Effectiveness of protected areas for bird conservation depends on guild

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Abstract

Aim: Protected areas are key conservation tools intended to increase biodiversity and reduce extinction risks of species and populations. However, the degree to which protected areas achieve their conservation goals is generally unknown for many protected areas worldwide. We assess the effect of protected areas on the abundance of 196 common, resident bird species. If protected areas were beneficial to avian biodiversity, we expect landscapes with a higher proportion of protected areas will have higher densities of species compared to landscapes with no protection.

Location: Greater Gauteng region, South Africa.

Methods: We analysed bird survey data collected over regular grid cells across the study area. We estimated bird abundance in relation to the proportion of a grid cell that was protected with the Royle–Nichols model and fitted the model once for each of the species. We examined variation in estimated abundance as a function of avian guild (defined by the type of food a species preferentially ate and its foraging mode) with a regression tree analysis.

Results: Abundance was significantly positively related to the proportion of protected areas in grid cells for 26% of the species, significantly negatively related in 15%, and not significantly related in 59% species. We found three distinct guild groups which differed in their average abundance, after accounting for associated variance. Group 1 consisted of guilds frugivores, ground-feeders, hawkers, predators, and vegivores and average abundance was strongly positively related to the proportion of protected areas. Group 2 included granivores, and average abundance was strongly negatively related to proportion of protected areas. Group 3 included gleaners only, and average abundance was not related to proportion of protected areas.

Main conclusion: We conclude that the network of protected areas within the greater Gauteng region sustained relatively higher abundances of common birds and thus perform an important conservation role.

KEYWORDS
Avian conservation, citizen science, hierarchical models, protected areas, species abundance

1 | INTRODUCTION

Protected areas are geographic areas set aside and managed for conservation of nature, ecosystem services and cultural values (IUCN, 1994). They are a key tool used to conserve biodiversity and are central to virtually all national and international conservation efforts (Gaston et al., 2008). The successful contribution of protected areas to biodiversity conservation is globally recognized, and every year billions of U.S. dollars are spent to maintain, improve and develop protected areas (Balmford, Gaston, Blyth, James, & Kapos, 2003). In 2011, there were approximately 160,000 protected areas worldwide, covering an estimated 12% of the earth's land surface (IUCN, 2011). One of the Aichi targets specifically aims to increase this to 17% by 2020 (United Nations, 2013), testament to protected areas' perceived importance for conservation of the world's biodiversity.

Most protected areas are developed and maintained to conserve particular species or habitats. For example, the Addo Elephant National Park in South Africa was designed to conserve elephants (Swemmer & Taljaard, 2011), or the Great Barrier Reef Marine Park in Australia was designed to protect corals and associated marine communities (GBRMPA, 2009). A substantial body of work examining the effect of protected areas on biodiversity confirms that these parks are effective at conserving the target species or habitat (Geldmann et al., 2013; Owen-Smith, Kerley, Page, Slotow, & van Aarde, 2006; Watson et al., 2011). However, it is not clear whether protected areas are generally also effective at protecting non-target species. Despite some keystone species or focal habitats benefiting within large, national protected areas, some of the remaining biodiversity may decline (Craigie et al., 2010; Hoekstra, Clark, Fagan, & Boersma, 2002; Watson, Dudley, Segan, & Hockings, 2014). For example, the Maasai Mara National Reserve is a wildlife sanctuary situated in the south of Kenya and was inaugurated in 1961. Its primary conservation goals include conserving mammalian wildlife, specifically, endangered carnivores. This goal has largely been achieved as lion densities have remained high since the onset of conservation programmes (Ogutu & Dublin, 2002), although other non-target species have declined in density, such as wildebeest (Newmark, 2008; Ottichilo, De Leeuw, & Prins, 2001), vultures (Virani, Kendall, Njoroge, & Thomsett, 2011) and ungulates (Ogutu, Owen-Smith, Piepho, & Said, 2011). Thus, managing an area for protection of one group or species does not necessarily protect all wildlife species, nor does it ensure the presence of specific species or taxa (van Jaarsveld et al., 1998). This suggests that there are still critical gaps in knowledge of how effective protected areas are at protecting biodiversity in general.

