expectations, the proximity to remnant natural habitats is not always influential in structuring urban bird communities (Parsons et al. 2003). Novel risks (e.g. carnivorous domestic animals (Parsons et al. 2006, Paker et al. 2013)) and benefits (e.g. supplementary feeding and water (Galbraith et al. 2015)) in gardens may also influence urban adjustment.

The responses of nectarivorous birds are particularly important because of the mutualistic bird-pollinated plants

that depend on them. Pollination systems are expected to be affected by land-use changes and the manner in which they are affected will depend on pollinator foraging and dispersal behaviour and the vulnerability of mutualisms (Phillips et al. 2010). Habitat fragmentation, due to land-use change, can disrupt pollinator movement and result in lower seed set in pollinator-dependent plants (Volpe et al. 2016). However, there are also examples of pollinating birds that are tolerant of urban areas and continue to provide pollination services in these areas (Fontúrbel et al. 2017). This highlights the variation in responses among species and the need to investigate this in different parts of the world. Thus far, evidence from the Americas, India and Australia show that nectarivorous birds range from urban avoiders to urban exploiters (Blair 1996, Conole and Kirkpatrick 2011, Leveau 2013, Verma and Murmu 2015). Some of the biological and garden traits that determine species' responses include diet specialisation (Verma and Murmu 2015) and the abundance of flowering plants (Wood 1993). Nectar specialists (primarily dependent on nectar) and nectar opportunistic birds (occasionally feeding on nectar) (Johnson and Nicolson 2008, Brown et al. 2009) sometimes show different urban tolerances (Conole and Kirkpatrick 2011, Verma and Murmu 2015). In most cases studied so far, nectarivorous birds seem to prefer native over exotic garden plants (French et al. 2005, Daniels and Kirkpatrick 2006, Davis and Wilcox 2013, Paker et al. 2013).

The nectarivorous birds of Cape Town, South Africa, play an unusually important ecological role because of the highly asymmetrical pollination mutualism between birds and plants in this biodiversity hotspot (Rebelo et al. 1984, Myers et al. 2000). This city lies within the fynbos biome that hosts approximately 318 bird-pollinated plant species (Rebelo 1987), but only four resident nectar specialist bird species (Rebelo et al. 1984) and a number of nectar opportunistic species. What is more, the functional diversity of these birds is of importance since they are relatively specialised in terms of the plant species on which they feed (Rebelo et al. 1984, Brown et al. 2008, Geerts and Pauw 2009a) and consequently one species cannot necessarily replace another as a pollinator (Geerts 2016). Some of the nectar specialist species in Cape Town appear to be very sensitive to urban areas and do not penetrate deep into suburbia (Pauw and Louw 2012). Furthermore, one of these species, the Cape sugarbird *Promerops cafer*, seem to experience higher stress levels closer to urban areas, since these sugarbirds have a higher incidence of fluctuating asymmetry and stress bars on feathers (Mackay et al. 2017). There is thus a need to determine what the important factors are that facilitate urban adjustment of these birds. Such a study would also contribute to our knowledge gap of African urban bird ecology (Ortega-Álvarez and MacGregor-Fors 2011).

In this study, we assess garden bird assemblages in Cape Town to address two questions: 1) which biological traits of nectarivorous birds affect the assembly of urban bird

communities most? 2) Which garden traits are the most important predictors of the community assembly of nectar specialist and opportunistic species? To answer these questions we recorded biological traits including: habitat and diet specialisation, longevity, nesting location; and garden traits such as distance to natural habitat, garden size, plant diversity, numbers of carnivorous domestic animals and the presence of bird baths and sugar water and other bird feeders.

Methods

Study area

Cape Town, located in the southwest of South Africa, is one of the country's largest cities and the only one that contains a national park (Cilliers and Siebert 2012). The lowlands in this area have been extensively urbanised, but most of the mountains are currently protected and conserved (Rebello and Siegfried 1990). The city contains a remarkable 19 endemic vegetation types and 190 endemic plant species (Holmes et al. 2012). The native biodiversity is still highly threatened by urbanisation (Rebello et al. 2011). Fortunately, this city leads urban conservation management in South Africa (Holmes et al. 2012) by conserving habitat fragments. The study was focused on the Cape Town metropolitan (33°57'S, 18°24'E) and adjacent Drakenstein Municipal area, which encompasses 11027 km².

