



The relative importance of environment, human activity and space in explaining species richness of South African bird orders

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ABSTRACT

Aim To assess the relative importance of environmental (climate, habitat heterogeneity and topography), human (population density, economic prosperity and land transformation) and spatial (autocorrelation) influences, and the interactions between these predictor groups, on species richness patterns of various avifaunal orders.

Location South Africa.

Methods Generalized linear models were used to determine the amount of variation in species richness, for each order, attributable to each of the different predictor groups. To assess the relationships between species richness and the various predictor groups, a deviance statistic (a measure of goodness of fit for each model) and the percentage deviation explained for the best fitting model were calculated.

Results Of the 12 avifaunal orders examined, spatially structured environmental deviance accounted for most of the variation in species richness in 11 orders (averaging 28%), and 50% or more in seven orders. However, orders comprising mostly water birds (Charadriiformes, Anseriformes, Ciconiiformes) had a relatively large component of purely spatial deviance compared with spatially structured environmental deviance, and much of this spatial deviance was due to higher-order spatial effects such as patchiness, as opposed to linear gradients in species richness. Although human activity, in general, offered little explanatory power to species richness patterns, it was an important correlate of spatial variation in species of Charadriiformes and Anseriformes. The species richness of these water birds was positively related to the presence of artificial water bodies.

Main conclusions Not all bird orders showed similar trends when assessing, simultaneously, the relative importance of environmental, human and spatial influences in affecting bird species richness patterns. Although spatially structured environmental deviance described most of the variation in bird species richness, the explanatory power of purely spatial deviance, mostly due to nonlinear geographical effects such as patchiness, became more apparent in orders representing water birds. This was especially true for Charadriiformes, where the strong anthropogenic relationship has negative implications for the successful conservation of this group.

Keywords

Avifaunal orders, environmental factors, human activities, macroecology, patchiness, South Africa, spatial autocorrelation, water birds.

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INTRODUCTION

Today, the distribution and diversity of life at intermediate scales covary mainly with the geographical patterns of two main groups of explanatory variables: anthropogenic activities (e.g. land transformation, Gaston, 2005) and environmental variables (e.g. energy availability, Currie, 1991; O'Brien, 1998; Gaston, 2000). Although human population dynamics and resource demands contribute most to recent changes in the spatial patterns of biodiversity (Gaston, 2005), studies often neglect the influence of human activity. For example, few studies incorporate factors such as human population growth, advancement and development into model building (e.g. systematic conservation planning models, Margules & Pressey, 2000; Gaston *et al.*, 2001) or studies relating to ecosystem functioning (McDonnell & Pickett, 1990; O'Neill & Kahn, 2000; Fairbanks *et al.*, 2002). Neglecting the effects of anthropogenic activity on biodiversity's geographical patterns could therefore jeopardize our understanding of the mechanisms that account for changes in environmental variables and that translate into altered species richness patterns.

Species richness patterns are also influenced by the species richness of surrounding areas, because species richness tends to be spatially autocorrelated (Legendre & Fortin, 1989; Borcard *et al.*, 1992; Legendre, 1993; Schiegg, 2003). Similarly, as the distribution patterns of birds are affected by environmental, biological and anthropogenic factors, the spatial structure present in those factors may also have spill-over effects on species richness patterns (Legendre & Fortin, 1989; Legendre & Legendre, 1998; van Rensburg *et al.*, 2002; Diniz-Filho *et al.*, 2003). The assumption of data independence in statistical techniques therefore rarely holds in examinations of broad-scale biodiversity patterns (spatial autocorrelation, Legendre & Fortin, 1989; Borcard *et al.*, 1992; Legendre, 1993; Schiegg, 2003), and spatial autocorrelation in ecological data must be accounted for when attempting to understand the mechanisms driving species' biogeographical patterns.

A positive relationship between species richness and available energy is another commonly observed pattern (Currie, 1991; van Rensburg *et al.*, 2002; Bonn *et al.*, 2004; Koh *et al.*, 2006), although some controversy exists about the mechanisms accounting for such a relationship (cf. Rosenzweig & Abramsky, 1993; Wright *et al.*, 1993; Srivastava & Lawton, 1998; Waide *et al.*, 1999). In a previous study on South African birds, van Rensburg *et al.* (2002) indicated that, after examining several environmental variables, the spatially structured component of the variation in the environmental variables, specifically energy availability, accounted for most of the variation in species richness patterns. Chown *et al.* (2003) also highlighted that areas with high human density and avian species richness values show high levels of spatial congruence across South Africa due to similar responses of humans and avifauna to net primary productivity (for similar conclusions elsewhere see Balmford *et al.*, 2001). Consequently, priority conservation areas are expected to face increased socio-economic pressures associated with large and growing human

populations. While such studies may give a useful indication of the size of future conservation conflicts concerning birds in general, they are limited by uncertainty as to how different taxonomic groups, habitat-specific species and individual species react to anthropogenic pressures.

