

Alien and native birds in South Africa: patterns, processes and conservation

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Abstract The spatial distribution of alien species richness often correlates positively with native species richness, and reflects the role of human density and activity, and primary productivity and habitat heterogeneity, in facilitating the establishment and spread of alien species. Here, we investigate the relationship between the spatial distribution of alien bird species, human density, and anthropogenic and natural environmental conditions. Next, we examined the relationship between the spatial distribution of alien bird species and native bird species richness. We examined alien species richness as a response variable, using correlative analyses that take spatial autocorrelation into account. Further, each alien bird species was examined as a response variable, using logistic regression procedures based on binary presence–absence data. A combination of human density and natural habitat heterogeneity best explained the spatial distribution of alien species richness. This contrasts with the results for individual alien species and with previous studies on other non-native taxa showing the importance of primary productivity and anthropogenic habitat modification as explanatory variables. In general, native species richness is an important correlate of the spatial distribution of alien

species richness and individual alien species, with alien species being more similar to common species than to rare species.

Keywords Alien birds · Habitat heterogeneity · Human activities · Human population density · Native birds · Primary productivity · Species richness

Introduction

Many studies indicate a positive spatial correlation between native and alien species richness at coarse resolutions and the regional scale (Lonsdale 1999; Stohlgren et al. 1999; McKinney 2001; Pyšek et al. 2002; Stohlgren et al. 2003, 2006; Evans et al. 2005; Richardson et al. 2005; Williams et al. 2005). The opposite effect is often expected due to local competitive exclusion of alien species (also known as exotic species or introduced species) by natives; however, competitive exclusion by natives appears to be a relatively weak force that is mainly manifested at fine resolutions, if at all (Case 1996; Stohlgren et al. 1999; Kennedy et al. 2002; Levine et al. 2004). A coarse resolution positive relationship is not necessarily causal (Lonsdale 1999; Stohlgren et al. 1999). Indeed, Duncan et al. (2003) suggest that factors such as natural and anthropogenic environmental conditions and introduction effort are much more important than species traits and interactions in

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determining the colonisation and distribution of alien bird species. It is more likely that alien and native species richness covary at regional spatial scales due to positive responses to similar environmental conditions, leading to higher native and alien species richness in areas with a great diversity of habitat types and favourable environmental conditions such as high primary productivity or energy availability (Lonsdale 1999; Stohlgren et al. 1999, 2006; Evans et al. 2005; Richardson et al. 2005; Williams et al. 2005).

Alien species richness is often higher in areas with high human density, because humans and human activities are often the source of alien species (Hodkinson and Thompson 1997; Dean 2000; McKinney 2001, 2002; Pyšek et al. 2002; Le Maitre et al. 2004; Richardson et al. 2005; Williams et al. 2005; Stohlgren et al. 2006). Further, disturbance of natural habitat by humans also facilitate the colonisation and spread of alien species (Case 1996; Dean 2000; Fine 2002; Le Maitre et al. 2004). Spatial variation in human density is, in turn, often determined by the same environmental conditions that determine native and alien species richness, further promoting a widespread positive correlation between these variables (McKinney 2001; Chown et al. 2003; Evans and Gaston 2005). Thus, areas with high native species richness are most at risk from the harmful effects of invasive alien species and human activities such as habitat transformation, degradation, and destruction, and overexploitation of natural resources including species (see Vitousek et al. 1997, for a review).

Most of the studies mentioned so far focussed on or included alien plant species richness, for which adequate distribution atlases are often available (e.g. the Southern African Plant Invaders Atlas used by Richardson et al. 2005). These studies are essential because of the high prevalence of alien plant species (Rapoport 2000; Richardson et al. 2005) and the severity of detrimental ecological and economical impacts caused by alien plant invasions (Gordon 1998; Van Wilgen et al. 2001; Le Maitre et al. 2004). Spatial distribution of alien plant species richness in South Africa is determined by the natural environmental factors primary productivity and habitat heterogeneity, and the human factors population density, road density, and percentage urban and transformed area (Richardson et al. 2005).

Fewer studies have been done on the spatial distribution of alien animal species richness, examples being studies done on fish (McKinney 2001, 2002; Irz et al. 2004; Stohlgren et al. 2006), and birds (Case 1996; Evans et al. 2005; Germaine et al. 1998; Stohlgren et al. 2006). The basic variables and mechanisms found to govern the spatial distribution of alien plant species richness are often extended in the literature to animal species (e.g. Evans et al. 2005; Stohlgren et al. 1999), one difference being that animals are known to have greater dispersal abilities than plants (Rapoport 2000). The spatial distribution pattern of alien animal species richness is therefore assumed to be similar to native animal species richness distribution patterns, and to reflect the response of alien species to environmental conditions (e.g. primary productivity and habitat heterogeneity), their source of introduction (e.g. humans and human activities), and anthropogenic disturbance to ecosystems (e.g. habitat transformation).

Data on South African birds provide an ideal opportunity to investigate these assumptions and as far as we are aware, no studies have been done on the spatial patterns and the underlying mechanisms of alien animal species richness at the national scale for South Africa. The Southern African Bird Atlas Project (SABAP, Harrison et al. 1997) provides bird distribution data at the quarter-degree square (QDS) resolution (the area of QDS grid cells in South Africa vary from 635 km² in the South to 712 km² in the North) which have been used successfully in many previous studies (e.g. Van Rensburg et al. 2002; Chown et al. 2003; Evans et al. 2006; Hugo and Van Rensburg 2008), and includes 11 bird species that are non-native (Harrison et al. 1997; Hockey et al. 2005).