Data collection

To gain information on garden characteristics and bird assemblages, hard copy and online questionnaires were distributed to members of two urban bird clubs and other garden owners in the study area (Fig. 1). The questionnaire was aimed at citizens that are knowledgeable on bird and plant identification, but pictures were provided to avoid confusion of names. The questions were not limited to a specific season or time period and no information was gathered about the age of the garden, respondents' knowledge or their intensity of observations. Although respondents' observation efforts may be correlated with numbers of birds seen in a garden, all respondents were interested in birds and thus we do not expect large variation in their observation efforts. A total of 193 complete responses were returned.

We listed nine nectarivorous bird species in the questionnaire, and respondents reported the maximum number of each species seen at one time (applicable all year round), henceforth referred to as the number of birds. This included 5 nectar specialist species (*Promerops cafer*, *Anthobaphes violacea*, *Cinnyris chalybeus*, *Nectarinia famosa* and *Chalcomitra amethystina*) and 4 nectar opportunistic species (*Zosterops virens*, *Pycnonotus capensis*, *Ploceus capensis* and *Onychognathus morio*) (Supplementary material Appendix 1 Table A1). Birds were classified as specialist nectarivores if nectar was their main food source (as reported in Hockey et al. (2005)),

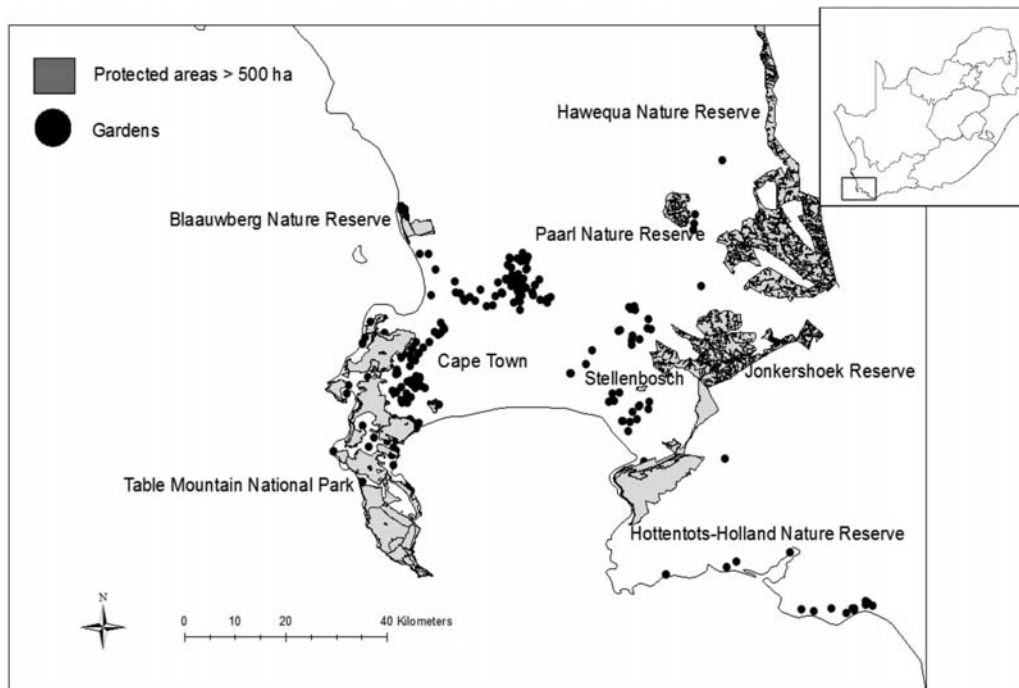


Figure 1. Location of study area and gardens. The insert on the right shows South Africa and indicates the location of the study area (enlarged map) with a black square. On the enlarged map, the black dots surrounding City of Cape Town and the town of Stellenbosch shows the 193 gardens included in this study. The grey areas represent protected areas and the white terrestrial areas include other natural as well as non-natural areas.

and the rest were classified as opportunists. All of these species (or close relatives) have been reported to pollinate flowers legitimately (Rebello 1987, Botes et al. 2008).