Using an integrated approach, we examined the relationships between bird species richness (from selected orders), energy availability, anthropogenic activities and spatial autocorrelation. We are aware that when measuring the fraction of variation in species data explained simultaneously by more than one predictor variable, the results should be interpreted with caution (Borcard *et al.*, 1992; Legendre, 1993). Nevertheless, several studies have achieved this successfully after including three predictor components: mainly environmental and spatial influences together with human activity (Barbosa *et al.*, 2001; Real *et al.*, 2003; cf. Vaughn & Taylor, 2000). Our aim is thus to assess simultaneously the relative importance of environmental, human and spatial influences, as well as the importance of combined influences, between the respective predictor groups, on species richness patterns of different avifaunal orders in South Africa.

METHODS

Study area

For the purpose of our study, we considered South Africa a suitable study area due to the availability of comprehensive data on bird distribution and human activity, as well as appropriate environmental data. To determine the relationships between avian species richness and environmental, human and spatial variables, we used the finest national scale data available: the quarter-degree grid cell resolution (15'×15', QDC). Grid cells that included land and ocean surfaces simultaneously were eliminated from the data set, resulting in 1795 cells considered for analysis. For each QDC, data were obtained on biotic and abiotic variables.

The Southern African Bird Atlas Project (SABAP; Harrison *et al.*, 1997), which summarizes information on reporting rates of species at the QDC resolution, provided the most comprehensive information available on southern African bird distributions. Using SABAP data, the number of bird species within each of the 1795 QDCs was determined. Those species that are deemed insignificant for South African terrestrial conservation purposes (marine, vagrant, marginal and introduced species) were not included. Only avifaunal orders containing 12 or more species were analysed (Table 1), resulting in a total of 602 species analysed, as they were considered to be more representative of the study area examined.

Biological data collected over large spatial and temporal scales often suffer from survey biases: high survey intensity along roads and close to city centres, and low intensity in more isolated areas (Blackburn & Gaston, 2002; Rouget *et al.*, 2004). To reduce spurious data collection to some extent, the SABAP opted for standardized and spatially representative collection

Table 1 Percentage deviance in each species richness group explained by exclusive environmental influences (*E*), exclusive human influences (*H*), and exclusive spatial influences (*S*), as well as proportions of richness explained by environment and space interactions (*ES*), environment and human interactions (*EH*), human and space interactions (*HS*) and interactions between the three predictor groups combined (*EHS*).

	<i>E</i>	<i>H</i>	<i>S</i>	<i>S1</i>	<i>S2</i>	<i>ES</i>	<i>EH</i>	<i>HS</i>	<i>EHS</i>	Total
Coraciiformes	1.5	1.4	17.1	2.1	5.8	50.5	3.7	4.4	1.3	77.6
Piciformes	3.1	2.4	13.2	1.4	5.8	42.3	0.0	3.1	6.0	73.3
Passeriformes	4.8	2.7	15.5	0.5	5.5	34.6	0.0	1.8	8.6	72.6
Galliformes	1.9	3.1	15.4	0.8	3.7	31.5	0.3	7.3	1.3	62.3
Cuculiformes	4.0	3.0	9.9	1.1	5.2	37.9	0.0	3.0	0.5	62.2
Falconiformes	3.4	4.4	9.2	2.1	3.5	34.1	0.0	2.4	0.8	57.7
Collumbiformes	7.1	2.8	6.7	0.7	4.3	27.0	0.9	0.5	9.6	54.4
Charadriiformes	7.1	3.8	10.8	1.6	4.5	5.9	6.4	10.0	3.8	48.4
Strigiformes	1.5	3.9	6.9	0.9	1.3	28.6	0.6	3.8	0.7	46.8
Anseriformes	0.8	2.6	11.7	0.7	5.8	13.6	1.2	6.6	10.2	46.7
Ciconiformes	3.8	1.6	12.4	1.5	8.1	14.5	1.2	5.0	7.5	46.0
Gruiformes	1.0	4.7	9.0	1.6	2.7	17.0	1.1	1.5	7.8	41.9

S1 and *S2* are explained in the text and represent components of pure spatial deviance. Bold values denote the predictor group(s) that explain most of the species richness variation in each order.

efforts over South Africa (Harrison *et al.*, 1997). Allan *et al.* (1997b) showed that survey bias in the SABAP is statistically insignificant. In addition, Evans *et al.* (2006) concluded that sampling effort in the respective QDCs did not alter the strength of the species richness–human relationship after the results from two different SABAP data sets representing different sampling efforts were compared. These data have been used successfully to address several macro-ecological questions (van Rensburg *et al.*, 2002; Bonn *et al.*, 2004; Lennon *et al.*, 2004).

