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Article:

Structure of the species–energy relationship

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The relationship between energy availability and species richness (the species–energy relationship) is one of the best documented macroecological phenomena. However, the structure of species distribution along the gradient, the proximate driver of the relationship, is poorly known. Here, using data on the distribution of birds in southern Africa, for which species richness increases linearly with energy availability, we provide an explicit determination of this structure. We show that most species exhibit increasing occupancy towards more productive regions (occurring in more grid cells within a productivity class). However, average reporting rates per species within occupied grid cells, a correlate of local density, do not show a similar increase. The mean range of used energy levels and the mean geographical range size of species in southern Africa decreases along the energy gradient, as most species are present at high productivity levels but only some can extend their ranges towards lower levels. Species turnover among grid cells consequently decreases towards high energy levels. In summary, these patterns support the hypothesis that higher productivity leads to more species by increasing the probability of occurrence of resources that enable the persistence of viable populations, without necessarily affecting local population densities.

Keywords: species–energy relationship; species–area effect; productivity; occupancy; species turnover

1. INTRODUCTION

The covariation between the number of species in an area and the availability of environmental energy is fundamental to an understanding of spatial variation in species richness (Wright 1983; Turner *et al*. 1988; Currie 1991; Gaston 2000; Kaspari *et al*. 2000; Hurlbert & Haskell 2003). Studies so far have primarily concerned the establishment of the form and occurrence of species–energy relationships. These have variously been found to be positive, negative and hump-shaped. Some examples of the first two comprise the extremes of the third, but others apparently do not, and there is growing evidence for dependence of the form of observed patterns on spatial scale (Waide *et al*. 1999; Mittelbach *et al*. 2001; Whittaker *et al*. 2001; Chase & Leibold 2002; Van Rensburg *et al*. 2002). Such complexity has, perhaps inevitably, led to a multitude of explanations for species–energy relationships, rooted in a variety of evolutionary and ecological processes (Kerr & Packer 1997; Rohde 1997; Rosenzweig & Sandlin 1997; Srivastava & Lawton 1998; Allen *et al*. 2002; Storch 2003).

As with other macroecological patterns, untangling the causes of the species–energy relationship is problematic, because the large-scale nature of the pattern does not allow direct experimental testing (although manipulations of 'model' systems at smaller scales may prove informative (Gaston & Blackburn 1999)). However, although it is difficult to definitively prove or reject the importance of any particular process potentially leading to the relationship, it is possible to strengthen the support for some hypotheses and weaken that for others, by detailed analysis of the structure of the pattern; i.e. of the distribution of individual species along the energy gradient. In practice, although some other predictions of mechanisms proposed to determine species–energy relationships have been tested (e.g. Srivastava & Lawton 1998; Gaston 2000; Kaspari *et al*. 2003), this approach has not, to our knowledge, been used.

Assuming a linearly increasing species–energy relationship, we can distinguish two extreme types of species distribution along the energy gradient. First, species may exhibit a nested occurrence pattern, such that those present at a given level of energy availability always occur at higher ones (figure 1*a*; note that this pattern leads to a decrease in the average range of species occurrence along the gradient). Second, species can occupy equally narrow ranges along the gradient, regardless of the energy level (figure 1*b*). Real patterns of species distribution will probably lie somewhere between these two extremes. However, patterns closer to the 'nested' one indicate that greater energy availability increases the chance of persistence of most species independently to each other, i.e. in an individualistic manner. On the contrary, the other extreme type of distribution supports the role of processes affecting whole species assemblages, either as a result of the evolution of separate species pools in areas with different energy levels (e.g. faster evolution in areas with higher levels of energy (see Rohde 1997; Allen *et al*. 2002)), or as a result of the sorting of species along the gradient by interspecific competition (Rosenzweig & Abramsky 1993; Rosenzweig 1995) or other evolutionary processes.