Biological traits

In order to test the effect of biological traits of birds on garden bird communities, we calculated bird frequency across all gardens for each species separately (the proportion of gardens in which a species is present). Frequencies were used instead of the maximum number seen, since the latter may be inflated for species that forage in groups. The amethyst sunbird *Chalcomitra amethystina* is a recent immigrant to the study area and thus its numbers were judged to be not comparable to the other resident species. Therefore, it was excluded from this analysis.

Biological 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 1, Supplementary material Appendix 1 Table A1): mean body mass, maximum adult longevity, number of habitats used by a species (habitat generalisation), nectar rank (the importance of nectar in their diet: 3 = main food, 2 = secondary food or 1 = occasional food), diet generalisation (number of food types used), mean annual clutch size and nest site (tree, shrub or any suitable structure).

Garden traits

Lastly, to test the effect of garden traits on bird communities, the number of birds reported in the questionnaires were summarised into four response variables: number of nectar specialist birds per garden; number of nectar opportunistic birds per garden; species richness of nectar specialists per garden and species richness of nectar opportunists per garden (Table 1).

Information on garden traits was gathered through the questionnaires (Table 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 georeferenced in Google Earth Maps and then imported into ArcGIS 10 (ESRI 2010) and combined with maps of the City of Cape Town Biodiversity Network and Drakenstein Critical Biodiversity Areas, compiled by the South African National Biodiversity Inst. (<<http://bgis.sanbi.org>>). 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 designated protected area, larger than 500 ha, was measured. The matrix between each garden and the nearest protected area was also scored as the predominant land use type along the straight line. This was scored as natural (greenbelts and conserved areas) or non-natural (urban, agricultural or plantations).

The estimated garden sizes (in square meters) and the percentages of gardens comprised of plants (including

Table 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 [†]			
Species frequency across all gardens	numerical	0.188–0.906	per species
Predictor variables [†]			
Longevity	numerical	6–20	years
Number of habitats used	numerical	1–8	
Nectar rank	integer	1–3	
Nest site	categorical	shrub/tree/all	
Effect of garden traits			
Response variables [†]			
Total max. no. of nectar specialist birds	numerical	0–53	per garden
Total max. no. of nectar opportunistic birds	numerical	0–118	per garden
Number of nectar specialist bird species	integer	0–5	per garden
Number of nectar opportunistic bird species	integer	0–5	per garden
Predictor variables [†]			
Distance to nearest protected area	numerical	0.001–20.887	km
Matrix	categorical	natural/non-natural	
Size of planted area	numerical	80–534 600	m ²
No. of indigenous plant genera	numerical	0–12	per garden
No. of introduced plant genera	numerical	0–4	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	

[†]Information obtained from questionnaires.

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

trees, shrubs and herbs and excluding lawn and hard surfaces) were also reported and were multiplied to obtain the size of area that is planted in the garden. Although this is a subjectively estimated variable, it is not biased in favour of or against the hypotheses. In the questionnaire, respondents reported the presence/absence of 17 locally common bird-pollinated garden plant genera. This included 13 native genera (*Protea*, *Mimetes*, *Leucospermum*, *Erica*, *Watsonia*, *Chasmanthe*, *Tecoma*, *Strelitzia*, *Aloe* and *Kniphofia* (grouped together), *Leonotus*, *Schotia* and *Erythrina*) and 4 introduced genera (*Eucalyptus*, *Hibiscus*, *Callistemon* and *Phormium*). For each garden, the total numbers of indigenous plant genera and introduced plant genera present were then calculated. Respondents also reported the numbers 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). A limitation of the study is that sugar water feeders and bird-pollinated plants may increase the detectability of nectarivorous birds rather than their true abundance. However, it seems unlikely that the results are solely due to this effect. Without exception, the nectarivorous birds in this study are highly visible and vocal. The observation period was sufficiently long to ensure that these birds would have been seen if they were present, regardless of the presence or absence of sugar water feeders.