In this study, we use bird abundances to explore the broadscale ecological effectiveness of protected areas on avian biodiversity. Birds are good group to study because they are easily monitored, widespread, well-studied and occupy many niches (Furness & Greenwood, 1993). Furthermore, they are mobile and easily travel between areas with different land uses, which should allow them to react more quickly to changes in habitat quality. We consider common, resident bird species over the study area. Common species tend to be abundant, widespread, and in general,

drive patterns in biodiversity and ecosystem functionalities such as community assemblages, species richness, primary productivity and nutrient cycling (Gaston & Fuller, 2008; Lennon, Beale, Reid, Kent, & Pakeman, 2011; Winfree, Fox, Williams, Reilly, & Cariveau, 2015). Even slight declines in common species can have disproportionately negative effects on ecosystem functioning and indicate significant losses of ecosystem health (Gaston, 2010; Winfree et al., 2015). Therefore, monitoring how well common species fare in protected areas can give insight into the ecological health of protected areas. Here, we examine how the abundance of common species is affected by protected areas. If protected areas are beneficial for avian biodiversity in general, we expect higher bird abundances within protected areas relative to non-protected areas.

2 | METHODS

2.1 | Species detection/non-detection data

We used data from the second Southern African Bird Atlas Project (SABAP2). This project was initiated in June 2007 (Harebottle, Smith, Underhill, & Brooks, 2007) and was still ongoing in 2017. Because the statistical models we used assume abundances of common birds remain similar for the duration of the study, we restricted the analysis to data from years 2014 to 2015. These were the most data-rich years and together made up 62% of the total data volume collected during SABAP2, up to February 2016. Registered volunteers collected checklists of all bird species observed within a regular, pre-defined area called a pentad, which is a $5' \times 5'$ grid cell (approximately 61 km^2). Our study area covers 576 pentads (a 24 pentad by 24 pentad grid), for which 10,400 checklists were submitted at an average of 18 checklists per pentad; the maximum number of checklists submitted for a single pentad was 468, and the minimum was 1 (all pentads were visited). Similar to Broms, Johnson, Altwegg, and Conquest (2014), we used at most 100 checklists per pentad. Where pentads had more checklists than this, 100 were randomly selected. This was done because some pentads were extremely well sampled relative to the others.

Submitted checklists must have involved at least 2 hr of dedicated birding and can be collected over a period of up to five consecutive days. Volunteers were asked to record each species only once, regardless of how many individuals were seen. Not all areas inside the pentad were surveyed, but observers were asked to try to sample all habitats. Submitted checklists were examined thoroughly to identify possible misidentifications. When a species was reported from a pentad in which it had not previously been recorded, a vetting committee requested more information from the volunteer and then accepted or rejected the record (Harebottle et al., 2007).