Methods

It is known that in South Africa, native bird species richness, and accordingly, perhaps also alien bird species richness, is positively correlated to human density, primary productivity (especially where primary productivity has been artificially increased by irrigation), and natural and anthropogenic habitat heterogeneity (Van Rensburg et al. 2002; Chown et al. 2003; Hugo and Van Rensburg 2008). Further, as mentioned in the “[Introduction](#)”, alien species might benefit from land transformation, and they are

reputedly associated with urban and cultivated areas (Brooke et al. 1986; Case 1996; Dean 2000; Hockey et al. 2005; Peacock et al. 2007). Thus, to determine the relative importance of different anthropogenic and natural environmental factors to spatial distribution in alien species, we investigated all of the above mentioned variables as predictors of the spatial distribution of total number of alien bird species per QDS (i.e. alien species richness). In addition to this, following Evans et al. (2005), we modelled each alien species as individual response variables in relation to the predictor variables mentioned above. Doing this would allow the exploration of their separate contributions to the overall spatial distribution of alien species richness (i.e. alien species combined). For these two sets of multivariate regression analyses we report only the models that best predicted variation in the response variables. ‘Best’ models included only predictors that contribute significantly (0.05 level of probability) to the model.

Primary productivity was represented by January normalised difference vegetation index (NDVI) values averaged between 1982 and 1991. NDVI is obtained by satellite imaging, and it correlates strongly with net primary production and plant biomass (Kerr and Ostrovsky 2003). The NDVI values used in the current study were obtained from the African Real Time Environmental Monitoring using Meteorological Satellites (Artemis) programme of the Food and Agriculture Organisation (<http://www.fao.org/geonetwork/srv/en/main.home>). We specifically used NDVI for January, because compared with other NDVI metrics, it exhibits the most marked spatial variation and explains more of the spatial variation in human density and avian species richness (Evans et al. 2006). Natural habitat heterogeneity was represented by the number of vegetation types in each QDS according to Low and Rebelo (1996).

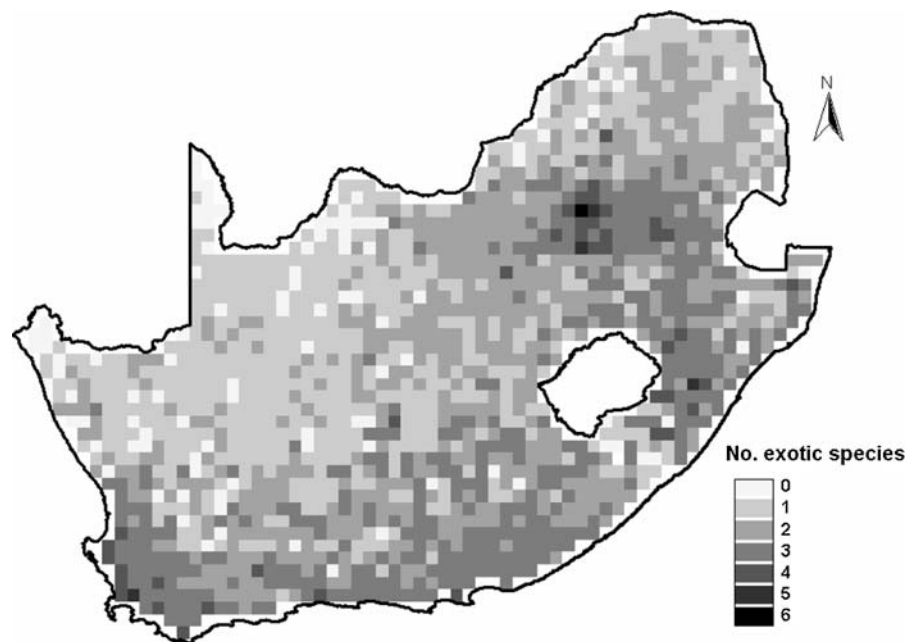
Human population density values were derived from the 2001 national population census (Anonymous 2001). Total percentage land transformation per QDS and percentage cultivated and urban area per QDS were based on the transformed land-cover data captured by Landsat TM satellite imagery (six main transformed land cover types were recorded mainly between 1994 and 1995: cultivated land, degraded land, plantations, water bodies, urban build-up, and mines and quarries), provided by Thompson (1996). We calculated anthropogenic habitat heterogeneity as

the number of transformed land cover types in each QDS. A spatial distribution map of irrigated areas was published by the Agricultural Research Council—Institute for Soil, Climate, and Water (2000), and was downloaded from the Agricultural Geo-Referenced Information System website (http://www.agis.agric.za/agis_metadata/).

To study the spatial relationship between alien and native bird species richness, we investigated native species richness as a predictor of the spatial distribution of alien species richness (response). Further, we investigated native species richness as a predictor of the spatial distribution of each alien species separately (Evans et al. 2005). We investigated three native species richness categories, representing different range size categories calculated for each QDS: (1) all 651 species, (2) the 25% most widespread species (each occupying a minimum of 610 QDSs) representing the category ‘common species’, and (3) the 25% most range restricted species (each occupying a maximum of 98 QDSs) representing the category ‘rare species’. This was done because the distribution patterns of common and rare species differ, and common species contribute more towards overall species richness distribution patterns than rare species (i.e. most of the spatial variation is caused by a minority of the most common species) with the result that rare species distribution patterns would be obscured in an analysis that do not separate the two (Lennon et al. 2004; Vázquez and Gaston 2004). Although the 25% cutoff values are arbitrary, they are commonly used to define range size categories (see Gaston 1994). For these analyses, we report all models regardless of whether the predictor was significant.

All spatial information datasets have been converted to a QDS resolution using ArcView GIS of ESRI Inc. (1998). We removed QDSs overlapping the border of the country (i.e. those overlapping with the coast or neighbouring countries) from the datasets (Fig. 1), as information in these cells are incomplete and could be misleading ($n = 1,669$ QDSs used). For this reason alien species restricted to the coast (chaffinch, *Fringilla coelebs*; chukar partridge, *Alectoris chucar*; house crow, *Corvus splendens*) were omitted from the study. The eight species that were included in the study were common myna (*Acridotheres tristis*), common starling (*Sturnus vulgaris*), house sparrow (*Passer domesticus*) and rock dove (*Columba livia*) which are widespread in South

Fig. 1 The number of exotic bird species per quarter-degree square in South Africa, as provided by the Southern African Bird Atlas Project (Harrison et al. 1997)



Africa, and budgerigar, *Melopsittacus undulates*, mallard (*Anas undulate*), rose-ringed parakeet (*Psittacula krameri*) and mute swan (*Cygnus olor*), which are narrowly distributed in South Africa (Harrison et al. 1997).