Different evolutionary or ecological mechanisms can also lead to different patterns of local species abundances across the energy gradient. The 'more individuals' hypothesis (e.g. Wright 1983; Srivastava & Lawton 1998; Gaston 2000; Kaspari *et al*. 2003) assumes that there is a direct

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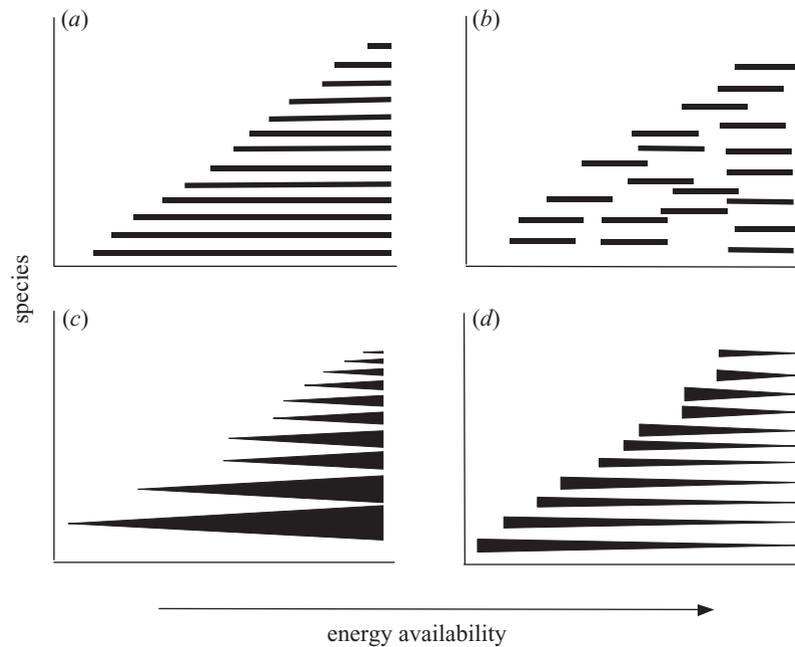
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Figure 1. Extreme patterns in species distribution along an energy gradient leading to higher richness at higher energy levels. (*a*) The nested distribution: all species can occur in higher energy levels, but not all can thrive in low levels of available energy. (*b*) Species range sizes are not related to energy level, but more species are confined to higher energy levels. (*c*) Species abundances increase with increasing energy, enabling the persistence of less common species. (*d*) Species abundances decrease with increasing energy, as a consequence of increasing interspecific competition or environmental heterogeneity.

relationship between energy availability, the overall amount of resources in an area, the total number of individuals that can thus be maintained, and consequently the number of species. This predicts that individual species will probably be more abundant with increasing energy availability (figure 1*c*), that they will occupy more sites with increasing energy availability, and also that at lower energy levels there will be higher turnover in species identities among sites than at higher ones (at which most species can maintain viable populations in most places). By contrast, what we shall call the 'specialization' hypothesis assumes that higher energy levels enable finer sub-division of available resources, either because of reductions in niche breadth or through the generation of greater resource diversity or habitat heterogeneity (e.g. Abrams 1995; Kerr *et al.* 2001). This predicts that individual species may become less abundant with increasing energy availability (figure 1*d*), that they will occupy fewer sites at higher energy availability, and also that there will tend to be higher turnover of species among sites at higher levels of energy availability than among sites at lower availability (see Whittaker 1960; Gaston & Williams 1996; Brown & Lomolino 1998).

In this paper, we determine the key features of the structure of a species–energy relationship, focusing on the distribution of individual species along the energy gradient. We use as a case study the avian species assemblage of South Africa and Lesotho, for which the existence of such a relationship is already well established (Van Rensburg *et al.* 2002). First, we describe (i) the observed pattern and test whether the observed species–energy relationship is attributable to (ii) the species–area relationship, as the existence of such an effect could influence subsequent considerations (Rosenzweig 1995). Then we analyse (iii) the relationship between energy and species' environmental

and geographical ranges. We subsequently test whether higher energy levels lead to higher levels of (iv) occupancy and (v) abundance of species. Finally, we analyse (vi) trends in species turnover along the energy gradient.

2. METHODS

(a) *Data*

Avian species-richness data for South Africa and Lesotho were obtained from the Southern African Bird Atlas Project (Harrison *et al.* 1997), which compiled information, mainly collected between 1987 and 1992, on species occurrences on a quarter-degree grid ($15' \times 15' \approx 676$ km²). We consider presence or absence and reporting rate data for 651 native species excluding marine, vagrant, marginal and introduced or escaped species. Reporting rates are the proportion of checklists submitted for each grid cell with presence records for a given species, and reflect broad differences in local abundances (Robertson *et al.* 1995).