2.1.1 | Species selection

Within the study area, we chose 207 common, resident bird species as defined by Hockey, Dean, and Ryan (2005). We included data that
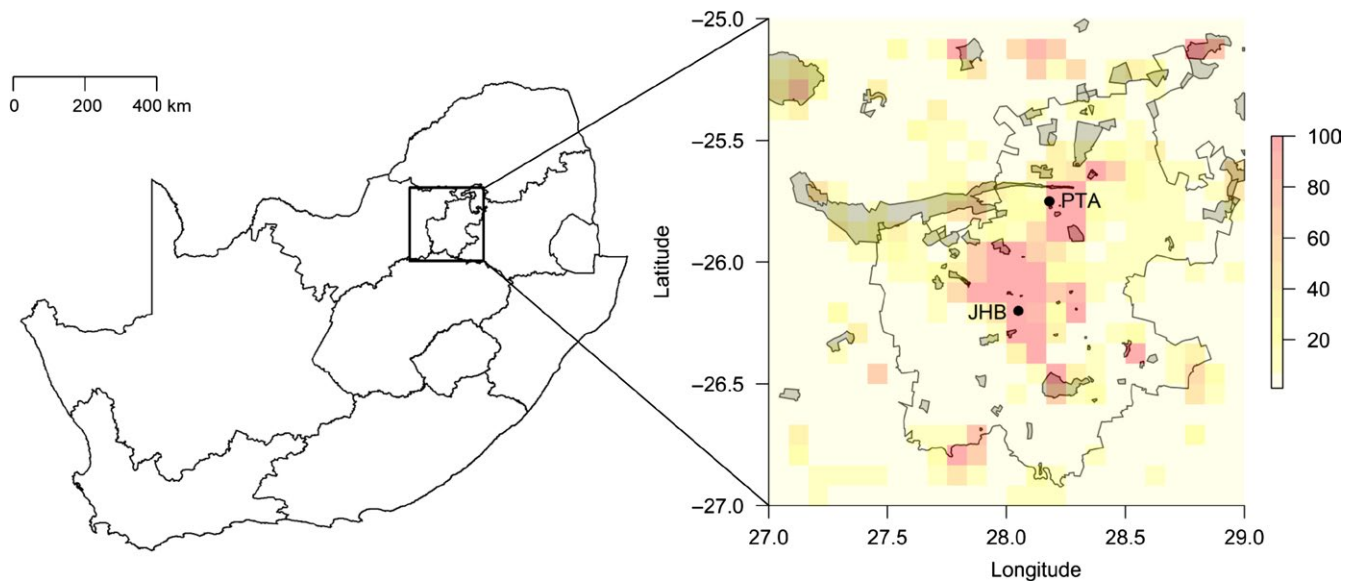
FIGURE 1 The study area was the greater Gauteng region of South Africa and covers approximately 35,000 km². The left panel shows South Africa, and the relative location of the study area. The right panel is the enlarged study area. Coloured squares show the pentads (one pentad is a 5′ × 5′ grid cell), and the colour scale indicates sampling effort (the minimum was one checklist, and we capped the maximum at 100). The shape outlined by a dark line is Gauteng Province in South Africa. The areas shaded in grey are protected areas (public and private) [Colour figure can be viewed at wileyonlinelibrary.com]

were collected between 1 January 2014 and 31 December 2015 and had been submitted to the project by February 2016.

2.2 | Study area

We selected the greater Gauteng Province, South Africa, as the study area (comprising of a square with coordinates NW: 25S 27E, SE:27S 29E) because of its good mix of protected areas and heavily modified landscapes situated near to each other (Figure 1). Gauteng is the most densely populated province in South Africa with average human density of 675.1 people per km² (Statistics South Africa, 2012). This ensures the study area was well atlassed, and that our data were of sufficient volume for our analyses (see below) and accurately represented the bird community. The study area covered approximately 35,000 km², of which 6.4% (approximately 2,240 km²) is protected (South African National Biodiversity Institute, 2009), either privately or publicly. The proportion of protected areas per pentad ranges from 0 to 1. The study area incorporates 81 protected areas, ranging in size from 0.08 km² to 816.70 km², at an average of 27.65 km². Vegetation is a major driver of bird diversity in our study area, which contained the vegetation types savanna (in the north) and grassland (in the south).

2.3 | Analyses

2.3.1 | Abundance models

We used abundance models to estimate bird abundances across the study area. Abundance models fall under the broader category of occupancy models (MacKenzie et al., 2006; Royle & Nichols, 2003), which are often used to analyse ecological atlas data. They recognize

that species can go undetected during surveys of sites where they occur. Occupancy models account for this by including a component which models the detection process separately from the biological process (abundance in this case). Failure to account for the detection process may lead to biased results (Altwegg, Wheeler, & Erni, 2008; Bailey, Mackenzie, & Nichols, 2014; Kéry, 2011).

Model structure

We used the Royle–Nichols abundance model (Royle & Nichols, 2003) to estimate the average latent abundance of individuals in pentad i (N_i). The model exploits the relationship between species detection probability, individual detection probability and latent abundance, with the following equation:

$$p_{ij} = 1 - (1 - r_{ij})^{N_i}, \qquad (1)$$

where p_{ij} indicates the probability of detecting the species in pentad i during survey j, r_{ij} the probability of detecting an individual in pentad i during survey j and N_i the latent abundance in pentad i.

The detection probability for a single individual in pentad i during survey j (r_{ij}) is modelled as a Bernoulli process:

$$\omega_{ij} \sim \text{Bernoulli}\,(r_{ij}), \qquad (2)$$

and variation in r_{ij} was modelled with survey specific covariates using a logit link function:

$$\text{logit}(r_{ij}) = \alpha_0 + \alpha_1 \times \hbar_{ij}, \qquad (3)$$

where $\hbar_{ij}$ indicates the log of the number of hours spent birding in pentad i during survey j, and the α are coefficients to be estimated by the model.