Our analysis estimated the effects of environmental, anthropogenic (human) and spatial variables in affecting bird species diversity using a variance partitioning procedure pioneered by Whittaker (1984). This procedure has subsequently been adapted for different types of data using sums of squares from stepwise regression analysis (Real *et al.*, 2003); canonical eigenvalues from canonical correlation analysis (Borcard *et al.*, 1992); and deviance values from generalized linear models (GzLM; Lobo *et al.*, 2002).

Environmental factors (Env)

Van Rensburg *et al.* (2002) found that net primary productivity (NPP); precipitation (PPT, which is also strongly correlated with NPP); absolute minimum temperature (MIN); and, at coarser resolutions, habitat heterogeneity (VEG) are significant positive correlates of avian species richness in South Africa. For our analysis, we included the same variables. However, as topography has often been identified as an important explanatory variable for species richness patterns (Owen, 1990; Allan *et al.*, 1997a; Patterson *et al.*, 1998), we also included altitudinal range (maximum height a.s.l. minus minimum height a.s.l., in metres) derived from standard 1 : 250,000 topographical information for South Africa (South African Surveyor General, 2004).

Human activity (Hum)

Human population density, economic prosperity and land transformation, often used in the literature as surrogates for measuring anthropogenic impact on natural areas (Kerr & Currie, 1995; Naidoo & Adamowicz, 2001; Harcourt & Parks, 2003; Reyers, 2004), were used as indicators of human activity. The 1996 South African population census data (Statistics South Africa, 1998) were used to estimate the density of humans (number of people per km²) in each QDC. The average gross income per capita (the remuneration received from all economic activities per capita; Statistics South Africa, 1995), and poverty (considered as the proportion of the population earning less than ZAR200 per month; Statistics South Africa, 1998) were obtained for each QDC. Finally, the extent of land transformation was obtained by calculating and summing the percentage of each land-cover class in each QDC, based on the six transformed land-cover classes identified by Fairbanks & Thompson (1996) and Fairbanks *et al.* (2000). These classes are based on seasonally standardized Landsat Thematic Mapper satellite imagery captured primarily during 1994–95, and included anthropogenic effects such as forest plantations, artificial water bodies, urban/built-up areas, cultivated lands, degraded land as well as mines/quarries. For coordination with avian distribution and environmental data, all human activity data were converted to a spatial scale at the QDC level using ARCVIEW GIS 3.2 (ESRI Inc., Redlands, CA, USA) – all human activity data thus represent weighed averages/QDC.

Spatial situation (Spa) including linearity and degree of patchiness characteristics

Nine different spatial variables were used to measure the influence of spatial autocorrelation on species richness

patterns. Longitude (Lo), latitude (La) and LoLa describe linear spatial trends, while the other six variables of a cubic trend-surface polynomial of both spatial terms (Lo^2 , La^2 , Lo^3 , La^3 , Lo^2La , $LoLa^2$) are sufficient to extract more complex features (or patterns) such as patches or gaps of diversity (Borcard *et al.*, 1992; Legendre, 1993; van Rensburg *et al.*, 2002; Real *et al.*, 2003).

Data analysis

Statistical analyses were conducted using STATISTICA ver. 6 (StatSoft Inc., Tulsa, OK, USA). For each avifaunal order, analyses using GzLM (McCullagh & Nelder, 1989) were used to determine the amount of variation in species richness attributable to each of the different predictor groups. The analyses were performed using a Poisson error structure and a logarithmic link function (examination of the residuals revealed that the correct error distribution was used) (for analysis when using count data see Blackburn & Duncan, 2001; Maggini *et al.*, 2002). To account for overdispersion (Agresti, 1996), the deviance statistic/df values were examined and, where needed, standard errors were scaled using the deviance values as an estimate of the dispersion parameter.