We used the normalized difference vegetation index (NDVI) as a measure of energy availability. A mean 9 year average NDVI for the first decade in January (1982–1991) for each quarter-degree grid cell was obtained from the African Real Time Environmental Monitoring using Meteorological Satellites program (ARTEMIS) of the Food and Agriculture Organization (FAO; see http://metart.fao.org/default.htm). In January, differences in the NDVI index were most pronounced and ranged from 0 to 0.63 across the whole of Africa at a 0.01 resolution. The means for quarter-degree grid cells across the region of interest span 0.04 to 0.50 (at the original spatial resolution of 7.6 km² the values span 0.0 to 0.54). Substantially higher levels than these are only met by moving considerable distances beyond the borders of South Africa (figure 2).

Measures of NDVI were used as measures of energy because they were available at a finer resolution than the half-degree
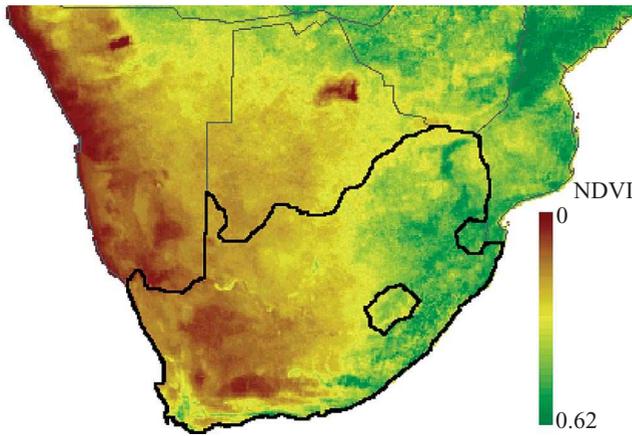
Figure 2. A map of the southern part of the African continent showing NDVI levels. The study area, South Africa and Lesotho, is delineated with bold black boundaries. NDVI classes are relatively contiguous in the study area, and the areas of intermediate productivity exhibit the greatest surface area and areal coverage.

measures of net primary productivity (NPP) (Woodward *et al.* 2001) that have previously been employed in documenting a species–energy relationship for the South African avifauna (Van Rensburg *et al.* 2002). However, at a half-degree resolution the two are closely correlated ($r^2 = 0.81$, $p < 0.001$). Moreover, the following analyses, when performed using NPP as the energy variable at the broader resolution, arrived at similar results.

(b) *Analyses*

We recognize two scales of analysis. The first is that of the quarter-degree grid cell, and the number of species occurring in a cell is termed grid-cell species richness. The second is that of the NDVI class, and the total number of species occurring in one or more grid cells within a class is termed NDVI class species richness. The grid cells fall into 47 classes from lowest to highest NDVI values, with 0.01 increments of NDVI (finest possible resolution).

To determine relationships between species richness and NDVI, linear and quadratic regressions were performed. When quadratic effects were found significant, we used a statistical test developed by Mitchell-Olds & Shaw (1987) (see also Chase & Leibold 2002) to test for the significance of a hump-shaped relationship, determining whether the estimated maximum of species richness in intermediate levels of NDVI is significantly greater than species richness at both low and high NDVI levels.

As spatial autocorrelation may systematically distort classical tests of association, we implemented spatial correlation models for analyses at the grid-cell level using the PROC MIXED procedure (Littell *et al.* 1996). An exponential covariance structure was used as it gave a better fit to the null model, as assessed by Akaike's Information Criteria and Schwarz's Bayesian Criteria.

To test for potential species–area effects on the species–energy relationship, the number of cells falling within each NDVI class was used as a measure of the surface area of that class. Because species richness can be affected not only by the number of respective grid cells within an NDVI class, but also by their geographical dispersion, the geographical extent of each class was measured as the logarithm of the product of the maximum latitudinal and maximum longitudinal extent, and as the logarithm of the product of the standard deviation of the latitudinal and longitudinal coordinates, respectively. Because the latter

measure for geographical extent gives essentially the same results as the former, only those using the former are reported.

Mean percentage occupancy of species within an NDVI class was measured as the average percentage of occupied grid cells per species present within the class. Mean reporting rate, as a measure of the abundance of a species, was the average reporting rate per species within an NDVI class. In a second step, only grid cells with presence records were considered for this analysis to make this measure independent of occupancy. Thus, mean percentage occupancy relates to the species abundance at the larger energy scale, i.e. the NDVI class, whereas mean reporting rate for grid cells with presence records relates to local population density at the grid-cell level. Both measures were calculated for NDVI classes with 10 or more grid cells, i.e. for NDVI classes from 0.06–0.48.