Statistical analyses

Data exploration

All data exploration and analyses were conducted in R software (R Core Team). 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 variable. Collinearity was tested between explanatory variables (Zuur et al. 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 (Supplementary material Appendix 1 Table A2), but these were all weak relationships (correlation coefficients < 0.5) and thus all variables were included in the analyses.

Biological traits

For both biological traits and garden traits, an information-theoretic approach (Burnham et al. 2011) was used to determine which variables, or combinations of variables, best predict bird communities. A model set of 10 models was created with different combinations of the four selected biological traits. Each model was fitted with a generalised linear model with binomial error structures due to the non-normality of frequency data. 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 et al. 2011) using the MuMIn package in R (Barton 2012).

Garden traits

The prediction strength of ten garden traits was tested on the four response variables. For each response variable a set of 27 models was created (Supplementary material Appendix 1 Table A4). 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.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b20q512> (Coetzee et al. 2018).

Results

Biological traits

The model that included habitat generalism and nest site location as predictors of the frequency of the eight different bird species in gardens received full support ($w_i = 1$) (Table 2). Thus, species with greater habitat generalism and that nest in trees were more likely to occur in gardens than species that lacked these traits (Fig. 2, Supplementary material Appendix 1 Table A1 and Table A3).

Garden traits

The effect of garden traits could be analysed for 174 gardens. The number of specialist birds was strongly influenced by the combination of indigenous plants and sugar water feeders in gardens (Table 3). The two most supported models described the additive and interaction effects between these

Table 2. The set of five best-supported models describing which biological traits of nine nectarivorous birds predict their numbers in gardens. Models were tested with generalized linear models. 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†	K	L	AICc	Δ AICc	w_i
Habitats + nest site	4	−62.77	146.88	0	1
Longevity + habitats	3	−155.91	323.82	176.941	0
Habitats	2	−176.58	359.57	212.693	0
Habitats + nectar rank	3	−176.27	364.54	217.66	0
Nectar rank + nest site	4	−171.99	365.31	218.437	0

†habitats=number of habitats used by a species; nest site=tree, shrub or all; nectar rank=importance of nectar in the diet.

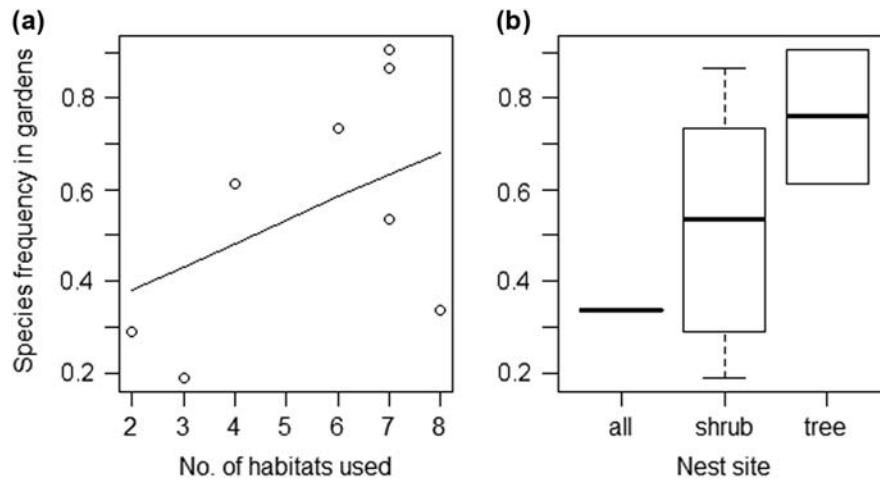


Figure 2. The biological traits that most strongly predicted the frequency of nectarivorous birds in gardens were (a) the number of habitats that a species uses and (b) its nest site location. Species frequency was positively related to habitat versatility ($z=10.55$, $p < 0.001$) and differed significantly based on the species' preferred nest site location (in trees, shrubs or on any suitable structure) ($z=9.43$, $p < 0.001$). Each point shows the frequency of a species across all sampled Cape Town gardens. In box plots, the solid line indicates the median, the box indicates the interquartile range, and whiskers show the range.

two predictor variables and had a collective Akaike weight of 0.974. The number of these birds was increased by higher plant diversity (Fig. 3a, $z=4.61$, $p < 0.001$) and by the presence of sugar water feeders (Fig. 3b, $z=3.68$, $p < 0.001$).