We reduced heteroscedasticity in all variables by logarithmically transforming the data to the base 10, before applying the relevant statistical procedures. If zero values were present within a dataset, we added an incremental value, 1, to all values in that dataset before applying log transformation.

To detect collinearity, we examined the tolerance value for each predictor variable. Tolerance, as defined by Neter et al. (1996), is 1 minus the squared multiple correlation of a predictor variable with all other independent variables in the regression equation (Statsoft, Inc. 1999); the lower the tolerance of a given variable, the stronger the correlation between the variable in question and one or more of the other predictors (Quinn and Keough 2002). Following Quinn and Keough (2002), those variables with tolerance values smaller than 0.1, should be eliminated from subsequent analyses. However, as none of the explanatory variables were found to be redundant, all were included in the analyses.

We used the SAS version 9.1 procedure 'PROC MIXED' (SAS Institute, Inc. 2004) to investigate the spatial distribution of alien species richness. Data

from contiguous grid cells are often spatially auto-correlated, which violates the assumption of independent errors on which many classical statistical tests are based (Legendre et al. 2002). Therefore, using 'PROC MIXED', we implemented spatial correlation models in which spatial variation in the response variable is tested for spatial autocorrelation (null spatial models are compared with the independent errors models with a likelihood ratio test giving a χ^2 value and level of significance) (Littell et al. 1996). Further, 'PROC MIXED' fits a spatial covariance matrix to the data to adjust the test statistics (Littell et al. 1996). We used an exponential spatial covariance structure in all analyses, as this always provided a better fit to the null model compared with the five others: spherical, Gaussian, linear, linear log and power. Variation in the response variable was significantly ($P < 0.0001$) spatially autocorrelated in each analysis done with 'PROC MIXED' in this study, i.e. a significant proportion of spatial variation in the response variable can be explained by spatial autocorrelation, which results in smaller F statistics and significance levels for the predictor variables compared to models assuming independent errors.

To investigate the spatial distribution of the individual alien species we used the SAS version 9.1 procedure 'PROC LOGISTIC' (SAS Institute, Inc. 2004), which is a logistic regression procedure

that allows the use of presence-absence (i.e. binary) data to model the probability of occurrence of a species in relation to various predictor variables (Evans et al. 2005). There is no test that controls for spatial autocorrelation when performing binary regressions, consequently for analyses using ‘PROC LOGISTIC’ we could only report models based on the independent errors assumption.

To test the ‘goodness of fit’ of different models, the ‘PROC MIXED’ and ‘PROC LOGISTIC’ procedures supply Akaike’s information criterion (AIC) values, of which smaller (or more negative) values indicate a better model. AIC values do not mean anything by themselves and are only used to compare models with different predictor variables and the same response variable (SAS Institute, Inc. 2004). Thus, AIC values could not be used to compare different subsets of a dataset. Rare species occupy fewer QDSs at the national scale, i.e. the rare species dataset is a subset of QDSs occupied by all and common species. Therefore, to compare different models of the relationship between alien and native species, the common and all species datasets were reduced so that the area covered matched that of the rare species in size and location (i.e. the same QDSs were analysed, $n = 1,011$).

To detect simple nonlinear relationships, the square term of each variable was included into the models together with the variable concerned (Evans and Gaston 2005). An increase in the ‘goodness of fit’ (i.e. a decrease in the AIC value), indicate a nonlinear relationship.

Sampling intensity in the SABAP differed widely among QDSs (Harrison et al. 1997). To determine the influence of sampling effort, we followed Evans et al. (2006) by repeating all analyses using a dataset from which poorly sampled QDSs (i.e. those QDSs for which fewer than ten bird species checklists have been received) had been excluded, and comparing the results with that of the complete dataset. Like Evans et al. (2006) we found only negligible differences and therefore we only report the results based on the complete dataset.

Results

Of all the predictor variables investigated, only total transformed area was not included in any model of

any analysis. This could be due to some level of collinearity with one or more of the other predictors, despite having a tolerance value larger than 0.1 (see “Methods”).

Human density ($F = 181.83$; $P < 0.0001$) and natural habitat heterogeneity ($F = 13.39$; $P = 0.0003$) are the only human and natural environmental factors included in the best model explaining the spatial distribution pattern of alien species richness. Both have a positive correlation with alien species richness. For both these predictors, $n = 1,668$, the numerator $df = 1$, and the denominator $df = 1,666$.

The probability of occurrence of common myna (the response variable) was best predicted by a combination of human density, cultivated area, and primary productivity with which it was positively correlated, and urban build-up with which it was negatively correlated (Table 1). Judging from the Chi-square values, primary productivity was the predictor that contributed most to the model. The square terms (which may or may not have been positively correlated to the response variable) of human density and urban build-up were included in the model, meaning that, compared to the remaining predictor variables, these predictors were nonlinearly correlated with the response variable.

The probability of occurrence of common starling was best predicted by human density, cultivated area, irrigated area, primary productivity and vegetation heterogeneity (Table 1). Primary productivity contributed most to the model, although it was negatively correlated to the probability of occurrence of common starling. Of the other predictors only cultivated area had a negative correlation with the response variable. Human density, irrigated area and vegetation heterogeneity had nonlinear relationships with the response variable.

The probability of occurrence of the house sparrow was best predicted by human density and irrigated area to which it was positively correlated and cultivated area to which it was negatively correlated (Table 1). Cultivated area had a nonlinear relationship with the response variable. Human density seemed to have contributed most to the model.