Latent abundance in pentad i (N_i) was modelled using a Poisson process with rate parameter λ in the following form:

$$N_i \sim \text{Poisson}(\lambda_i), \tag{4}$$

λ was modelled with pentad-specific covariates using the log link function:

$$\log(\lambda_i) = \beta_0 + \beta_1 \times PA_i + \beta_2 \times S_i, \tag{5}$$

where for pentad i, PA_i is the proportion of protected areas, and S_i the proportion of savanna vegetation. Grassland and savanna are the major vegetation types in the study region, and together make up 99% of the vegetation in the study area (therefore, only savanna or grassland vegetation need be included in the model; including both will confound the model). The β are coefficients to be estimated by the model, and we fitted a single model for each of the 207 species considered.

β_1 estimates the relationship between abundance and the proportion of the grid cell covered by protected areas. We interpret positive β_1 estimates as an indication that the species benefits from protected areas and is more abundant inside protected areas than outside. We interpret negative β_1 estimates as an indication that the species is relatively more abundant outside protected areas than inside them. We included the vegetation parameter (β_2 in equation 5) to account for the effects of vegetation on bird abundance and to estimate the effects of protected areas on abundance more accurately. Therefore, we do not focus on parameter β_2 in extensive detail here.

As the N_i are unknown, it is necessary to sum over reasonable values for species abundance (K) when maximizing the model likelihood. We used an estimate $K = 100$ for all species in the models and checked that the estimated abundances were always well below this value.

A key assumption of the Royle–Nichols abundance model is that the population remains demographically closed over the study period (i.e., no gains and losses of individuals). We restricted our analysis to common, resident species whose densities were unlikely to change significantly over the duration of the study. We used package "unmarked" (Fiske & Chandler, 2011) in program R version 3.0.1 (R Development Core Team, 2016) to run the abundance models.

2.3.2 | Regression tree and guilds

We further examined variation among species in β_1 using a regression tree implemented with the R package RPART (Therneau, Atkinson, & Ripley, 2017). Regression trees group observations as a function of multiple predictor variables (Breiman, Friedman, Olshen, & Stone, 1984). They recursively split the response up into nodes, dependent on the predictor variables, in a way that minimizes the remaining variance. The node after which there are no more splits is termed a "terminal" node. Each terminal node can be viewed as a group or cluster, as they are similar in terms of their response.

To account for the variable precision with which the β_1 were estimated, we weighted them by the inverse of their standard error to obtain a weighted β_1 ($w\beta_1$). This gives a higher weight to the more

precisely estimated coefficients (i.e., those with a smaller standard error) in the overall average calculation.

We assigned species to guild level, based on the type of food the species preferentially consumes and its primary foraging mode, taken from Hockey et al. (2005). We identified seven different guilds: frugivores (primarily consume fleshy fruit), gleaners (insects and invertebrates from foliage), ground-feeders (insects and invertebrates from the ground), granivores (seeds and grains), hawkers (insects and invertebrates from the air), predators (vertebrate carnivores) and vegivore (vegetative plant matter). In our regression tree model, we modelled the weighted β_1 estimates of each species as a function of the guild to which each species belongs.

3 | RESULTS

3.1 | Estimated abundance in relation to proportion of area protected

A single Royle–Nichols abundance model was fitted for each of the 207 species. Models for 11 species failed to converge, likely due to data sparsity. This left 196 species to which the remainder of the results refer. The parameter β_1 measures the slope of the linear (on the log scale) relationship between mean local abundance of each species and the proportion of protected areas per pentad, while accounting for the observation process. Species with a positive estimate for β_1 were relatively more abundant in pentads with a high proportion of protected areas, and this was interpreted as the species having higher abundance inside protected areas, whereas a negative estimate for β_1 indicates the opposite. On average across all species, estimated abundance was shown to be higher inside protected areas than outside because mean $\hat{\beta}_1$ was slightly positive (0.12, range from −4.53 to 4.23 across species). Of the 196 species, 50 (26%) had a positive $\hat{\beta}_1$ and confidence intervals; 30 species (15%) had negative $\hat{\beta}_1$ and confidence intervals; 116 species (59%) had their confidence intervals overlap zero (Figure 2).