To assess the relationships between species richness and the various predictor groups, the deviance statistic (a measure of goodness of fit for each model) and the percentage deviation explained for the best fitting model were calculated (McCullagh & Nelder, 1989; Collet, 1991; Dobson, 2002) using the formula:

$$\% \text{ deviance explained} = \left[\frac{(\text{null deviance statistic} - \text{full deviance statistic})}{\text{null deviance statistic}} \right] \times 100$$

Before the GzLM was performed, the effects of possible collinearity between the different predictor variables were taken into account. This is a concern when applying explanatory models where each collinear variable in the logarithmic function has its own explanation rationale. To detect collinearity, the tolerance value for each predictor variable was examined. Tolerance could be defined as 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. Following Quinn & Keough (2002), those variables with tolerance values < 0.1 were eliminated from subsequent analyses. None of the predictor variables was shown to be redundant due to collinearity. However, the spatial variables were not subjected to collinearity tests as the current spatial model attempts to capture maximum species richness variation; eliminating spatial variables would jeopardize this purpose. The relative importance or contribution of each predictor group exclusively, as well as interactions between these groups (e.g. between space and human influence, indicating how human influence that is in itself spatially structured explains species richness patterns)

were estimated, following three steps. First, we determined the amount of deviation explained by the three groups of predictor variables simultaneously ($Env \cup Hum \cup Spa$): each avifaunal group's species richness was regressed onto all the variables together (the full model). This provided an indication of the total amount of deviation explained by all the variables simultaneously. Second, we determined the degree to which each of the three individual groups of predictor variables (Env , Hum and Spa) explains geographical species richness patterns within each avian order. Spatial data for each order were regressed against the variables within each group of predictor variables. Third, we estimated the sizes of the components of each of the main sets of predictor variables (Fig. 1). Predictor variables may counteract or have additive effects on one another (Borcard *et al.*, 1992). Therefore we can expect a difference between the total amount of deviation of species richness explained by the three explanatory groups combined ($Env \cup Hum \cup Spa$ from step 1 above), and the sum of the amounts of variation of species richness that can be explained by each of the three groups in isolation ($Env + Hum + Spa$ from step 2). Thus the variation in each avian group's species richness was divided into two components: (a) that due to a predictor group exclusively (components E , H and S in Fig. 1); (b) interactions between the three different predictor groups (components SE , SH , EH and ESH in Fig. 1). The effect of spatial predictor variables excluding all interaction (S) was estimated by calculating the deviation explained by human activity and environmental variables together (the union $Env \cup Hum$, obtained by regressing species richness onto the environmental (Env) and human (Hum) variables simultaneously. Following Real *et al.*'s (2003) variance-partitioning procedure, the proportion of the variation explained exclusively by the spatial variables (S) was obtained with the

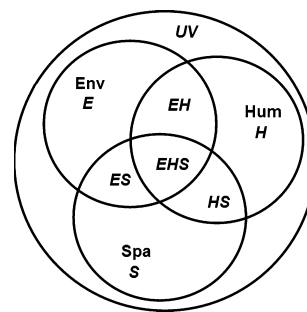


Figure 1 Diagram indicating the components of each predictor group exclusively, as well as interactions between these groups, in explaining avian species richness patterns. Spa = spatial autocorrelation; Hum = human activity; Env = environmental conditions. E , H and S are the exclusive effects of environmental conditions, human activity and spatial autocorrelation, respectively. ES , EH , HS and EHS represent the interactions between environment and space, between environment and human activity, between human activity and space, and finally between all three predictor variables. UV represents the unexplained variation.

subtraction $(\text{Env} \cup \text{Hum} \cup \text{Spa}) - (\text{Hum} \cup \text{Env})$. The proportions explained exclusively by humans (H) and exclusively by environment (E), respectively, were obtained in a similar fashion. To assess the influence of interactions between environment and human activity (EH) on species richness patterns, the simultaneous influence of these predictor variables was calculated with the subtraction $(\text{Env} \cup \text{Hum} \cup \text{Spa}) - \text{Spa} - E - H$. The interactions between humans and space (HS) and between environment and space (ES) were obtained similarly. Finally, the extent to which interactions among all three groups of predictor variables (EHS) contributed towards spatial variation in species richness was obtained using the subtraction $(\text{Env} \cup \text{Hum} \cup \text{Spa}) - E - H - S - EH - ES - HS$.

A subsidiary analysis was performed to estimate the separate effects of the linear components of spatial variation (the first-order terms among the spatial variables that explain linear trends such as large-scale rainfall gradients) and the higher-order terms (that describe nonlinear geographical structures such as patchiness of populations). This was performed by subdividing Spa into two components: Spa1 (linear) and Spa2 (higher-order). As for the other predictor variables described above, the degree to which Spa1 and Spa2 were related to richness patterns was estimated by regressing them onto geographical diversity patterns for each avian order. For excluding interactions that Spa1 and Spa2 have with other variables, the corresponding spatial variables that exclude any interactions were calculated as: $S1 = (\text{Env} \cup \text{Hum} \cup \text{Spa1} \cup \text{Spa2}) - \text{Hum} - \text{Env} - \text{Spa2}$. The corresponding value $S2$ was estimated in a similar way.