The number of nectar opportunistic birds was best predicted by two models that described the additive and interaction effects between the size of planted area and distance from protected area, with a collective Akaike weight of 0.804

Table 3. A summary of the top five models of garden traits predicting the number of nectarivorous birds in gardens. Predictions were made for the number of birds and the number of species of the specialist and opportunistic 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. An \times indicates interactions between variables.

Model*	K	L	AICc	Δ AICc	w_i
No. of specialist birds					
Indig. plants + sugar water feeder	4	-495	998.24	0	0.712
Sugar water feeder \times indig. plants	5	-494.94	1000.24	2	0.262
Indig. plants + bird bath	4	-499.23	1006.7	8.461	0.01
Distance PA + sugar water feeder	4	-500.04	1008.31	10.072	0.005
Indig. plants	3	-501.19	1008.51	10.274	0.004
No. of opportunistic birds					
Distance PA + planted area	4	-669.86	1347.95	0	0.546
Planted area \times distance PA	5	-669.55	1349.45	1.5	0.258
Planted area + sugar water feeder	4	-671.41	1351.06	3.104	0.116
Indig. plants + sugar water feeder	4	-672.42	1353.07	5.123	0.042
Sugar water feeder \times indig. plants	5	-671.85	1354.05	6.101	0.026
No. of specialist species					
Indig. plants + bird bath	3	-275.56	557.26	0	0.39
Indig. plants + sugar water feeder	3	-275.74	557.62	0.357	0.326
Sugar water feeder \times indig. plants	4	-275.48	559.19	1.93	0.149
Indig. plants	2	-277.69	559.46	2.193	0.13
Sugar water feeder + matrix	3	-280.93	567.99	10.73	0.002
No. of opportunistic species					
Sugar water feeder \times indig. plants	4	-281.61	571.45	0	0.52
Indig. plants + sugar water feeder	3	-283.53	573.21	1.758	0.216
Indig. plants + bird bath	3	-283.67	573.49	2.035	0.188
Indig. plants	2	-286.66	577.4	5.943	0.027
Planted area + bird bath	3	-286.33	578.8	7.346	0.013

*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); indig. plants=number of indigenous plant genera.

