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Species Richness, Environmental Correlates, and Spatial Scale: A Test Using South African Birds

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ABSTRACT: Energy and habitat heterogeneity are important correlates of spatial variation in species richness, though few investigations have sought to determine simultaneously their relative influences. Here we use the South African avifauna to examine the extent to which species richness is related to these variables and how these relationships depend on spatial grain. Taking spatial autocorrelation and area effects into account, we find that primary productivity, precipitation, absolute minimum temperature, and, at coarser resolutions, habitat heterogeneity account for most of the variation in species richness. Species richness and productivity are positively related, whereas the relationship between potential evapotranspiration (PET) and richness is unimodal. This is largely because of the constraining effects of low rainfall on productivity in high-PET areas. The increase in the importance of vegetation heterogeneity as an explanatory variable is caused largely by an increase in the range of vegetation heterogeneity included at coarse resolutions and is probably also a result of the positive effects of environmental heterogeneity on species richness. Our findings indicate that species richness is correlated with, and hence likely a function of, several variables, that spatial resolution and extent must be taken into account during investigations of these relationships, and that surrogate measures for productivity should be interpreted cautiously.

Keywords: energy availability, habitat heterogeneity, primary productivity, potential evapotranspiration, grain.

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A recurrent theme emerging from recent studies is that energy either has a primary role in generating spatial variation in species richness or is an important modulating factor (Currie 1991; O'Brien 1998; Chown and Gaston 1999; Gaston 2000; Morin 2000). Studies have shown not only that energy is strongly correlated with species richness (Currie 1991; O'Brien 1998) but also that there is a clear set of mechanisms that can account for the way in which changes in energy availability translate to alterations in numbers of individuals and the way these individuals, in turn, are partitioned between species (Kerr et al. 1998; O'Brien 1998; Chown and Gaston 1999; Currie et al. 1999; Kerr and Currie 1999; Kaspari et al. 2000a, 2000b). However, several other factors are thought to be responsible for some, perhaps large, component of spatial variation in species richness (Rosenzweig 1995). Of particular interest is the idea that at the highest energy levels, energy loses its grip on species richness and other factors become more significant (Kerr and Packer 1997; Chown and Gaston 1999). At least in some terrestrial systems, habitat heterogeneity is thought to account for the remaining variation (Kerr and Packer 1997).

That habitat heterogeneity is likely to explain some proportion of the variance in species richness is not surprising. The literature is replete with studies showing that species richness is correlated with habitat heterogeneity and complexity at local, regional, and continental scales (e.g., MacArthur 1964; Verner and Larson 1989; O'Connor et al. 1996; Wiebe and Martin 1998; Ricklefs and Lovette 1999; Boone and Krohn 2000b). Moreover, many studies have provided insight into the way heterogeneity might cause changes in species richness by influencing the presence or abundance (Verboom et al. 1991; Villard et al. 1995), movements (Wegner and Merriam 1979; Machtans et al. 1996), and persistence (Hanski et al. 1994) of species.

Nonetheless, few investigations have sought to determine simultaneously the relative influences of energy availability and habitat heterogeneity on species richness. This is particularly important because energy availability is thought to have a direct effect on habitat heterogeneity (Wylie and Currie 1993; Waide et al. 1999; Morin 2000),

which in turn has an effect on species richness that increases in importance from the local to regional scales (Wright et al. 1993). At least one regional-scale study has suggested that the extent to which habitat heterogeneity serves as a correlate of species richness is also dependent on the spatial grain of the study, increasing in importance with a decline in spatial resolution (Fraser 1998). This may occur for both statistical and biological reasons. A decline in spatial resolution means larger sampling units, which in turn incorporate greater climatic and, hence, habitat variability. Thus, fewer sampling units cover a wider range of vegetation types. In consequence, the strength of the relationship between vegetation heterogeneity and species richness is likely to increase as spatial resolution declines (see Currie 1993 for discussion of this effect in another context). At the same time, a change in spatial resolution may result in a difference in the importance of habitat heterogeneity as a correlate of species richness because of an increase in the heterogeneity of resource production characteristics, which in turn has an influence on species richness (Wright et al. 1993).

The aim of this article is, therefore, to examine the extent to which species richness is related to abiotic variables (some of which provide measures or reasonable surrogates of ecosystem productivity and others, of environmental energy) and habitat heterogeneity at a regional scale and how these relationships depend on the resolution (spatial grain) of the study when the spatial extent is kept constant. For this purpose, we use the South African avifauna as a test case. We do this because there are marked spatial variations in the abiotic environment across South Africa, specifically a marked east-west aridity gradient (Schulze 1997*a*; see also O'Brien 1993, 1998; O'Brien et al. 1998), and because it has long been maintained that vegetation complexity accounts for most variation in bird species richness in the region (Winterbottom 1978; Osborne and Tigar 1992; Allan et al. 1997).