Finally, to investigate further the patterns in water-living bird species related to anthropogenic activities, we raised the question of the extent to which and the direction in which these species are being affected by artificial water bodies at the broad regional scale. To do this, we compared the effect of the total surface area covered by water bodies (km^2) on threatened and non-threatened water species richness in statistical models that did and did not take artificial water into account. Relationships were examined using two SAS ver. 9.1 procedures (SAS Institute Inc., Cary, USA): PROC GLM (assuming independent errors) to implement general linear models; and PROC MIXED to take spatial autocorrelation into account (for more information on how this procedure fits a spatial covariance matrix to the data, see Littell *et al.*, 1996). To reduce heteroscedasticity, species richness values and percentage of water body areas were logarithmically transformed to base 10. This was achieved after adding values of one to each variable in order to best transform all zero numbers.

RESULTS

Spatially structured environmental deviance (ES) explained most of the deviance in species richness across 11 of the 12 avifaunal orders examined (averaging 28%; SD 13%), followed by purely spatial deviance (S , averaging 12%; SD 3%) (Table 1). From the bivariate human relationship and all combinations examined (excluding EHS), spatially structured

human impacts (HS) accounted for most deviance, although this explanatory power was very low (averaging 4%; SD 3%). This factor together with pure spatial deviance did, however, explain 21% of the species richness variation in the order Charadriiformes (Table 1).

Of the total deviance in species richness explained by the variables included in the model, spatially structured environmental factors explained 50% or more of the deviance in seven of the 12 orders examined (Table 1). Of these, Coraciiformes, Cuculiformes and Strigiformes showed the highest percentage values (65, 61 and 61, respectively). In the case of the order Charadriiformes, where purely spatial deviance accounted for most of the deviance, 22% of its deviance was accounted for by this factor (Table 1).

Although some general trends were similar among the different bird orders (e.g. the dominance of spatially structured variables in describing bird species richness), clear differences in pattern were also evident among the orders. First, the proportion of the total deviance for each order explained by the variables included in the model varied (42–78%, averaging 57%; SD 12%; Table 1). This means that the model used provided a much better fit for some orders, while being somewhat less successful for others. For the water birds (Charadriiformes: waders; Anseriformes: waterfowl; Ciconiiformes: herons and storks; Gruiformes: cranes and rails), the model explained < 50% of the total deviance.

Second, three of the four orders comprising mostly water birds (Charadriiformes, Anseriformes, Ciconiiformes) have a relatively large component of purely spatial deviance compared with spatially structured environmental deviance (Table 1). For instance, the purely spatial deviance for the Charadriiformes is larger than the spatially structured environmental deviance. In the case of the Anseriformes and the Ciconiiformes, these two sources of deviance were almost of equal size. The Gruiformes and Galliformes have an intermediate position in this respect, with pure spatial deviance being about half the magnitude for spatially structured environmental deviance. In the other taxa, the spatially structured environmental deviance is substantially larger than the purely spatial deviance.

Third, the Charadriiformes and Anseriformes had a relatively important component of spatially structured human deviance, accounting for 21% and 14%, respectively, of their total deviances. The other water bird orders (Gruiformes and Ciconiiformes) have a low-to-intermediate position in comparison with the remaining orders. The comparatively important component of spatial congruence between anthropogenic activities and water-living bird species therefore complements the additional analysis to better understand the extent to which these species are being affected by the total area covered by artificial water bodies. Both before and after taking artificial water bodies into account, the statistical estimates of the slopes of the species–natural water relationships remained extremely weak (Tables 2 & 3). This consistency was evident from both the independent error models and spatial models showing no significant differences when comparing the slopes' 95% confidence intervals (Table 4). The independent error model

Table 2 Effect of natural water bodies on water-living bird species richness in South Africa in univariate tests.

Response	Model	log ₁₀ natural water (%)	(log ₁₀ natural water) ² (%)	Model fit
Threatened water bird species	GLM	$F_{1,1791} = 1.90$ +ns	$F_{1,1791} = 0.17$ +ns	$r^2 = 0.015$
	Spatial	$F_{1,1791} = 4.92$ +	$F_{1,1791} = 0.09$ -ns	AIC = -411.8
Non-threatened water bird species	GLM	$F_{1,1791} = 2.36$ +ns	$F_{1,1791} = 0.01$ +ns	$r^2 = 0.013$
	Spatial	$F_{1,1791} = 6.78$ ++	$F_{1,1791} = 0.02$ -ns	AIC = -357.5

Positive effects: +ns, $P \geq 0.05$; +, $P < 0.05$; ++, $P < 0.01$; negative effects: -ns, $P \geq 0.05$.