3.2 | Regression tree and guilds

The regression tree identified three distinct groups that differed markedly in their $\hat{\beta}_1$ estimate. Group 1 consisted of guilds frugivores, ground-feeders, hawkers, predators and vegivores. On average, and accounting for error associated with each $\hat{\beta}_1$ estimate, they were strongly more abundant inside pentads with a higher proportion of protected areas, ($w\hat{\beta}_1 = 0.34$, $n = 121$; Table 1), which we infer as being more abundant within protected areas than outside of them. Group 2 comprised of gleaners, which neither increased nor decreased in average estimated abundance with an increase in protected areas ($w\hat{\beta}_1 = 0.0$, $n = 30$; Table 1). From this, we infer that on average, gleaners were as abundant within protected areas as they were outside of them. Group 3 included granivores, which were, on average, much less abundant within pentads with a higher proportion of protected areas ($w\hat{\beta}_1 = −0.35$, $n = 45$; Table 1). Thus, we infer granivores were, on average, much less abundant within protected areas than outside

of them. Model results for each species, and the guild group to which it belongs are located in the supporting information (Table S1).

3.3 | Relative estimated abundances per group across the study area

To examine spatial patterns in estimated abundance in more detail, we predicted the average estimated abundance in each pentad for each species, using the coefficients as estimated by the Royle–Nichols model, and the pentad-specific covariate values. We then calculated the average estimated abundance for each of the three groups for each pentad (Figure 3). This figure clearly shows a higher estimated average abundance of group 1 species inside protected areas, a lower estimated average abundance of group 3 species
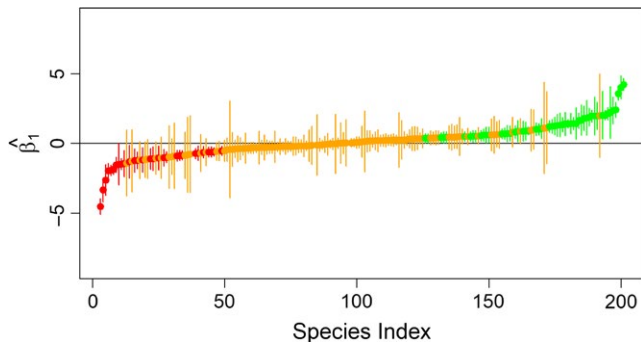

FIGURE 2 Estimated slope of the linear (on the log scale) relationship between abundance and proportion of protected area per pentad for 196 common bird species in the greater Gauteng area in South Africa over the period January 2014–December 2015. The species are sorted by magnitude of this slope, and the vertical lines are 95% confidence intervals. Red dots and lines indicate species with estimated mean and confidence intervals <0 (assumed to be less abundant inside protected areas). Green dots and lines represent those species with estimated mean and confidence intervals >0 (assumed to be more abundant inside protected areas). Orange dots and lines represent species with confidence intervals that overlapped zero and were not significantly influenced by the proportion of protected areas [Colour figure can be viewed at wileyonlinelibrary.com]

inside protected areas, and on average, similar estimated abundances for group 2 species inside and outside of protected areas. Confirming the importance of vegetation for avian diversity, estimated abundances for gleaners were higher in the northern part of our study area, occupied by savanna vegetation. Grassland occupies the southern half.

4 | DISCUSSION

Protected areas are one of the most important tools for biodiversity conservation. It is therefore critical to know how well they perform this function. In this study, we examined how protected areas affected the abundance of common, resident bird species in South Africa. As birds are well monitored, easy to observe (this particularly applies to common birds) and are good indicators of ecosystem health (Furness & Greenwood, 1993; Gaston, 2010; Winfree et al., 2015), decreases in their abundance, especially within protected areas, can indicate a decline of ecosystem functionality. We found that for most species, estimated abundance increased with the proportion of protected area within a pentad. However, this relationship varied strongly among species and was in part explained by differences in guild.