The probability of occurrence of the rock dove was best predicted by all predictors except total transformed area and irrigated area (Table 1). Only cultivated area had a negative relationship with the

Table 1 The Chi-square (χ^2) values and significance levels of all predictors included in the best model predicting the probability of occurrence of each alien bird species

Predictor	Common myna	Common starling	House sparrow	Rock dove	Budgerigar	Mallard	Rose-ringed parakeet
Human density	$\chi^2 = 4.73^*$	$\chi^2 = 50.01^{*****}$	$\chi^2 = 20.70^{*****}$	$\chi^2 = 62.38^{*****}$	$\chi^2 = 12.71^{\dagger\dagger\dagger}$	NI	$\chi^2 = 25.04^{*****}$
Human density ²	$\chi^2 = 3.89^\dagger$	$\chi^2 = 42.63^{\dagger\dagger\dagger}$	NI	$\chi^2 = 45.61^{\dagger\dagger\dagger\dagger}$	NI	NI	NI
Cultivation	$\chi^2 = 17.14^{*****}$	$\chi^2 = 7.09^{\dagger\dagger}$	$\chi^2 = 14.14^{\dagger\dagger\dagger}$	$\chi^2 = 7.56^{\dagger\dagger}$	$\chi^2 = 10.85^{**}$	$\chi^2 = 9.73^{**}$	NI
Cultivation ²	NI	NI	$\chi^2 = 15.22^{*****}$	$\chi^2 = 14.53^{***}$	NI	NI	NI
Irrigation	NI	$\chi^2 = 18.97^{*****}$	$\chi^2 = 11.23^{***}$	$\chi^2 = 13.17^{***}$	$\chi^2 = 15.38^{*****}$	NI	NI
Irrigation ²	NI	$\chi^2 = 4.60^\dagger$	NI	NI	NI	NI	NI
Urban build-up	$\chi^2 = 10.47^{\dagger\dagger}$	NI	NI	$\chi^2 = 34.47^{*****}$	$\chi^2 = 12.44^{***}$	$\chi^2 = 56.99^{*****}$	NI
Urban build-up ²	$\chi^2 = 17.00^{*****}$	NI	NI	NI	NI	NI	NI
Primary productivity	$\chi^2 = 116.12^{*****}$	$\chi^2 = 95.46^{\dagger\dagger\dagger}$	NI	$\chi^2 = 4.10^*$	NI	NI	NI
Anthropogenic heterogeneity	NI	NI	NI	$\chi^2 = 7.94^{**}$	NI	NI	NI
Anthropogenic heterogeneity ²	NI	NI	NI	$\chi^2 = 14.69^{\dagger\dagger\dagger}$	NI	NI	NI
Vegetation heterogeneity	NI	$\chi^2 = 4.01^*$	NI	$\chi^2 = 9.87^{**}$	NI	NI	NI
Vegetation heterogeneity ²	NI	$\chi^2 = 12.80^{***}$	NI	NI	NI	NI	NI

All predictors were log-transformed to the base ten

NI not included

Significance levels: positive effects, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; negative effects, † $P < 0.05$; †† $P < 0.01$; ††† $P < 0.001$; †††† $P < 0.0001$

response variable. Human density, cultivated area, and anthropogenic habitat heterogeneity had nonlinear relationships with the response variable. Human density contributed most to the model.

The probability of occurrence of the budgie was best predicted by human density, with which it was negatively correlated, and cultivated area, irrigation and urban build-up, with which it was positively correlated (Table 1). Irrigation contributed most to the model.

The probability of occurrence of the mallard was best predicted by cultivated area and urban build-up (Table 1). Both predictors had positive correlations with the response variable, and urban build-up contributed most to the model.

The probability of occurrence of the rose-ringed parakeet was best predicted by human density only, with which it had a positive relationship (Table 1).

Mute swan was omitted from the individual species analyses because it is present in only two QDSs of the dataset, and thus does not provide enough data for the analysis to be conducted.

The spatial distribution of alien species richness was significantly positively correlated to all three native species richness categories, although it had a nonlinear correlation with common native species richness. The AIC values indicated that common species richness ($F = 10.87$, $P = 0.001$) and its square term ($F = 19.47$, $P < 0.0001$; $AIC = -1,526.8$) were the predictors that best describe spatial patterns in alien species richness, followed by all species richness ($F = 213.83$; $P < 0.0001$; $AIC = -1,467.6$), and then rare species richness ($F = 61.55$; $P < 0.0001$; $AIC = -1,338.5$). For all these analyses, $n = 1,011$, the numerator $df = 1$, and the denominator $df > 1,008$.

Generally, the probability of occurrence of an alien bird species in a QDS increased with an increase in the number of native bird species occurring in that QDS. However, negative relationships were found for the probability of occurrence of rock dove (common native species richness), and house sparrow (all and common native species richness) (Table 2). Further, the probability of occurrence of budgies increased significantly only with common native species richness (Table 2). Nonlinear relationships were present for the probability of occurrence of common myna (rare native species), common starling (all three native species richness categories), mallard (rare native species), rock dove

(all categories), and house sparrow (all and common native species richness categories) (Table 2). As indicated by the AIC values, probability of occurrence of four species (budgie, mallard, rock dove and house sparrow) were best predicted by common native species richness, whereas probability of occurrence of three alien species (common myna, common starling and rose-ringed parakeet) were best predicted by the native species richness category 'all species' (Table 2). Again, mute swan was omitted from this analysis.

Discussion

One of the most noticeable results of this study is that there is limited agreement between the models concerning the spatial distribution of alien bird species richness and the models concerning the spatial distributions of individual alien bird species. Further, models predicting the occurrence of individual alien species differ substantially from one another in terms of the combination of factors predicting their occurrence (Table 1). This result is supported by the fact that the South African distribution ranges of these alien bird species differ substantially and some, like common myna and common starling, show hardly any overlap with each other (Harrison et al. 1997).