General linear models assumed independent errors, spatial models accounted for spatial autocorrelation. F ratios and associated significance levels are provided. Akaike's information criterion (AIC) values were used to assess the fit of spatial models. The model selection process was based on the lowest AIC value, as smaller values indicate a better fit. Response and predictor variables were logarithmically transformed prior to analysis.

Table 3 Minimum adequate models of water bird species–water relationships that control for artificial water bodies.

Response	Model	log ₁₀ natural water (%)	(log ₁₀ natural water) ² (%)	log ₁₀ artificial water (%)	(log ₁₀ artificial water) ² (%)	Model fit
Threatened water bird species	GLM	$F_{1,1789} = 1.92$ +ns	$F_{1,1789} = 0.17$ +ns	$F_{1,1789} = 33.60$ ++++	$F_{1,1789} = 8.66$ --	$r^2 = 0.043$
	Spatial	$F_{1,1789} = 5.07$ +	$F_{1,1789} = 0.10$ -ns	$F_{1,1789} = 7.94$ ++	$F_{1,1789} = 1.47$ -ns	AIC = -419.2
Non-threatened water bird species	GLM	$F_{1,1789} = 2.59$ +ns	$F_{1,1789} = 0.01$ +ns	$F_{1,1789} = 96.89$ ++++	$F_{1,1789} = 34.68$ ----	$r^2 = 0.077$
	Spatial	$F_{1,1789} = 7.10$ ++	$F_{1,1789} = 0.03$ -ns	$F_{1,1789} = 29.97$ ++++	$F_{1,1789} = 9.38$ --	AIC = -392.5

Positive effects: +ns, $P \geq 0.05$; +, $P < 0.05$; ++, $P < 0.01$; ++++, $P < 0.0001$; negative effects: -ns, $P \geq 0.05$; --, $P < 0.01$; ----, $P < 0.0001$.

General linear models assumed independent errors, spatial models accounted for spatial autocorrelation. F ratios and associated significance levels are provided. Akaike's information criterion (AIC) values were used to assess the fit of spatial models. The model selection process was based on the lowest AIC value, as smaller values indicate a better fit. Response and predictor variables were logarithmically transformed prior to analysis.

Table 4 Estimates of the slopes of water bird species–water relationships (95% CI) obtained from univariate models and those that take artificial water bodies into account.

Response	Model	Estimate of slope without artificial water		Estimate of slope with artificial water	
		log ₁₀ natural water (%)	(log ₁₀ natural water) ² (%)	log ₁₀ natural water (%)	(log ₁₀ natural water) ² (%)
Threatened water bird species	GLM	-0.045 to 0.260	-0.100 to 0.153	-0.044 to 0.257	-0.098 to 0.151
	Spatial	0.016 to 0.254	-0.110 to 0.081	0.018 to 0.255	-0.111 to 0.079
Non-threatened water bird species	GLM	-0.039 to 0.316	-0.142 to 0.152	-0.031 to 0.312	-0.140 to 0.143
	Spatial	0.039 to 0.278	-0.103 to 0.089	0.042 to 0.279	-0.104 to 0.086

General linear models assumed independent errors, spatial models accounted for spatial autocorrelation.

and the spatial model suggested that, compared with natural water bodies, spatial patterns in artificial water bodies were stronger and more significantly related to the richness patterns of water birds (Table 3), although the overall amount of variance explained by the water bodies was low. While non-threatened species richness patterns seem to be stronger and more significantly related to artificial water bodies compared with threatened species (Table 3), the overall results, at least at the broad spatial resolution of QDC, seem to indicate that artificial water bodies were having a positive influence on water bird species richness.

With purely spatial variation accounting for a significant amount of deviance among water birds, the question arises as to how much of this spatial deviance is due to linear gradients

in species richness (S1), as opposed to higher-order spatial effects such as patchiness (S2). Understanding the nature of such spatial deviance could be relevant when assessing how human activity may alter natural species richness patterns. In all the avian orders examined, the higher-order spatial effects were larger than the gradient effects (Table 1). Especially for the water birds, the higher-order spatial effects tended to be relatively much larger than the linear effects, although they did not differ quantitatively from the remaining orders. Spatial autocorrelation due to higher-order spatial effects were therefore important, indicating relatively large degrees of complex spatial patterns in bird richness across all orders. The combined values of the linear (S1) and higher-order sources (S2) of purely spatial deviance were much lower than the

combined purely spatial deviance (S) (Table 1). This suggests a significant interaction between the linear and nonlinear components of pure spatial variation, $S1 \cap S2$.