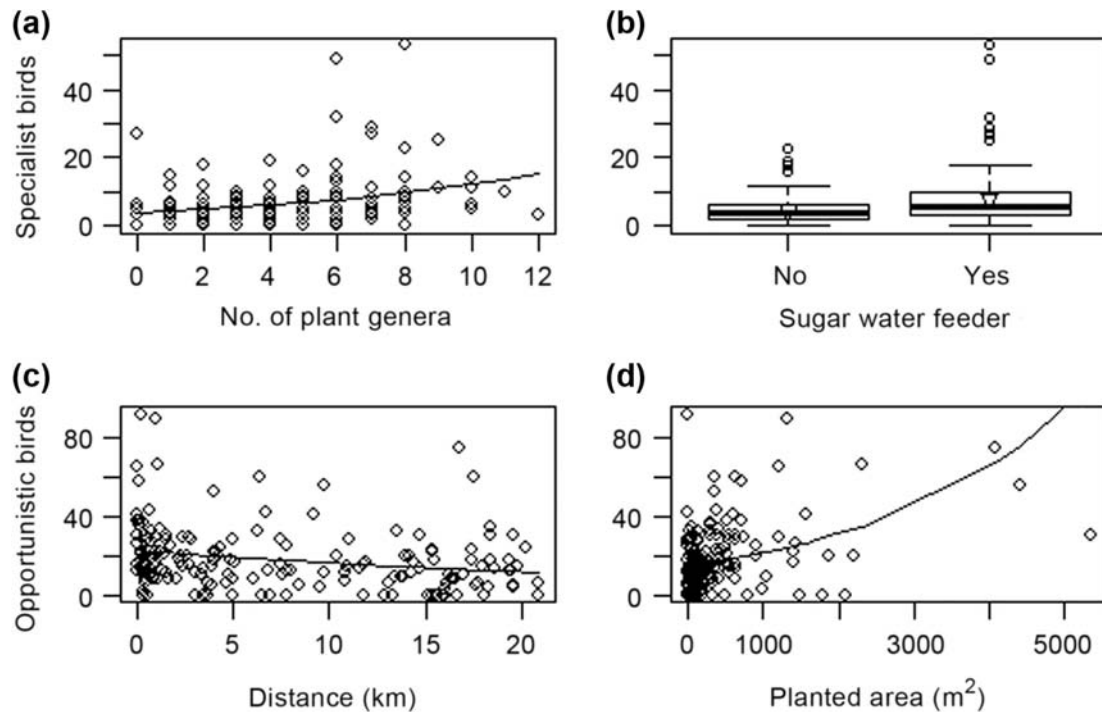


Figure 3. Garden traits identified as the most important predictors of the numbers of nectarivorous birds in gardens in Cape Town, South Africa. All relationships were significant. In scatter plots, regression lines are estimated by generalized linear models. In box plots, thick solid lines indicate medians, triangles show the means, the boxes indicate the interquartile ranges, whiskers show the ranges and dots are outliers.

(Table 3). Their numbers decreased with greater distance from protected area (Fig. 3c, $z = -2.99$, $p = 0.003$) and increased in larger planted area (Fig. 3d, $z = 3.58$, $p < 0.001$).

For species richness of specialist birds, the top three models differed by less than two AICc values and had a collective weight of 0.865 (Table 3). These models represent the collective presence of indigenous plants with bird baths and with sugar water feeders. Specialist bird species richness increased with indigenous plant diversity (Fig. 4a, $z = 4.64$, $p < 0.001$) and the presence of sugar water feeders (Fig. 4b, $z = 2.86$, $p = 0.004$) and bird baths (Fig. 4c, $z = 2.86$, $p = 0.004$).

Similarly, the species richness of nectar opportunistic birds was also increased by greater plant diversity (Fig. 4d, $z = 3.52$, $p < 0.001$) and the presence of sugar water feeders (Fig. 4e, $z = 2.69$, $p = 0.007$). The top two models contained the combination of these two predictor variables with a collective Akaike weight of 0.736. In most cases, models that included the number of introduced plant genera, cats and/or dogs were not well supported (Supplementary material Appendix 1 Table A5).

Discussion

This study shows that habitat generalism, tree nesting ability, the presence of dispersal barriers, and supplemental food and water sources in gardens most strongly affect the guild

of urban nectarivorous birds. In contrast, introduced plants and carnivorous domestic animals seem to be unimportant in structuring these communities.

Habitat generalism and tree nesting promote urban adjustment. In North American birds, innovation rate is related to versatile habitat use (Overington et al. 2011), thus an innovative ability may make species more likely to adapt to urban habitats (Tryjanowski et al. 2016). Habitat specialist species, on the other hand, may lack innovative abilities and may be much more easily stressed by novel environments (Deikumah et al. 2015). Ecological specialisation may be one of the most important factors that prevent species across all taxa from adjusting to urban areas (Concepción et al. 2015). The prevalence of canopy nesting birds in urban areas have been noted across continents (Chace and Walsh 2006, Croci et al. 2008, Conole and Kirkpatrick 2011), which may be due to a lower vulnerability to disturbance and cat predation in urban environments.