Methods

Data

The Southern African Bird Atlas Project (SABAP; Harrison et al. 1997) provides the most comprehensive information available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992 at a spatial resolution of a quarter-degree grid (15 min \times 15 min \approx 676 km²) for Lesotho, Namibia, South Africa, Swaziland, and Zimbabwe and on a half-degree grid (30 min \times 30 min \approx 2,500 km²) for Botswana (for a detailed description of methods, see Harrison et al. 1997). For the purpose of this study, the analyses were restricted to South

Africa and Lesotho because of the availability of appropriate environmental data.

To determine the effect of variation in spatial resolution on the relationship between species richness and environmental variables, we divided South Africa into three different geographical quadrant resolution systems consisting of 1,858 quarter-degree grid cells (approximately equal area, but varying from 635 km² in the north to 712 km² in the south), 458 half-degree grid cells, and 102 one-degree grid cells (\sim 100 km \times 100 km). Grid cells including both land and ocean surfaces simultaneously were excluded from the analysis. The number of bird species occurring in each quarter-degree cell was determined using the SABAP data. Bird species richness within the section of a grid cell extending outside the study area (e.g., into Botswana) was assumed to be equivalent to the species richness inside the study area (although the overall proportion of such grid cells in the study was low at 4%, 3%, and 3% of the total number of grid cells for each resolution, respectively). Marine, vagrant, marginal, and escaped bird species were excluded from the analysis (651 species were analyzed).

For each quarter-degree cell, values were calculated for each of seven abiotic environmental variables (some acting as surrogates for energy availability) that were selected a priori on the basis of an assessment of which of these were biologically most meaningful in the context of our investigation (see also Currie 1991; Kerr and Packer 1997; O'Brien et al. 1998; Andrews and O'Brien 2000). These variables were mean absolute monthly minimum (MIN) and mean absolute monthly maximum (MAX) temperatures ($^{\circ}$ C) averaged over the year; mean monthly minimum (MINMO) and mean monthly maximum (MAXMO) temperatures ($^{\circ}$ C) of the coldest and hottest months, respectively; mean annual precipitation (PPT; mm yr⁻¹); mean annual solar radiation (SRAD; MJ m⁻² yr⁻¹); and mean annual potential evapotranspiration (PET; an unscreened A-Pan equivalent; mm yr⁻¹). These values were calculated using monthly data based on interpolated climate surfaces for the past 30–50 yr; these data were supplied to us by the South African Computing Center for Water Research (see Schulze 1997*b*). In the central and western parts of the study area, these surfaces may be subject to greater error given a paucity of meteorological stations from which data for the interpolations could be gathered.

Abiotic and richness data at the quarter-degree resolution were rescaled to half-degree and one-degree grid cell sizes. For the richness data, duplicate species were removed, and for the abiotic data, the mean value of participating quarter-degree grid cells was assigned to the appropriate half- or one-degree grid cell. For measuring productivity, we obtained data on mean annual net primary productivity (NPP; g C m⁻² yr⁻¹) and leaf area index (LAI;

the total one-sided leaf area over a unit area of ground, i.e., area of leaf divided by area of ground) based on model simulation outputs only at the half-degree resolution (see Woodward et al. 2001 for information on the SDGVM model used to generate these simulated data sets). The data were then similarly rescaled to a one-degree grid cell size.

For measuring habitat heterogeneity, we enumerated the number of vegetation types (VEG) occurring in each quarter-degree cell based on Low and Rebelo (1996). These authors define "vegetation type" as a coherent array of communities that share common species (or abundances of species), have similar vegetation structure, and share the same set of ecological processes. Number of vegetation types is commonly employed as a measure of habitat heterogeneity or habitat complexity (Reed 1981; Kohn and Walsh 1994); VEG was also rescaled for half- and one-degree grid cell sizes, which provided one way of measuring habitat heterogeneity within a grid cell. A second method used evenness of vegetation-type cover. Low and Rebelo's (1996) map of 68 vegetation types across South Africa was digitized and replotted in ArcInfo. This software was used to calculate the percentage of vegetation-type coverage of each cell at each resolution (Albers equal area projection). As in the case of bird species richness, vegetation-type cover within the section of a grid cell extending outside the study area was assumed to be equivalent to that of the grid cell section inside the study area. From these vegetation-type proportion values in each cell, the Shannon-Wiener function was used as a measure of vegetation-type evenness (E) for each cell at each resolution (Krebs 1999). Evenness values vary between 0 and 1, with higher values indicating more evenly distributed vegetation types and, therefore, greater heterogeneity within a cell.

Regression Analysis

For each resolution, we used linear and curvilinear regressions to investigate relationships between all pairs of environmental variables and between avian species richness and each independent environmental variable (bivariate relationships). Tabulated regression results were subject to sequential Bonferroni corrections (Rice 1989). We subsequently explored the data in greater depth using models that included all combinations of two explanatory variables, but only those providing the best significant fits after sequential Bonferroni correction are reported. Stepwise variable selection procedures were not used because of significant collinearity and because of the problems associated with interpretation of model outputs (James and McCulloch 1990). Because O'Brien et al. (1998) found that a combination of PPT and minimum monthly PET

(PEMIN) explained a considerable portion of the variation of woody plant richness in southern Africa, we also assessed the ability of their multivariate model to explain avian species richness.