Finally, to assess whether the variation in total number of species across the avian groups influenced the percentage deviance in richness explained by the different predictor groups, we used linear and nonlinear regressions to investigate the relationships between species richness (including all avian groups examined) and the explanatory power of each predictor group, respectively. Relationships were weak (correlation coefficients varying between -0.30 and 0.19) and non-significant (P values varying between 0.14 and 0.94). Curvilinear relationships did not improve the fit of the models. These results therefore suggest that the variation in total species number across avian groups had no significant influence on the explanatory power found for the different predictor groups used.

DISCUSSION

Spatially structured environmental deviance accounted for most of the variation exhibited in avian bird orders at the scale of QDC in South Africa, when compared with measures of human activity. This result is consistent with previous studies conducted at this (regional) scale on overall bird species richness patterns in South Africa (van Rensburg *et al.*, 2004b) and other taxa elsewhere (Barbosa *et al.*, 2001; Real *et al.*, 2003). Even after examining a highly transformed region within South Africa, it was concluded that biogeographical patterns in birds can be recovered using modern data, despite landscape transformation (for explanations as to why this may be true, see van Rensburg *et al.*, 2004b and references therein).

Much of this covariation between richness and the environmental variables is a consequence of the strong east–west gradient in precipitation, and associated gradients in both productivity and vegetation heterogeneity across South Africa (Schulze, 1997a,b) to which species richness patterns respond positively (e.g. mammals, Andrews & O'Brien, 2000; plants, O'Brien *et al.*, 2000; birds, van Rensburg *et al.*, 2002). This undoubtedly also explains the small proportion of richness accounted for solely by the environment (a common feature of regional-scale studies; Borcard *et al.*, 1992).

Spatial effects on species richness of water birds

Perhaps more interestingly, compared with all the avian orders examined, it is clear that the variation accounted for solely by space indicates that the three orders comprising mostly water birds (Charadriiformes, Anseriformes and Ciconiiformes) show significant spatial autocorrelation independent of the spatial structure of the explanatory variable in question. This was true especially for Charadriiformes, where the pure spatial deviance component was larger than the environmentally structured spatial deviance (Table 1). Our study suggests that the spatial autocorrelation within the avian species richness patterns was characterized mostly by higher-order spatial effects ('spatial

clumpedness') as opposed to linear gradients, indicating more complex patterns (e.g. patchy or humped-shaped distributions; Borcard *et al.*, 1992; Legendre, 1993), especially in species richness of birds that are directly related to water sources (water-living bird orders). The complex and highly spatially autocorrelated richness patterns in water birds are probably a reflection of the spatial distribution of natural and human-made water bodies in a relatively arid region. That is, both are showing higher-order spatial effects describing a nonlinear geographical structure such as a patchy ($S2$) distribution across the South African landscape (Fairbanks & Thompson, 1996; Fairbanks *et al.*, 2000).

Anthropogenic effects on species richness of water birds

The idea of significant anthropogenic effects, especially on water-related birds, was supported further with human structured spatial deviance being an important component in explaining variation in Charadriiformes and Anseriformes richness patterns when compared with all avian orders examined (Table 1). Different species react differently to the same predictor variable. For example, many so-called 'weedy' taxa (Harcourt & Parks, 2003) benefit from human activities and consequently occur in high densities in altered areas, which are otherwise unoccupied by species sensitive to human activities. Avifaunal assemblages in built-up areas are often dominated by introduced species such as the common myna (*Acridotheres tristis*), the house sparrow (*Passer domesticus*) and the rock dove (*Columba livia*) (e.g. Hockey *et al.*, 2005), while many threatened bird species rarely enter such areas (Barnes, 2000). This interaction between positively and negatively influenced species might conceal the true extent of human activity on biodiversity. Through the creation of various artificial water bodies in areas devoid of water, human activity allowed many Charadriiform species (more resilient species and those not threatened) to colonize areas that would otherwise be unoccupied (Harrison *et al.*, 1997; Fairbanks *et al.*, 2002; Hockey *et al.*, 2005). Consistent with this idea, the results from our study suggested a positive and significant relationship, albeit weak, at the broad regional scale between the spatial distribution of artificial water bodies and richness patterns of both threatened and unthreatened water birds.