Our results suggest that, on average, ground-feeding and hawking insect eaters, frugivores, vegivores and predatory birds were more abundant in pentads with a higher proportion of protected areas, whereas granivores were relatively less abundant in such pentads. The estimated average abundance of gleaners was not affected by the proportion of protected areas (Table 1). Our results are consistent with other studies conducted in South Africa which find that in general, common species are more abundant within protected areas compared with outside of them (Child, Cumming, & Amano, 2009; Greve, Chown, van Rensburg, Dallimer, & Gaston, 2011), as well as elsewhere throughout the world (Coetzee, Gaston, & Chown, 2014; Gray et al., 2016; Laurance et al., 2012). Thus, our results show that protected areas are supporting a rich diversity of common bird species. Because common birds are good indicators of ecosystem health and functioning (Furness & Greenwood, 1993;
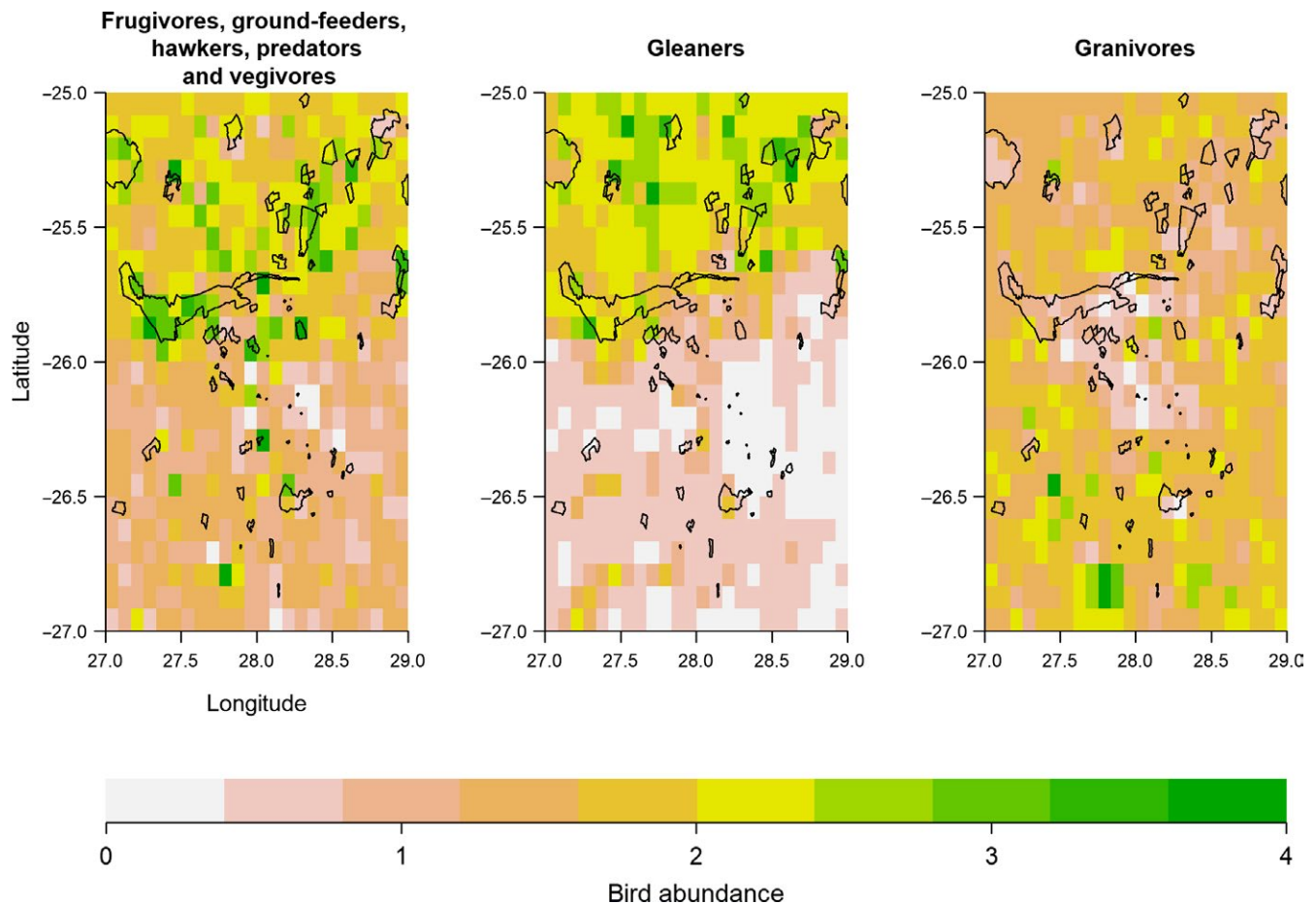
TABLE 1 Summary statistics of groups identified by a regression tree analysis modelling the relationship between estimated abundance and the proportion of protected area per pentad ($\hat{\beta}_1$ estimates taken from the Royle–Nichols abundance model) as a function of guild. $w\hat{\beta}_1$ indicates the weighted mean of $\hat{\beta}_1$ (see Methods text for details on this calculation). We considered only common and resident bird species in the greater Gauteng area of South Africa over the period 2014–2015, totalling 196 species. A positive estimate for $w\hat{\beta}_1$ indicates that group is, on average, more abundant within pentads with a higher proportion of protected areas, and the opposite is true for negative $w\hat{\beta}_1$ estimates