Spatial Data Analysis

The presence of spatial autocorrelation within ecological data results in a lack of independence of data points and, consequently, an overestimation of the number of degrees of freedom in an analysis (Clark 1982; Legendre and Legendre 1998; Boone and Krohn 2000a). Moreover, variation in a given variable such as species richness may result from spatial autocorrelation of the variable itself, from relationships between the variable of interest and another variable that is spatially structured or from relationships between the two variables that are independent of space (Legendre and Legendre 1998). Unlike many previous analyses that have generally downplayed or glossed over the problems associated with spatial structuring of the data, here we employed partial regression analyses to address both issues. Variation in avian species richness was partitioned into four components: (a) nonenvironmental spatial: that component of the spatial variation in species richness that is not shared with the environmental variables; (b) spatially structured environmental: spatial structuring in the species richness data that is shared with the environmental variable data; (c) nonspatial environmental: that component of the spatial variation in species richness that can be explained by the environmental variables independent of any spatial structure; and (d) unexplained (residual) variation (Legendre and Legendre 1998).

The spatial component of avian species richness for each resolution was modeled using a third-order polynomial of the form

$$f(x, y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3, \quad (1)$$

where x and y represent longitude and latitude, respectively. This expression is sufficient to extract any linear gradients from the data as well as more complex features such as patches or gaps (Legendre 1990; Borcard et al. 1992). The coefficient of determination (r^2) for this relationship was used as a measure of that component of the variation in bird species richness that is explained by a combination of the nonenvironmental spatial component (component a) and the spatially structured environmental component (component b). The r^2 values of the bivariate or multivariate relationships between species richness and environmental variables, obtained from the previous analyses, were used as a measure of the variation

explained by a combination of the spatially structured environmental component (component *b*) and the nonspatial environmental component (component *c*). The variation in species richness explained by components *a* + *b* + *c* was determined from a model incorporating both the environmental and spatial variables. Tabulated partial regression model results were subject to sequential Bonferroni corrections. By subtraction we estimated the amount of variation accounted for by each of the components separately.

To understand further the form of the spatial autocorrelation in the data, we investigated spatial patterns in avian species richness and the most significant environmental correlates of this variation at the one-degree grid square resolution. To do this, we used spatial autocorrelation analysis (Moran's *I*; see Legendre and Legendre 1998) and, specifically, SAAP-PC Version 4.3 (Exeter Software; Wartenberg 1989; program limitations precluded analysis at the other scales). Correlograms based on 15 equal-distance classes (123 km; covering the full spatial extent of the data) were used to graphically represent the changes in the autocorrelation coefficients with physical distance between pairs of grid cells (Legendre and Legendre 1998). Distance classes with less than 1% of the total number of point pairs (the two largest distance classes) were considered unreliable and were not interpreted (Legendre and Fortin 1989). We used Bonferroni approximation (correcting for multiple comparisons) to evaluate the overall significance of each correlogram (Legendre and Fortin 1989). All correlograms proved significant at the Bonferroni corrected level $\alpha = 0.001$.

Results

Bird species richness at each resolution generally exhibited highly significant linear relationships with the environmental variables (table 1). Weak curvilinear relationships were found in only a few instances and generally did not greatly improve the fit of the models (e.g., for species richness and PET at the half-degree resolution, *r* increased from 0.59 to 0.64). Species richness was most strongly correlated with PPT at both the quarter- and one-degree resolutions and with NPP or LAI at the half-degree resolution (table 1; fig. 1). Strong relationships were also found between PET and species richness at each resolution (table 1; fig. 2). Correlations between species richness and the environmental variables increased with a decline in the spatial resolution of the data in six (PET, MAX, PPT, MAXMO, SRAD, and VEG) of the eight variables that were available for all three resolutions. This was especially true for both measures of habitat heterogeneity (table 1).

Five successive jackknife analyses were conducted for each environmental variable to investigate the robustness

Table 1: Pearson's correlation coefficients between avian species richness and environmental variables at each resolution before taking spatial autocorrelation into account

Environmental variables	Avian species richness		
	Quarter degree <i>r</i>	Half degree <i>r</i>	One degree <i>r</i>
PET	-.52***	-.64***	-.71***
MAX	.02 NS	.02 NS	-.25*
MIN	.39***	.42***	.27**
PPT	.65***	.77***	.82***
MAXMO	-.12***	-.13**	-.28**
MINMO	.42***	.45***	.29**
SRAD	-.47***	-.49***	-.60***
VEG	.32***	.43***	.70***
EVVEG	.04 NS	.10 NS	.22*
NPP		.79***	.71***
LAI		.80***	.71***

Note: Significance was calculated after a sequential Bonferroni correction was applied; *df* = 1, 1,856 at quarter degree; *df* = 1, 456 at half degree; *df* = 1, 100 at one degree. PET = mean annual potential evapotranspiration (mm yr⁻¹); MAX and MIN = mean absolute monthly maximum and minimum temperatures (°C) averaged over the year; PPT = mean annual precipitation (mm yr⁻¹); MAXMO and MINMO = mean monthly maximum and minimum temperatures (°C) of the hottest and coldest months; SRAD = mean annual solar radiation (MJ m⁻² yr⁻¹); VEG = number of vegetation types; EVVEG = evenness of vegetation type cover; NPP = mean annual net primary productivity (g C m⁻² yr⁻¹); LAI = leaf area index.