Generally, the models predicting the probability of occurrence of individual alien species included more variables than the models that best predicted spatial variation in alien species richness. It should be kept in mind that 'PROC LOGISTIC', used to model the distributions of each individual alien species, is a less stringent analysis than the 'PROC MIXED' analysis that take spatial autocorrelation into account. For this reason, it is possible that the models concerning individual alien species included some predictors that would have been excluded from a more stringent analysis. Therefore, one should be cautious when interpreting 'PROC LOGISTIC' results, and view the analyses concerning the probability of occurrence of individual alien species only as a supplement to the analyses concerning the spatial distribution of alien species richness.

Overall, human density seems to be the most important variable (of those investigated) determining the spatial distribution of alien bird species in

Table 2 The probability of occurrence of each alien bird species in relation to three categories of native bird species richness: all species, the 25% most widespread species (common species) and the 25% most range restricted species (rare species)

	Native species group	Native richness	Native richness ²	AIC
Common myna	All	$\chi^2 = 110.35^{*****}$	NI	800.7
	Common	$\chi^2 = 76.02^{*****}$	NI	852.5
	Rare	$\chi^2 = 38.28^{*****}$	$\chi^2 = 15.06^{\dagger\dagger}$	889.4
Common starling	All	$\chi^2 = 74.77^{*****}$	$\chi^2 = 76.27^{\dagger\dagger\dagger}$	1,004.4
	Common	$\chi^2 = 8.81^{**}$	$\chi^2 = 7.71^{\dagger}$	1,075.8
	Rare	$\chi^2 = 19.62^{*****}$	$\chi^2 = 26.06^{\dagger\dagger\dagger}$	1,106.6
House sparrow	All	$\chi^2 = 6.45^{\dagger}$	$\chi^2 = 8.22^{**}$	399.5
	Common	$\chi^2 = 13.35^{\dagger\dagger\dagger}$	$\chi^2 = 16.00^{*****}$	354.3
	Rare	$\chi^2 = 7.95^{**}$	NI	450.3
Rock dove	All	$\chi^2 = 10.53^{**}$	$\chi^2 = 6.88^{\dagger}$	1,081.3
	Common	$\chi^2 = 21.35^{\dagger\dagger\dagger}$	$\chi^2 = 29.83^{*****}$	893.9
	Rare	$\chi^2 = 44.49^{*****}$	$\chi^2 = 21.88^{\dagger\dagger\dagger}$	1,332.1
Budgerigar	All	$\chi^2 = 1.51$ NS	NI	85.8
	Common	$\chi^2 = 4.49^*$	NI	78.5
	Rare	$\chi^2 = 1.30$ NS	NI	86.4
Mallard	All	$\chi^2 = 13.91^{***}$	NI	240.6
	Common	$\chi^2 = 22.12^{*****}$	NI	212.2
	Rare	$\chi^2 = 12.78^{***}$	$\chi^2 = 10.51^{\dagger\dagger}$	234.5
Rose-ringed parakeet	All	$\chi^2 = 18.19^{*****}$	NI	89.6
	Common	$\chi^2 = 9.92^{**}$	NI	104.1
	Rare	$\chi^2 = 11.59^{*****}$	NI	113.1

Chi-square (χ^2) values and significance levels are provided for each predictor. All predictors were log-transformed to the base ten AIC Akaike's information criterion (smaller values indicate a better model); NI not included; NS not significant

Significance levels: positive effects, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; negative effects, $\dagger P < 0.05$; $\dagger\dagger P < 0.01$; $\dagger\dagger\dagger P < 0.001$; $\dagger\dagger\dagger\dagger P < 0.0001$

South Africa. The spatial distribution of alien species richness was mainly determined by human density, with which it had a positive correlation. Such a positive correlation is consistent with various other studies where alien taxa were examined (McKinney 2001, 2002; Pyšek et al. 2002; Richardson et al. 2005; Stohlgren et al. 1999). Further, human density also played a prominent positive role in models predicting the probability of occurrence of most of the individual alien bird species. This is generally consistent with local scale observations (Dean 2000; Hockey et al. 2005) of alien bird species in South Africa and with the QDS resolution analysis of common myna by Peacock et al. (2007), suggesting that alien bird species tend to be closely associated with humans. However, these results conflict with Evans et al. (2005) who found that human density is not significantly correlated to alien

bird species richness in Britain if energy availability is taken into account.

It is often suggested that human settlements and human-modified landscapes are important habitats to alien bird species, and that alien bird species may benefit from human activities and human-induced habitat modification (e.g. Case 1996; Germaine et al. 1998; Dean 2000; Fine 2002; Richardson et al. 2000; Le Maitre et al. 2004; Hockey et al. 2005; Peacock et al. 2007). According to the results from the current study, and depending on the bird species in question, cultivated and irrigated area, urban build-up and anthropogenically created habitat heterogeneity all played a (usually positive) role in determining the probability of occurrence of an individual alien bird species in South Africa at the QDS resolution. In contrast, none of these human-caused factors made a

significant contribution to explaining the spatial distribution of alien species richness if human density was taken into account.

It is likely that humans provide beneficial factors that promote alien species richness which were not accounted for in the current study due to its coarse resolution, e.g. the feeding of animals, either directly (e.g. bird feeders) or indirectly through alien vegetation or refuse (Emlen 1974; Mills et al. 1989; Morneau et al. 1999; Jokimäki et al. 2002). The alien species investigated in the current study often scavenge on human refuse, and feed from bird feeders and on the seeds and fruit of alien vegetation and crops (Brooke et al. 1986; Dean 2000; Hockey et al. 2005). Further, they use buildings, nest boxes, bridges and other man-made structures for nest sites, and incorporate man-made materials in their nests (Brooke et al. 1986; Dean 2000; Richardson et al. 2000; Hockey et al. 2005). These factors were determined from local scale observations and seem impractical to study at a coarser resolution, suggesting that the QDS resolution might be too coarse to study all of the factors that may promote the close association between alien species richness and human density.

Introduction effort (which is spatially associated with human densities, see “[Introduction](#)”) was also not considered in the current study; however, it is unlikely to be a reason for a strong contemporary species-human correlation in South Africa, because except for budgies and mute swans, most current populations of alien bird species are self-sustaining and do not require continuous introductions by humans to survive (Hockey et al. 2005). Moreover, well-established South African alien bird species are now found far from their initial sites of introduction (e.g. Hockey et al. 2005; Peacock et al. 2007).