Geographical ranges of species were measured as the number of grid cells in which the species had been recorded in the study region. The species' energy range was measured as the range of NDVI values of those grid cells. For geographical range size quartiles (RSQs), species were partitioned into four groups of *ca.* 163 species from the narrowest to widest ranging species (first to fourth RSQ).

Species turnover between all possible pairs of grid cells within an NDVI class was determined using β_{sim}

$$\beta_{sim} = \frac{1}{n} \sum_{i=1}^{n} (1 - S_i); \quad S_i = \frac{a_i}{a_i + \min(b_i, c_i)},$$

where n is the number of pairwise comparisons (Lennon *et al.* 2001). For each pairwise comparison, S_i, a is the total number of species shared by the two grid cells, and b and c are the total number of species unique to each cell, respectively. β_{sim} is independent of species-richness gradients, reflecting relative rather than absolute differences between compared units (Lennon *et al.* 2001; Koleff *et al.* 2003). As the turnover between grid cells is strongly affected by distance ($r = 0.536$, $p < 0.001$), pairwise comparisons, S_i, were calculated only for directly adjacent grid cells within NDVI classes. β_{sim} was calculated when five or more pairwise comparisons were possible.

3. RESULTS

(a) *Species–energy pattern*

Both grid-cell species richness and NDVI class species richness rise along the NDVI gradient (figure 3*a*). When controlling for spatial autocorrelation, grid-cell species richness increases monotonically with NDVI ($r^2 = 0.483$, $F_{1,1856} = 57.93$, $p < 0.001$) and a squared term of NDVI is not significant ($F_{1,1855} = 1.92$, n.s.). However, NDVI class species richness shows a marked hump-shaped relationship ($r^2 = 0.85$, $n = 47$, $p < 0.001$) reaching a ceiling at high but not the highest NDVI levels; the removal of the squared term results in a significant decrease in the model fit ($F_{change\ 1,46} = 89.15$, $p < 0.001$).

(b) *Species richness and area*

Maximum geographical extent and surface area of the NDVI classes correlate with NDVI class species richness (log–log transformation, $n = 46$: $r^2_{extent} = 0.38$, $p < 0.001$; $r^2_{area} = 0.20$, $p < 0.005$). However, this does not confound the relationship between NDVI and NDVI class species richness. On the contrary, controlling simultaneously for both factors by partial correlation changes the hump-shaped
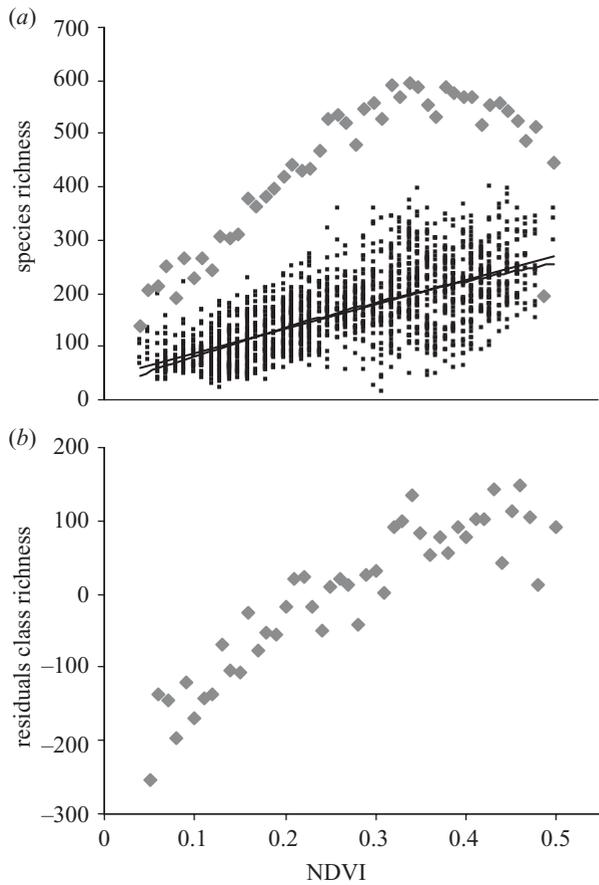
Figure 3. (*a*) Patterns of species richness along the NDVI gradient for grid-cell species richness (black squares, regression lines are given for linear and unimodal relationship) and for NDVI class species richness (diamonds). (*b*) Controlling for log surface area and log geographical extent reveals a more linear relationship between NDVI and NDVI class richness (unstandardized residuals plotted).