Group classifications	Guild	n	$w\hat{\beta}_1$ of Guild	$w\hat{\beta}_1$ of group
	Frugivores	9	0.35	
	Ground-feeders	63	0.34	
Group 1	Hawkers	11	0.24	0.34
	Predators	19	0.50	
	Vegivores	19	0.29	
Group 2	Gleaners	30	0.00	0.00
Group 3	Granivores	45	−0.35	−0.35
	Σ 196			

FIGURE 3 Estimated bird abundances per pentad averaged across all species within each of the three distinct groups identified by the regression tree analysis. Abundance predictions from Royle–Nichols abundance model run singly for each of the 196 common species examined within the greater Gauteng area over January 2014–December 2015. The plots from left to right correspond to groups 1–3 in Table 1. The colour of the pentad refers to the average abundance estimate: white pentads correspond to a lower estimated abundance and green (darker) ones to a higher abundance estimate. The outlined shapes are protected areas, both public and private. On average, guilds frugivores, ground-feeders, hawkers, predators and vegivores (group 1) were more abundant in pentads with a higher proportion of protected areas. Gleaners (group 2) were, on average, neither more abundant nor less abundant in pentads with a higher proportion of protected areas. Conversely, granivores (group 3) were less abundant, on average, in pentads with a higher proportion of protected areas [Colour figure can be viewed at wileyonlinelibrary.com]

Gaston, 2010; Winfree et al., 2015), our results suggest protected areas over the study area successfully maintain relatively healthy and functioning habitats.

The conservation benefit provided by protected areas to biodiversity can be dependent on the type of land surrounding them (DeFries, Hansen, Turner, Reid, & Liu, 2007; Hansen & Defries, 2007; Laurance et al., 2012). This is especially true for birds because they are a very mobile species and can travel easily between multiple land uses within a landscape. Our study primarily comprised of protected areas, urban and agricultural land use types. The level of protection provided by protected areas to a species may depend on the degree to which the species is able to adapt to neighbouring land use types (or, to habitats disturbed due to human-related activity). Group 1 includes many species recorded to adapt poorly to disturbed habitats (including human-modified landscapes), or are habitat specialists (Chace & Walsh, 2006; Greve et al., 2011; Rayner, Lindenmayer, Wood, Gibbons, & Manning, 2014; Santos,

Pino, Rodà, Guirado, & Ribas, 2008; Thomas et al., 2012). Thus, for these species, protected areas play an important conservation role, as they provide natural and undisturbed habitat in which they may persist. For example, in our case, these include ground-feeder species such as cape rock thrush (*Monticola rupestris*, $\hat{\beta}_1$ = 4.23), sentinel rock thrush (*Monticola exploratory*, $\hat{\beta}_1$ = 3.56), plain-backed pipit (*Anthus leucophrys*, $\hat{\beta}_1$ = 2.13); vegivores including the cape bunting (*Emberiza capensis*, $\hat{\beta}_1$ = 2.40) and red-winged francolin (*Scleroptila levaillantii*, $\hat{\beta}_1$ = 2.21); predators including African grass owl (*Tyto capensis*, $\hat{\beta}_1$ = 2.02), jackal buzzard (*Buteo rufofuscus*, $\hat{\beta}_1$ = 1.96), rock kestrel (*Falco rupicolus*, $\hat{\beta}_1$ = 1.82); hawkers including rock martin (*Ptyonoprogne fuligula*, $\hat{\beta}_1$ = 0.87), fiery-necked nightjar (*Caprimulgus pectoralis*, $\hat{\beta}_1$ = 0.81); and finally, frugivores including yellow-fronted tinkerbird (*Pogoniulus chrysoconus*, $\hat{\beta}_1$ = 1.11) and dark-capped bulbul (*Pycnonotus tricolor*, $\hat{\beta}_1$ = 0.61). Generally, our results indicate that protected areas play an important role to the persistence of many species within group 1.