* *P* < .05.

** *P* < .01.

*** *P* < .001.

of these bivariate correlations (see Krebs 1999, pp. 336–338). At each step, a random sample of 10% of the grid cells was excluded. Thus, in the final step, 50% of the grid squares had been excluded. The jackknife values for each of the comparisons were robust, leading to small standard deviations of the *r* values, which varied between 0 and 0.019 for all resolutions. Consequently, the correlation coefficients between species richness and each of the environmental variables were considered robust.

A combination of PPT and MIN or PPT and MINMO explained most variation in species richness at the quarter-degree resolution. At the half-degree resolution, a combination of PPT and MIN, NPP and MIN, or NPP and MINMO accounted for most variation in species richness, whereas combinations of PPT and habitat heterogeneity (VEG), or VEG and NPP or LAI, accounted for most of the variation in richness at the one-degree resolution (table 2). Despite pronounced collinearity among many of the independent variables, the relationships between these particular variables were generally not strong ($0.08 < r < 0.58$). The O'Brien et al. (1998) model, that is, species richness = PPT + (PEMIN – PEGIN²), provided a poorer fit than did the other variable combinations at all resolutions (table 2).

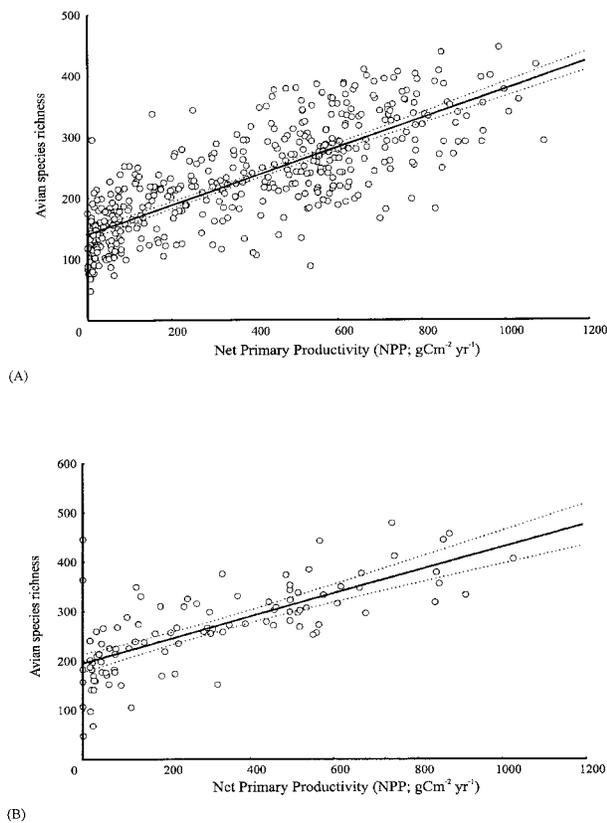


Figure 1: Relationships between avian species richness and NPP (mean annual net primary productivity). A, Half-degree resolution (avian species richness = $140.66 + 23.588 \times \text{NPP}$; $r = 0.79$). B, One-degree resolution (avian species richness = $195.61 + 23.100 \times \text{NPP}$; $r = 0.71$).

In most cases, spatially structured environmental variation accounted for most of the variation in bird species richness (tables 3, 4), as might be expected given strong and similar spatial autocorrelation patterns in both the dependent and independent variables (fig. 3). Nonetheless, a reasonable proportion of the variation in bird species richness was accounted for by space only, while the environment only accounted for a small proportion of variation in avian richness.

The use of approximately equal area grid cells limited the likelihood of a direct effect of variation in local area on the relationships between species richness and the environmental variables. However, area might have had a role at the regional level. For example, if in a positive relationship between species richness and some environmental variable the highest values of the environmental variable cover the largest area (Chown and Gaston 1999), then the relationships between species richness and the environmental variable in question might be the consequence of an underlying species-area relationship. To test

for this effect, we assigned grid cells to equal-sized classes for each of the abiotic environmental variables contributing most to variation in species richness (PPT, MIN, LAI). The precise number of classes used for each variable depended on the range of values in each case.