Natural habitat heterogeneity (i.e. vegetation type heterogeneity) also played a smaller significant role in explaining the spatial distribution of alien species richness, consistent with Lonsdale (1999) and Richardson et al. (2005). For the individual species analyses, natural heterogeneity seemed to play a small significant positive role only for common starling and rock dove.

Primary productivity was not a significant determinant of spatial distribution in alien bird species richness in South Africa, which conflicts with studies on alien plant species richness in South Africa (Richardson et al. 2005) and California, USA (Williams et al. 2005),

and alien bird species richness in Britain (Evans et al. 2005), in which significant positive correlations between primary productivity or energy availability (as a limiting factor of primary productivity) and alien species richness were reported. For the individual species analyses, primary productivity played an important role only for common myna (positive relationship) and common starling (negative relationship). Adaptation to the climatic conditions in their regions of origin possibly determined that the breeding range of common myna is mainly restricted to the warmer, more productive regions in the East of South Africa, whereas the breeding range of common starling is restricted to the cooler regions of South Africa (Brooke et al. 1986; Dean 2000; Richardson et al. 2000). Nevertheless, it seems that alien bird species in South Africa are generally more dependent on humans and human activities for food and shelter than on climatic conditions. For example, house sparrow and rock dove seem to occur across the country in almost any kind of climate, provided that there are humans or man-made structures present (Dean 2000; Richardson et al. 2000). In contrast, energy availability was an important predictor of the probability of occurrence of all alien bird species present in Britain (Evans et al. 2005). Evans et al. (2005) suggested that most of these species originated in countries that are warmer than Britain, hence the importance of energy availability.

Although positively correlated to all three native species richness categories, spatial distribution in alien species richness was more similar to that of common native species richness than rare native species richness, possibly indicating that alien species behave more similarly to common species. This idea is supported by the fact that human density is an important correlate of spatial variation in both alien (current study) and common native (Hugo and Van Rensburg 2008) species richness. Further, although the distributions of individual alien species were generally similar to the distribution of native species richness, they were never most similar to the distribution of rare native species richness. These observations should be expected, as common and rare species are known to react differently to anthropogenic disturbance. In particular, common species, many of which are generalists, are often able to take advantage of habitats altered by human activities, whereas rare or specialist species usually become rarer (McKinney and Lockwood 1999; Davies et al.

2004; Fairbanks 2004). Alien bird species that are successful at establishing a population and spreading are often pre-adapted for invasion by being opportunistic generalists that are closely associated with humans and tolerant of a wide range of environmental conditions (Dean 2000; Duncan et al. 2003). Similarly Dean (2000) suggested that common native species with the characteristics of a successful invader could also increase in number and expand their ranges. Thus common species with expanding ranges, as was shown for North America by La Sorte and Boecklen (2005) and La Sorte (2006), and invasive alien species may share many traits and may both respond positively to increased human densities. The pied crow (*Corvus albus*) is an example of a generalist species native to South Africa that benefits to a large extent from human activities and has made use of the human modification of habitats to expand its range in South Africa (Harrison et al. 1997).

Despite local scale observations of South African alien bird species mentioned previously throughout the “Discussion” (reviewed and summarised in Brooke et al. 1986; Harrison et al. 1997; Dean 2000; Richardson et al. 2000; Hockey et al. 2005), there is still a lack of fine resolution and local-scale studies of alien and native birds in South Africa. For example, the QDS resolution study by Fairbanks et al. (2002) suggest that the population density of invasive alien species and certain native generalists are often greater than the population density of rare native species in transformed areas, thus possibly threatening biodiversity through interspecific competition, and hybridization of alien and native species (Emlen 1974; Clout 2002). However, little is known about the local-scale interactions between populations of alien and native bird species in South Africa, although common myna are suspected to displace natives at a local scale and mallards are known to hybridize with native *Anas* species (Dean 2000; Richardson et al. 2000; Hockey et al. 2005; Peacock et al. 2007). There is also a lack of studies on the impacts of alien fauna on indigenous species and vegetation (Dean 2000; Richardson et al. 2000). Further, it can be seen that much of the knowledge gained about the factors that correlate with alien species at a QDS resolution differs from that gained from local-scale observations. For example, whereas the QDS-resolution

analysis of common starling in the current study showed no effect of urban build-up and a negative effect of cultivated area, local-scale observations revealed that common starling occur in urban areas and agricultural fields (Hockey et al. 2005). Studies are needed to clarify this scale-dependent effect.

Case (1996) and Germaine et al. (1998) conducted and reviewed local-scale studies, and reported that alien and native birds tend to occupy different habitats and might use different resources at a local scale. This suggests that spatial distributions of alien bird species richness and native bird species richness in South Africa might be negatively correlated at finer resolutions, at which different habitat types could be distinguished more clearly. Alien bird species are usually not abundant in pristine natural habitats (Case 1996; Dean 2000; Richardson et al. 2000; Hockey et al. 2005). It has been suggested that alien bird species in South Africa are competitively dominant and more prevalent than most native species in human-modified habitats, whereas natives are dominant and prevalent in pristine natural habitats (Dean 2000; Richardson et al. 2000). It is conceivable that, if interspecific competition would occur, it would be mainly between alien birds and the few generalist native birds that are closely associated with humans and could therefore come into regular contact with alien birds (Fairbanks et al. 2002).

In conclusion, alien bird species seem to be generally spatially associated with high human density and native bird species richness. However, not all assumptions regarding the factors that govern the spatial distribution in alien species richness are relevant for all taxa and all situations. Further, spatial correlates for alien bird species richness differs substantially from what was found for individual alien bird species, and in addition, individual alien bird species differ substantially from one another. In addition, the results from this QDS-resolution analysis differ from previous local-scale observations. Therefore, this study leaves many unanswered questions, particularly those that can be elucidated with further local-scale and fine-resolution studies.