Dispersal barriers and the sizes of vegetated areas influenced the numbers of nectar opportunistic birds in gardens. Firstly, the fact that their numbers gradually decreased with increasing distance to the nearest protected area suggests that the urban environment poses a barrier, even though it is penetrable. Importantly, this is not an artefact of several garden traits differing consistently with distance from protected area. This distance was only associated with the presence of sugar water feeders (Supplementary material Appendix 1 Table A2), thus the shortage of this supplemental food resource in the

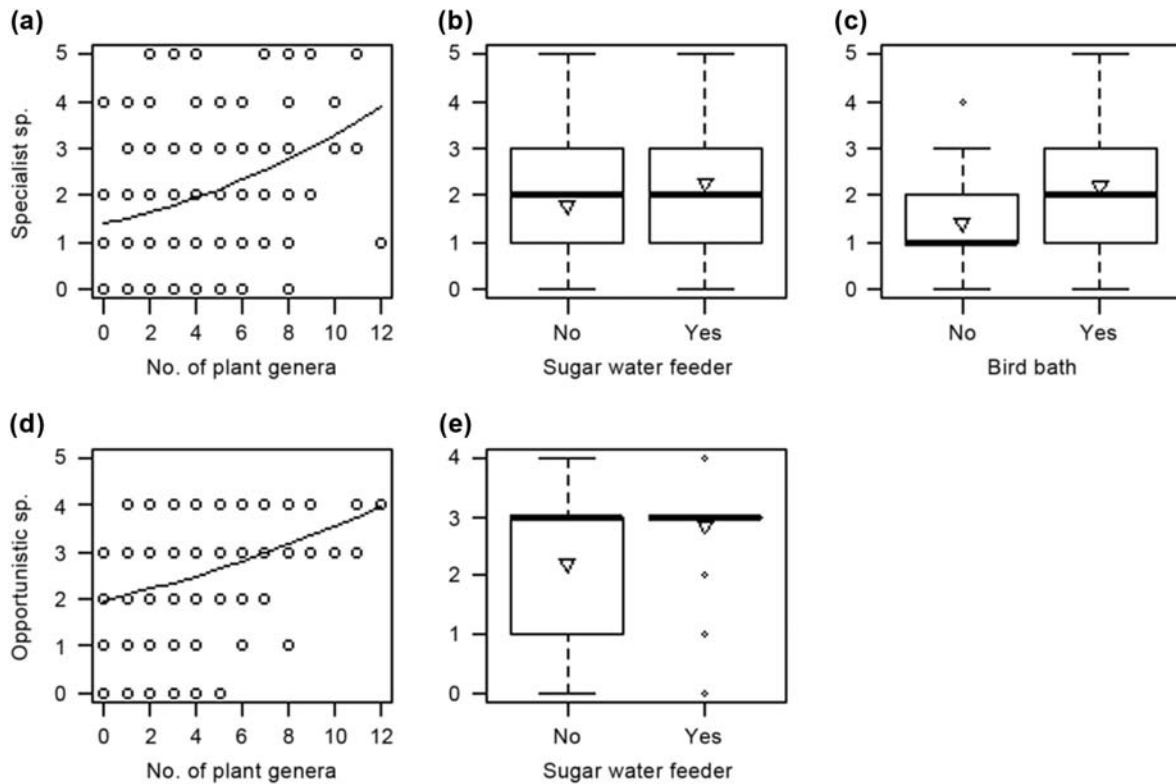


Figure 4. The most important garden traits predicting species richness of nectarivorous birds in gardens of Cape Town, South Africa. All relationships are significant. In scatter plots, regression lines are estimated by generalized linear models. In box plots, thick solid lines indicate medians, triangles show the means, the boxes indicate the interquartile ranges, whiskers show the ranges and dots are outliers.

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 to their proximity to protected areas (Sanz and Caula 2015). Urban environments are likely to pose even greater barriers to less mobile taxa (Concepción et al. 2015, Olivier et al. 2016). Secondly, the successful urban adjustment of nectar opportunistic birds is facilitated by large vegetated areas. Large planted areas provide shelter and nest sites, but it is probably the diversity of food types among plants that attract these species, since they are primarily insectivores and frugivores. In contrast, the nectar specialists were not sensitive to the size of planted area, despite the fact that sunbirds show a preference for dense vegetation in natural habitat (Larsson and Hemborg 1995).