For each of the classes and for each variable, we determined mean species richness and total area (number of grid cells) covered by each variable within each class. We examined the relationships between these variables using Pearson product-moment correlation coefficients, and then repeated this procedure for all resolutions. As we expected, species richness and the mean class value were

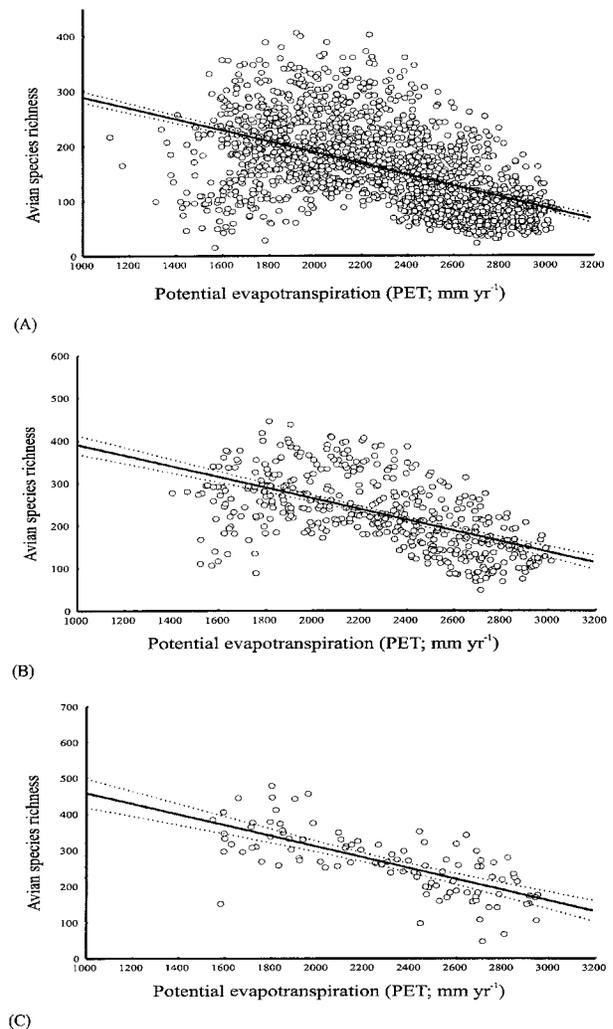


Figure 2: Relationships between avian species richness and PET (potential evapotranspiration). A, Quarter-degree resolution (avian species richness = $389.97 - 0.1009 \times \text{PET}$; $r = -0.52$). B, Half-degree resolution (avian species richness = $516.10 - 0.1261 \times \text{PET}$; $r = -0.64$). C, One-degree resolution (avian species richness = $606.79 - 0.1485 \times \text{PET}$; $r = -0.71$).

Table 2: Correlation coefficients for the best-fit explanatory models of bird species richness incorporating two variables, in order of their fit, without taking spatial autocorrelation into account

Spatial resolution with significant two-environmental variable models	<i>r</i>
Quarter degree:	
PPT and MIN	.728***
PPT and MINMO	.722***
PPT + (PEMIN – PEMIN ²)	.670***
Half degree:	
PPT and MIN	.830***
NPP and MIN	.815***
NPP and MINMO	.815***
PPT + (PEMIN – PEMIN ²)	.766***
One degree:	
PPT and VEG	.867***
LAI and VEG	.839***
NPP and VEG	.839***
PPT + (PEMIN – PEMIN ²)	.821***

Note: Significance was calculated after a sequential Bonferroni correction was applied; *df* = 2, 1,856 at quarter degree; *df* = 2, 456 at half degree; *df* = 2, 100 at one degree. PPT = mean annual precipitation (mm yr⁻¹); MIN = mean absolute monthly minimum temperatures (°C) averaged over the year; MINMO = mean monthly minimum temperatures (°C) of the coldest months; NPP = mean annual net primary productivity (g C m⁻² yr⁻¹); VEG = number of vegetation types; LAI = leaf area index. PPT + (PEMIN – PEMIN²) is the model proposed by O'Brien et al (1998).
*** *P* < .001.

positively correlated at all resolutions ($r > 0.748$). These relationships were all monotonic except for PPT, which exhibited a unimodal relationship at the quarter-degree resolution. The mean class value for PET also exhibited a unimodal relationship with species richness. Because the area covered by each class either tended to decrease (PPT and LAI, $r < -0.29$) or showed no change (PPT) with an increase in the mean value for that class, there were either no significant relationships or a negative (PPT at quarter-degree resolution, $r = -0.779$) or weak positive (MIN at quarter-degree resolution, $r = 0.325$) relationship between area covered by the variable and species richness. Thus, underlying species-area effects do not appear to have significantly affected the relationships between species richness and the environmental variables.