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References

- Anonymous (2001) Census 2001: key results. Statistics South Africa, Pretoria
- Brooke RK, Lloyd PH, de Villiers AL (1986) Alien and translocated terrestrial vertebrates in South Africa. In: Macdonald IAW, Kruger FJ, Ferrar AA (eds) The ecology and management of biological invasions in southern Africa: proceedings of the national synthesis symposium on the ecology of biological invasions. Oxford University Press, Cape Town, pp 63–74
- Case TJ (1996) Global patterns in the establishment and distribution of exotic birds. *Biol Conserv* 78:69–96. doi:[10.1016/0006-3207\(96\)00019-5](https://doi.org/10.1016/0006-3207(96)00019-5)
- Chown SL, Van Rensburg BJ, Gaston KJ, Rodrigues ASL, Van Jaarsveld AS (2003) Energy, species richness, and human population size: conservation implications at a national scale. *Ecol Appl* 13:1223–1241. doi:[10.1890/02-5105](https://doi.org/10.1890/02-5105)
- Clout MN (2002) Biodiversity loss caused by invasive alien vertebrates. *Z Jagdwiss* 48:51–58. doi:[10.1007/BF02192392](https://doi.org/10.1007/BF02192392)
- Davies KF, Margules CR, Lawrence JF (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85:265–271. doi:[10.1890/03-0110](https://doi.org/10.1890/03-0110)
- Dean WRJ (2000) Alien birds in southern Africa: what factors determine success? *S Afr J Sci* 96:9–14
- Duncan RP, Blackburn TM, Sol D (2003) The ecology of bird introductions. *Annu Rev Ecol Evol Syst* 34:71–98. doi:[10.1146/annurev.ecolsys.34.011802.132353](https://doi.org/10.1146/annurev.ecolsys.34.011802.132353)
- Emlen JT (1974) An urban bird community in Tucson, Arizona: derivation, structure, regulation. *Condor* 76:184–197. doi:[10.2307/1366729](https://doi.org/10.2307/1366729)
- Evans KL, Gaston KJ (2005) People, energy and avian species richness. *Glob Ecol Biogeogr* 14:187–196. doi:[10.1111/j.1466-822X.2004.00139.x](https://doi.org/10.1111/j.1466-822X.2004.00139.x)
- Evans KL, Warren PH, Gaston KJ (2005) Does energy availability influence classical patterns of spatial variation in exotic species richness? *Glob Ecol Biogeogr* 14:57–65. doi:[10.1111/j.1466-822X.2004.00134.x](https://doi.org/10.1111/j.1466-822X.2004.00134.x)
- Evans KL, Van Rensburg BJ, Gaston KJ, Chown SL (2006) People, species richness and human population growth. *Glob Ecol Biogeogr* 15:625–636. doi:[10.1111/j.1466-8238.2006.00253.x](https://doi.org/10.1111/j.1466-8238.2006.00253.x)
- Fairbanks DHK (2004) Regional land-use impacts affecting avian richness patterns in Southern Africa—insights from historical avian atlas data. *Agric Ecosyst Environ* 101:269–288. doi:[10.1016/j.agee.2003.09.009](https://doi.org/10.1016/j.agee.2003.09.009)
- Fairbanks DHK, Kshatriya M, Van Jaarsveld AS, Underhill LG (2002) Scales and consequences of human land transformation on South African avian diversity and structure. *Anim Conserv* 5:61–73
- Fine PVA (2002) The invasibility of tropical forests by exotic plants. *J Trop Ecol* 18:687–705. doi:[10.1017/S0266467402002456](https://doi.org/10.1017/S0266467402002456)
- Gaston KJ (1994) *Rarity*. Chapman and Hall, London
- Germaine SS, Rosenstock SS, Schweinsburg RE, Richardson WS (1998) Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. *Ecol Appl* 8:680–691. doi:[10.1890/1051-0761\(1998\)008\[0680:RABBHA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[0680:RABBHA]2.0.CO;2)
- Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecol Appl* 8:975–989. doi:[10.1890/1051-0761\(1998\)008\[0975:EOINIP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[0975:EOINIP]2.0.CO;2)
- Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (1997) *The atlas of Southern African birds*. Birdlife South Africa, Johannesburg
- Hockey PAR, Dean WRJ, Ryan PG (2005) *Roberts—birds of southern Africa*, 7th edn. The Trustees of the John Voelcker Bird book Fund, Cape Town
- Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. *J Appl Ecol* 34:1484–1496. doi:[10.2307/2405264](https://doi.org/10.2307/2405264)
- Hugo S, Van Rensburg BJ (2008) The maintenance of a positive spatial correlation between South African bird species richness and human population density. *Glob Ecol Biogeogr* 17:611–621. doi:[10.1111/j.1466-8238.2008.00391.x](https://doi.org/10.1111/j.1466-8238.2008.00391.x)
- Irz P, Argillier C, Oberdorff T (2004) Natives and introduced fish species richness in French lakes: local and regional influences. *Glob Ecol Biogeogr* 13:335–344. doi:[10.1111/j.1466-822X.2004.00109.x](https://doi.org/10.1111/j.1466-822X.2004.00109.x)
- Jokimäki J, Clergeau P, Kaisanlahti-Jokimäki M (2002) Winter bird communities in urban habitats: a comparative study between central and northern Europe. *J Biogeogr* 29:69–79. doi:[10.1046/j.1365-2699.2002.00649.x](https://doi.org/10.1046/j.1365-2699.2002.00649.x)
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reigh P (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638. doi:[10.1038/nature00776](https://doi.org/10.1038/nature00776)
- Kerr JT, Ostrovsky M (2003) From space to species, ecological applications for remote sensing. *Trends Ecol Evol* 18:299–305. doi:[10.1016/S0169-5347\(03\)00071-5](https://doi.org/10.1016/S0169-5347(03)00071-5)
- La Sorte FA (2006) Geographical expansion and increased prevalence of common species in avian assemblages: implications for large-scale patterns of species richness. *J Biogeogr* 33:1183–1191. doi:[10.1111/j.1365-2699.2006.01480.x](https://doi.org/10.1111/j.1365-2699.2006.01480.x)
- La Sorte FA, Boecklen WJ (2005) Temporal turnover of common species in avian assemblages in North America. *J Biogeogr* 32:1151–1160. doi:[10.1111/j.1365-2699.2005.01271.x](https://doi.org/10.1111/j.1365-2699.2005.01271.x)
- Legendre P, Dale MRT, Fortin M, Gurevitch J, Hohn M, Myers D (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25:601–615. doi:[10.1034/j.1600-0587.2002.250508.x](https://doi.org/10.1034/j.1600-0587.2002.250508.x)
- Le Maitre DC, Richardson DM, Chapman RA (2004) Alien plant invasions in South Africa: driving forces and the human dimension. *S Afr J Sci* 100:103–112
- Lennon JJ, Koleff P, Greenwood JJD, Gaston KJ (2004) Contributions of rarity and commonness to patterns of species richness. *Ecol Lett* 7:81–87. doi:[10.1046/j.1461-0248.2004.00548.x](https://doi.org/10.1046/j.1461-0248.2004.00548.x)
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic invasions. *Ecol Lett* 7:975–989. doi:[10.1111/j.1461-0248.2004.00657.x](https://doi.org/10.1111/j.1461-0248.2004.00657.x)
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) *SAS[®] system for mixed models*. SAS Institute Inc., Cary, USA, pp 303–330
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- Low AB, Rebelo AG (1996) *Vegetation of South Africa, Lesotho, and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria

- McKinney ML (2001) Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biol Conserv* 100:243–252. doi:[10.1016/S0006-3207\(01\)00027-1](https://doi.org/10.1016/S0006-3207(01)00027-1)
- McKinney ML (2002) Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Glob Ecol Biogeogr* 11:343–348. doi:[10.1046/j.1466-822X.2002.00293.x](https://doi.org/10.1046/j.1466-822X.2002.00293.x)
- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 10:450–453. doi:[10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)
- Mills GS, Dunning JB, Bates JM (1989) Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* 91:416–428
- Morneau F, Décarie R, Pelletier R, Lambert D, DesGranges J, Savard J (1999) Changes in breeding bird richness and abundance in Montreal parks over a period of 15 years. *Landsc Urban Plan* 44:111–121. doi:[10.1016/S0169-2046\(99\)00002-X](https://doi.org/10.1016/S0169-2046(99)00002-X)
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) *Applied linear statistical models*, 4th edn. Irwin, Illinois
- Peacock DS, Van Rensburg BJ, Robertson MP (2007) The distribution and spread of the invasive alien common myna, *Acridotheres tristis* L. (Aves: Sturnidae), in southern Africa. *S Afr J Sci* 103:465–473
- Pyšek P, Jarošík V, Kučera T (2002) Patterns of invasion in temperate nature reserves. *Biol Conserv* 104:13–24. doi:[10.1016/S0006-3207\(01\)00150-1](https://doi.org/10.1016/S0006-3207(01)00150-1)
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Rapoport E (2000) Remarks on the biogeography of land invasions. *Rev Chil Hist Nat* 73:367–380
- Richardson DM, Bond WJ, Dean WRJ, Higgins SI, Midgely GF, Milton SJ, Powrie LW, Rutherford MC, Samways MJ, Schulze RE (2000) Invasive alien species and global change: a South African perspective. In: Mooney HA, Hobbs RJ (eds) *Invasive species in a changing world*. Island Press, Washington, DC
- Richardson DM, Rouget M, Ralston SJ, Cowling RM, Van Rensburg BJ, Thuiller W (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience* 12:391–402. doi:[10.2980/i1195-6860-12-3-391.1](https://doi.org/10.2980/i1195-6860-12-3-391.1)
- SAS Institute, Inc. (2004) *SAS/STAT® 9.1 User's guide*. SAS Institute Inc., Cary, NC
- Statsoft, Inc. (1999) *STATISTICA for Windows*. Statsoft Inc, Tulsa
- Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y (1999) Exotic plant species invade hotspots of native plant diversity. *Ecol Monogr* 69:25–46
- Stohlgren TJ, Barnett DT, Kartesz TJ (2003) The rich get richer: patterns of plant invasions in the United States. *Front Ecol Environ* 1:11–14
- Stohlgren TJ, Barnett D, Flather C, Fuller P, Peterjohn B, Kartesz J, Master LL (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biol Invasions* 8:427–447. doi:[10.1007/s10530-005-6422-0](https://doi.org/10.1007/s10530-005-6422-0)
- Thompson M (1996) The standard land-cover classification scheme for remote-sensing application in South Africa. *S Afr J Sci* 92:34–42
- Van Rensburg BJ, Chown SL, Gaston KJ (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *Am Nat* 59:566–577. doi:[10.1086/339464](https://doi.org/10.1086/339464)
- Van Wilgen BW, Richardson DM, Le Maitre DC, Marais C, Magdalela D (2001) The economic consequences of alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. *Environ Dev Sustain* 3:145–168. doi:[10.1023/A:1011668417953](https://doi.org/10.1023/A:1011668417953)
- Vázquez LB, Gaston KJ (2004) Rarity, commonness, and patterns of species richness: the mammals of Mexico. *Glob Ecol Biogeogr* 13:535–542. doi:[10.1111/j.1466-822X.2004.00126.x](https://doi.org/10.1111/j.1466-822X.2004.00126.x)
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277:494–499. doi:[10.1126/science.277.5325.494](https://doi.org/10.1126/science.277.5325.494)
- Williams JW, Seabloom EW, Slayback D, Stoms DM, Viers JH (2005) Anthropogenic impacts upon plant species richness and net primary productivity in California. *Ecol Lett* 8:127–131. doi:[10.1111/j.1461-0248.2004.00706.x](https://doi.org/10.1111/j.1461-0248.2004.00706.x)