Several more detailed studies conducted at the finer local scale have shown that, at least from an avian conservation perspective, the negative consequences of natural water bodies being transformed outweigh those positive interactions related to artificial water bodies being created. For example, three of South Africa's five critically endangered bird species are threatened mainly by the destruction of suitable wetlands, for example through creation of dams and intensified agriculture (Barnes, 2000). Furthermore, most species that benefit from, or are associated with, artificial water bodies are not threatened (Hockey *et al.*, 2005). Artificial water bodies therefore contribute little to the conservation of the region's avifauna. With future water availability likely to decline in

South Africa (Schulze *et al.*, 2001; Erasmus *et al.*, 2002), subsequent resources and conservation conflicts are likely to escalate across most, if not all, the avian orders examined (for African mammal extinctions see Ceballos & Ehrlich, 2002; for taxa worldwide see <http://www.iucnredlist.org>). That is, fewer areas across South Africa, and probably also across the rest of Africa (Balmford *et al.*, 2001) and other regions, will be able to harbour both high species richness and greater human population densities than is presently the case (van Rensburg *et al.*, 2004a; cf. Koh *et al.*, 2006). Such a scenario will increasingly threaten species in the order Charadriiformes that are highly dependent on water to maintain viable populations. This is true even for those species currently favourably influenced by artificial water bodies, due to knock-on effects on biodiversity such as human demand for agricultural resources, especially water, as the human population continues to grow (Tilman *et al.*, 2001).

Compared with all the avian orders examined, purely human activities explained most of the diversity distribution for Gruiformes, which also contains the highest proportion (48%) of threatened species (e.g. the white-winged flufftail, *Sarothrura ayresi* and the wattled crane, *Grus carunculatus*; Barnes, 2000). The order Gruiformes is known to be sensitive to human-induced habitat loss, and many members face extinction in the near future due to this threat (Harrison *et al.*, 1997; Barnes, 2000; Hockey *et al.*, 2005). However, the variation accounted for by human activity (5%) was generally small compared with the spatially structured environmental variation component (17%). This is probably attributed to the low proportion of total deviance for Gruiformes species richness explained by the variables included in the model (42%; Table 1). This high unexplained variation (highest for all orders examined) is attributed to factors not considered in our study mainly as a result of its coarse spatial scale. Several factors identified as primary limiting factors in determining local bird distributions, and known to be influenced by humans, were not taken into account, such as food availability and habitat quality or structure. The idea of fine-scale explanatory variables not being captured in the models was supported by a general decrease in the total deviance explained for each order as the importance of the environmentally structured spatial deviance became less of an explanatory factor; the environmental component consisted mainly of climatic variables known to explain richness patterns at the regional scale (Currie, 1991).

Spatial patterns in species richness of savanna and forest birds

More generally, compared with all the orders examined, deviance in spatial patterns of the order Coraciiformes was best explained by all the combined variables included in the model, as well as for spatially structured environmental deviance only. Species within this order, for example kingfishers, bee-eaters and hornbills, are known to be strongly associated with savanna and forest habitats dominated by trees (Hockey *et al.*,

2005). At least for South Africa, tree richness is known to be highly positively correlated with environmental variables, particularly with a water–energy model (O'Brien *et al.*, 2000; O'Brien, 2006). Although all the avian orders examined had lower $S1$ values (linear gradients in richness values) than $S2$ values (more complex richness values), the ratio between $S1$ and $S2$ was $< 1 : 2$ for three of the 12 bird orders examined. Such a result suggests that these three orders (Falconiformes, including birds of prey; Strigiformes, owls; Gruiformes, cranes, korhaans, bustards and flufftails) also tend to show some strong component of linear gradients in their richness patterns. It is interesting to note that two of the three orders constitute raptor species; we are not sure what the explanation for this is. Raptors generally have a large body size (Hockey *et al.*, 2005) resulting in Falconiformes and Strigiformes being characterized, on average, with larger body sizes compared with the other bird orders examined. Generally, it is known that larger-bodied species tend to have larger, and therefore more continuous, range sizes compared with smaller-bodied species (reviewed by Gaston & Blackburn, 1996), and a concentration of such distribution patterns among species within a single bird order could favour a more linear gradient in species richness values compared with more complex richness values.

In conclusion, we found clear differences in the extent to which different avian orders are related to environmental, human and spatial variables, either combined or exclusively. Although it has been suggested that models developed at crude spatial resolutions (such as this study) must be interpreted cautiously as they do not adequately capture finer-scale predictor variables, we have demonstrated clearly that, at the broad scale, bird species richness patterns across South Africa are complex and patchy across all orders. These complex patterns became apparent especially in Charadriiformes (and to a lesser degree the remaining orders representing water birds) even in the absence of any predictor variables. Our results, however, suggest that a large amount of the complex spatial variation in the species richness of these water bird orders can be attributed to human influences, mostly with negative conservation consequences.

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