Discussion

Mean annual precipitation (PPT), mean annual productivity (LAI or NPP), mean absolute monthly minimum temperature averaged over the year (MIN), and, at the

coarser resolutions, the number of vegetation types (VEG), either singly or in combination, accounted for most of the variation in avian species richness across South Africa. Perhaps more significantly, it is clear that the spatially structured component of the variation in the environmental variables accounted for most of the variation in species richness. Few other studies explicitly account for the pronounced spatial autocorrelation that is characteristic of species richness (see, e.g., Currie 1991; O'Brien 1993; Kerr and Packer 1997; Jetz and Rahbek 2001), and investigations into the reasons for this spatial structure have generally been limited. In this case, it is clear that spatial structure of the environmental variables, which is plainly a reflection of the strong east-west gradients in precipitation, and associated gradients in both productivity and vegetation heterogeneity in South Africa (see fig. 3; Schulze 1997*a*, 1997*b*) are responsible for much of the variation in species richness. 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; Smith 1994; Boone and Krohn 2000*a*). Furthermore, the variation accounted for solely by space indicates that species richness shows spatial autocorrelation independent of the spatial structure of the explanatory variable in question, although this was generally small compared to the spatially structured environmental variation. Thus, much of the variation in avian species richness across southern Africa is strongly related to and likely a consequence of the east-west spatial gradient in the environmental variables, particularly primary productivity and rainfall.

That primary productivity is strongly correlated with species richness is not surprising. This is considered the least contentious aspect of species-energy theory, and there are sound mechanisms accounting for these relationships (Rosenzweig and Abramsky 1993; Wright et al. 1993; but see also Srivastava and Lawton 1998; Waide et al. 1999). The strong association between species richness and precipitation is also readily explained. Precipitation and primary productivity (measured as either NPP or LAI) are highly correlated, and there is a clear underlying causal relationship between these two variables. In semiarid areas such as South Africa, precipitation sets limits to primary productivity, giving rise to the strong association between the two variables (see O'Brien 1993; Schulze 1997*a*; O'Brien et al. 1998, 2000; Andrews and O'Brien 2000). Thus, the correlations found in this study between species richness and both productivity and precipitation likely reflect underlying causation, though it remains unclear exactly what the mechanisms are through which energy and water availability might have such a pronounced causal effect on avian species richness (see also Gaston 2000).

Unlike the other direct (NPP and LAI) and indirect

Table 3: Coefficients of determination for the relationships between avian species richness and the environmental variables with the best fit at each resolution

Spatial resolution with strongest single significant explanatory variables	The proportions of variation in avian species richness (r^2)				
	Total ($a + b + c$)	Environment only (c)	Spatial structured environmental variation (b)	Space only (a)	Spatial structured environmental variation and space only ($a + b$)
Quarter degree:					
Potential evapotranspiration	.622***	.007	.267	.346	.614***
Precipitation	.618***	.003	.415	.199	.614***
Half degree:					
Net primary productivity	.779***	.018	.603	.158	.761***
Leaf area index	.771***	.009	.631	.129	.761***
Potential evapotranspiration	.776***	.015	.409	.351	.761***
One degree:					
Precipitation	.805***	.002	.672	.131	.803***
Net primary productivity	.806***	.003	.512	.291	.803***
Leaf area index	.812***	.008	.493	.310	.803***
Potential evapotranspiration	.830***	.026	.474	.329	.803***

Note: Variables partitioned into (a) nonenvironmental spatial component, (b) spatially structured environmental variation component, (c) nonspatial environmental component, and (d) unexplained component. All partial regression values reached significance after a sequential Bonferroni correction was applied.

*** $P < .05$.

(PPT) measures of primary productivity, annual potential evapotranspiration (PET) was negatively related to species richness, with the latter showing a strong decline above $\sim 2,200 \text{ mm yr}^{-1}$ (fig. 2). The lack of available precipitation is clearly responsible for this relationship too. Although potential evapotranspiration is high in the western arid regions of southern Africa, the rainfall here is low (hence the negative relationship between PPT and PET; table 1). In other words, even though there is potentially a considerable amount of energy available to be utilized for primary productivity in the western arid regions of the country, there is insufficient moisture to support utilization of the energy by plants. In a series of papers, O'Brien and her coworkers (O'Brien 1993, 1998; O'Brien et al. 1998, 2000; Andrews and O'Brien 2000) have suggested that a capacity rule based on geographic variation in and interactions between energy and water availability can explain variation in woody plant species richness in most geographic regions. Our findings show that this may be true of birds too, although the precise nature of the relationship between avian species richness and available energy and water differs from the model proposed for woody plants.

The relationship between PET and species richness found here shows a number of similarities to and differences from that found by Currie (1991) for North American birds. Undoubtedly, some of these differences are a consequence of the fact that the A-Pan measure of PET used here differs from the one used by Currie (1991). In

particular, the absolute values of PET are likely to vary between methods, and the values we used are generally higher than those estimated using other models (see Rosenberg et al. 1979; Hulme et al. 1996). Nonetheless, these factors are unlikely to affect the comparison because the most significant issue at hand is the trend in species richness relative to PET rather than the absolute values of PET. In North America, the strong increase in PET is associated with a rapid rise in bird species richness from the Arctic to more temperate areas. In North America, there is likely to be little in the way of water limitation, and productivity rises rapidly in this region (or at least AET does, and this variable was used to estimate productivity in Currie's [1991] study). Indeed, it is clear from Currie's (1991) figure 5 that the relationship between avian species richness and productivity is positive in this region too. Thereafter, the relationship between PET and species richness is virtually asymptotic, with the variance increasing as PET increases. In southern Africa, there is also an initial rise in species richness in regions with low PET, but thereafter species richness declines dramatically, and it seems likely that this is caused by a water constraint that prevents PET from being translated into energy availability (see discussion above).