Natural and artificial nectar resources, in the form of indigenous bird-pollinated plants and sugar water feeders, seem to facilitate the existence of nectarivorous birds in urban areas. The diversity of indigenous plants increased the abundance of nectar specialists and species richness of both specialist and opportunistic nectarivorous birds. One of the reasons may be that a diversity of plant genera provides nectar for longer periods due to variation in flowering times among genera and species (Feinsinger 1976, Waser and Real 1979, Coetzee 2016). Furthermore, species richness may be increased due to the preferences of different bird species: *Promerops cafer*

feed largely from Proteaceae plants, *Anthobaphes violacea* feed predominantly on *Erica* (Rebello et al. 1984), while *Nectarinia famosa* forages mostly from very long-tubed flowers (Geerts and Pauw 2009a) and some nectar opportunistic species prefer flowers with hexose dominant nectar in low concentrations (Brown et al. 2010, 2012, Odendaal et al. 2010).

Sugar water feeders attracted a greater number of nectarivorous bird species and greater numbers of nectar specialist birds, likely because feeders provide a super abundant food source. Such feeders can facilitate urban adjustment by contributing to reducing birds' sensitivity to human disturbance (Møller et al. 2015). Evidence from a nectarivorous hummingbird species (Greig et al. 2017) and other bird species (Zuckerberg et al. 2017) shows that feeders may ultimately affect species' ranges. It is uncertain what the implications of artificial feeders are for the pollination mutualisms in which these birds are involved. 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 (Parsons et al. 2003, Davis and Wilcox 2013). 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 and Altizer 2007). Secondly, birds may

be overconsuming sugars at feeders that lead to imbalances in their diets, which would require them to consume more water and arthropods (their protein source) (Nicolson and Fleming 2003, Schaefer et al. 2003). Thirdly, these super abundant, easily accessible nectar sources may attract birds away from natural plants (Arizmendi et al. 2007), which rely on their pollination services. However, a recent study on hummingbirds found no negative effects of feeders on pollen deposition of bird-pollinated plants (Sonne et al. 2016). Still, the seasonal patterns of nectarivorous birds' use of urban nectar resources require investigation.

Bird baths tended to increase the species richness of nectar specialist birds in gardens. This may be due to both their benefit for drinking and bathing. Sunbirds are known to drink water to maintain water and energy balances (Nicolson and Fleming 2003). Experimental studies on *Sturnus vulgaris* show that recent bathing affects the feather structure so that it slows a bird's flight down, but allows more accurate escape flight (Brilot et al. 2009).

Although these nectarivorous birds have been recorded visiting introduced plant species (Geerts and Pauw 2009b), the diversity of introduced plants was not an important factor influencing community assembly. It may be that introduced plants are less preferred resources, but the result may also be due to the fact that we included only a few introduced plant genera in the questionnaire. Likewise, the presence of carnivorous domestic animals was not an important influence on the number of birds in gardens. The same result was found in studies of Australian garden birds (Daniels and 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 et al. (2015) showed that birds take longer to use feeders the more cats there are present.

In summary, this study identifies factors that inhibit urban adjustment of nectarivorous birds. South African urban nectarivorous bird communities were larger and more species rich in gardens with indigenous and artificial nectar sources. Habitat generalists and tree nesting species have adjusted better to urban areas, while dispersal barriers and small planted areas limit the number of nectar opportunistic birds. This knowledge may help to improve urban landscape planning so that connectivity between natural habitat fragments can be maintained and extinction risk of bird-pollinated plants can be reduced. The results also highlight that ecological specialists are more sensitive to new environments, and since they are often key role players in their ecosystems, extra effort may be required to improve their adjustment. In general, both biological traits (habitat and diet versatility) and habitat traits (food sources) can promote urban adjustment by nectarivorous birds.

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Supplementary material (Appendix JAV-01526 at <www.avianbiology.org/appendix/jav-01526>). Appendix 1.