Conversely, granivores were more abundant in pentads with lower proportions of protected areas (group 3, Table 1). Granivores can be opportunistic, adapt quickly to new environments (Beissinger & Osborne, 1982; Chace & Walsh, 2006) and benefit from additional food sources and variety of nesting and roosting spots available in urban and agricultural land use types (Chace & Walsh, 2006; Gaston & Evans, 2004). Thus, our study suggests granivores favoured the conditions offered in urban and agricultural land use types over those provided by protected areas. Indeed, granivores with the most negative $\hat{\beta}_1$ included the village indigobird (*Vidua chalybeate*, $\hat{\beta}_1 = -2.63$), scaly-feathered finch (*Sporopipes squamifrons*, $\hat{\beta}_1 = -1.93$), red-headed finch (*Amadina erythrocephala*, $\hat{\beta}_1 = -1.86$) and red-capped lark (*Calandrella cinereal*, $\hat{\beta}_1 = -1.55$), all of which have been shown to adapt well to agricultural land use types in South Africa (Barnard, 1997; Dean, 1997; Herremans, 1997a, 1997b). Gleaners, on the other hand, were on average as abundant within pentads with a high proportion of protected areas as they were in those with low proportions (group 2, Table 1). This is probably because gleaners may eat insects that are attracted into urban gardens (Chace & Walsh, 2006). For example, species in this group such as the black-chested prinia (*Prinia flavicans*, $\hat{\beta}_1 = -1.27$), grey-headed bush shrike (*Malaconotus blanchoti*, $\hat{\beta}_1 = 0.55$), tawny-flanked prinia (*Prinia subflava*, $\hat{\beta}_1 = 0.49$) and southern boubou (*Laniarius ferrugineus*, $\hat{\beta}_1 = 0.89$) are commonly observed in gardens of suburban areas (Berruti, 1997a, 1997b; Parker, 1997a, 1997b). Furthermore, in some cases, agricultural practices may increase the abundance and species richness of insects (although this depends on the intensity of farming, and the type of crop planted; Benton, Bryant, Cole, & Crick, 2002; Newton, 2004), which may support relatively dense populations of gleaning species in agricultural lands. Thus, the ecological benefit provided by protected areas to gleaning species appears to depend strongly on the land use types surrounding protected areas.

Like all observational studies, we cannot infer causal relationships. An alternative explanation for our findings could be that protected areas were in areas that can naturally sustain high abundances of birds, for example, if they were located in areas with higher productivity. However, productivity is less likely to have a direct influence on our findings as protected areas are generally placed in areas of low economic value and in unwanted space, and productivity is not a major factor in the establishment of protected areas (Joppa & Pfaff, 2009). Furthermore, our study consisted of 81 protected areas of varying sizes, scattered over the landscape matrix (as opposed to just one, large protected area), and we accounted for vegetation as one of the most important drivers of avian diversity in our area.

In conclusion, even though we cannot clearly attribute our findings to protection status in general, our results indicate that the current network of protected areas within the greater Gauteng region does sustain a relatively higher abundance for many of the species we investigated and thus perform an important conservation role. The next step in further understanding the role played by protected areas is to gain insight into the mechanisms by which they are able to sustain higher abundances of common species. This can be done by examining local colonization and extinction

dynamics using dynamic occupancy models. As we suggest here, land use types neighbouring protected areas may affect significantly the conservation performance of protected areas. A further consideration, then, is to understand carefully the ways in which neighbouring land use types affect the ability of protected areas to host large abundances of common species. Additionally, the conservation performance of protected areas can be significantly affected by management practices. Future studies should quantify how differences in management influence performance. Tackling these concepts will considerably increase our general understanding of the conservation role played by protected areas, and the value they provide to biodiversity.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.