In contrast, species richness in both regions increases monotonically with primary productivity over a similar range of productivity values. Thus, the important distinction between southern Africa and North America appears

Table 4: Coefficients of determination for the relationships between avian species richness and the two environmental variable models with the best fit at each resolution

Spatial resolution with most significant explanatory two-environmental variable models	The proportions of variation in avian species richness (r^2)				
	Total ($a + b + c$)	Environment only (c)	Spatial structured environmental variation (b)	Space only (a)	Spatial structured environmental variation and space only ($a + b$)
Quarter degree:					
PPT and MIN	.656***	.041	.489	.125	.614***
PPT and MINMO	.655***	.040	.481	.133	.614***
Half degree:					
PPT and MIN	.797***	.036	.653	.107	.761***
NPP and MIN	.794***	.032	.631	.129	.761***
NPP and MINMO	.797***	.035	.628	.133	.761***
One degree:					
PPT and VEG	.842***	.038	.666	.090	.757***
LAI and VEG	.847***	.043	.660	.143	.757***
NPP and VEG	.844***	.040	.663	.14	.757***

Note: Variables partitioned into (*a*) nonenvironmental spatial component, (*b*) spatially structured environmental variation component, (*c*) nonspatial environmental component, and (*d*) unexplained component. All partial regression values reached significance after a sequential Bonferroni correction was applied. PPT = mean annual precipitation (mm yr^{-1}); MIN = mean absolute monthly minimum temperatures ($^{\circ}\text{C}$) averaged over the year; MINMO = mean monthly minimum temperatures ($^{\circ}\text{C}$) of the coldest months; NPP = mean annual net primary productivity ($\text{g C m}^{-2} \text{yr}^{-1}$); VEG = number of vegetation types; LAI = leaf area index.

*** $P < .05$.

to be that of water limitation. In southern Africa, high-productivity areas are associated with areas of lower PET (i.e., a negative relationship between NPP and PET: $r = -0.71$ and -0.67 at the half- and one-degree resolution levels, respectively), whereas PET and productivity are more likely to be positively related in North America (see fig. 8 in Currie 1991) where water limitation is not as severe, at least over much of the range of PET. This influence of water availability on the translation of available energy into primary productivity (see also O'Brien et al. 1998, 2000) means that when surrogates of primary productivity are being used during investigations of species-energy relationships, care must be taken in interpreting the outcomes of the analyses.

In the multivariate analyses undertaken here, minimum temperature (both MIN, mean absolute monthly minimum temperatures averaged over the year, and MINMO, mean monthly minimum temperatures of the coldest months), which was not strongly correlated with NPP or PPT, entered most of the models as the most important explanatory variable together with either primary productivity or precipitation. Following the logic of Root (1988) and Blackburn et al. (1996), we propose that the importance of minimum temperature as a correlate of species richness is likely a consequence of interactions between resource abundance and the physiological capabilities (especially alterations of metabolic rate) of the species

involved. Nonetheless, this effect of minimum temperature is relatively weak, probably because most of the region in question has a subtropical to warm temperate climate (see also O'Brien 1993; Andrews and O'Brien 2000).

At the largest scales, minimum temperature was replaced by vegetation heterogeneity as the independent variable, second to primary productivity or precipitation, contributing most to variation in species richness. The increase in the explanatory importance of habitat heterogeneity with a decline in spatial resolution can be attributed largely to an increase in the range of habitat heterogeneity included in the analysis with an increase in grid cell size (from 1–8 [quarter degree] to 1–12 [one degree] vegetation types). For statistical reasons, this increase in the range of vegetation types is likely to mean an increase in the importance of VEG as an explanatory variable (see the introduction to this article). Nonetheless, the increase in the importance of vegetation heterogeneity might also be caused by the strong positive effects that environmental and habitat heterogeneity have on species richness (see Rosenzweig 1995; Ricklefs and Lovette 1999; Waide et al. 1999 for discussion). These findings suggest that studies investigating the relationship between species richness and habitat heterogeneity, which are undertaken at large spatial scales using coarse resolutions (the two parameters are usually varied simultaneously), are almost certain to conclude that habitat heterogeneity is an important explan-

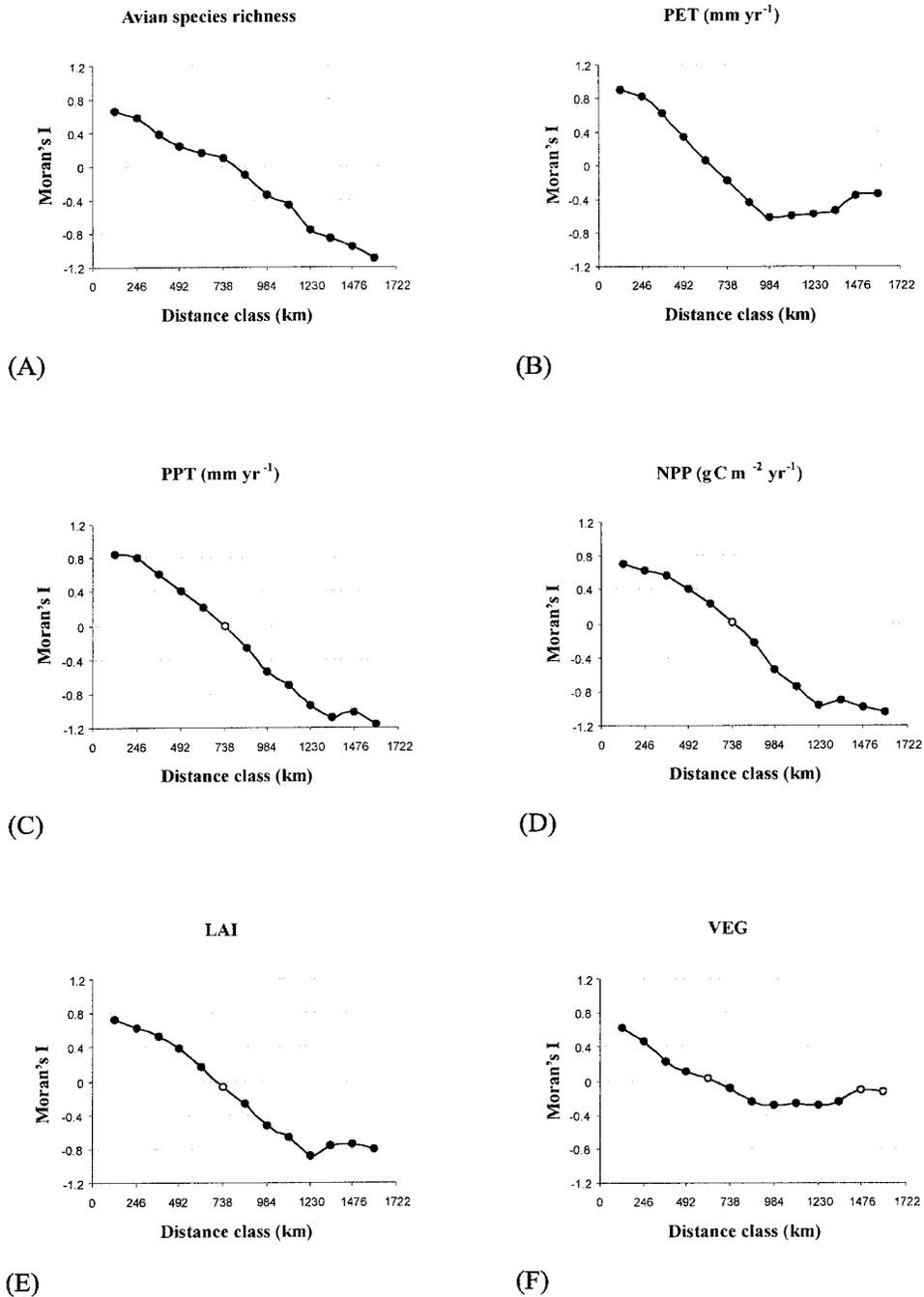


Figure 3: Spatial patterns in avian species richness and the most significant environmental correlates of this variation at the one-degree grid square resolution across South Africa based on equal distance classes (123 km). *Moran's I* = coefficient of autocorrelation. Sequential Bonferroni correction was applied at $\alpha = 0.001$ to evaluate each I value and the overall significance of each correlogram. All correlograms proved significant, and the closed circles represent significant I values. *PPT* = mean annual precipitation; *PET* = mean annual potential evapotranspiration; *NPP* = mean annual net primary productivity; *LAI* = leaf area index; *VEG* = number of vegetation types.

atory variable for species richness (see, e.g., Kerr and Packer 1997; Fraser 1998; Andrews and O'Brien 2000), even when this might not be the case. Thus, conclusions regarding the importance of vegetation heterogeneity in explaining species richness must be cautiously interpreted in the context of both the spatial extent and the resolution of the study being undertaken.

In conclusion, we have shown that spatial variation in avian species richness in southern Africa is correlated with and likely is the consequence of considerable spatial variation in precipitation and energy availability, which affects primary productivity. In addition, we have demonstrated that these results are consistent across several spatial resolutions but that vegetation heterogeneity is likely to increase in importance as an explanatory variable with declining spatial resolution, probably for statistical reasons. This provides at least a partial explanation for the conclusion of some studies (see, e.g., Kerr and Packer 1997; Fraser 1998) that, second to energy availability, vegetation heterogeneity forms a significant correlate of species richness. Finally, we have shown that surrogate measures of primary productivity must be interpreted cautiously when investigating species energy theory.

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