relationship into a more linear increase ($r^2 = 0.85$, $n = 46$, $p < 0.001$; although inclusion of the squared term still provides a better model fit, there is no significant internal maximum: $F_{\text{change } 1,41} = 84.25$, $p < 0.001$; figure 3*b*). Therefore, the strong hump-shaped relationship is an artefact of the wider coverage of intermediate levels of energy in South Africa (see figure 1), which consequently sample more species ranges. Not surprisingly, mean grid-cell species richness is only weakly affected by the two coverage parameters of the respective NDVI class (log–log transformation, $n = 46$: $r^2_{\text{extent}} = 0.09$, $p < 0.05$; $r^2_{\text{area}} = 0.02$, n.s.), and the relationship between NDVI and mean grid-cell species richness is not altered when controlling for both ($r^2 = 0.89$, $n = 46$, $p < 0.001$).

(c) *Energy ranges and geographical ranges along the energy gradient*

The mean energy range of species, i.e. the range of occupied NDVI classes, decreases with increasing NDVI, both when assessed for the species occurring in individual grid cells ($r^2 = 0.37$, $n = 1858$, $p < 0.001$) and for the species occurring in individual NDVI classes ($r^2 = 0.95$, $n = 47$, $p < 0.001$; figure 4*a*). The same is true for the mean geographical range of species occurring in individual
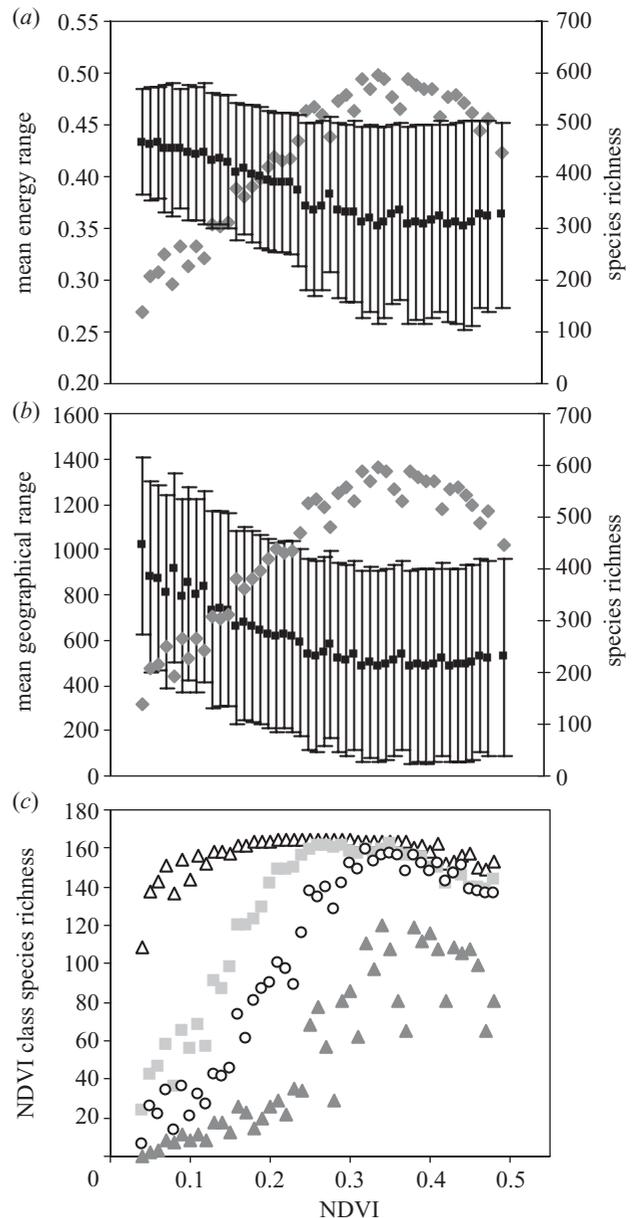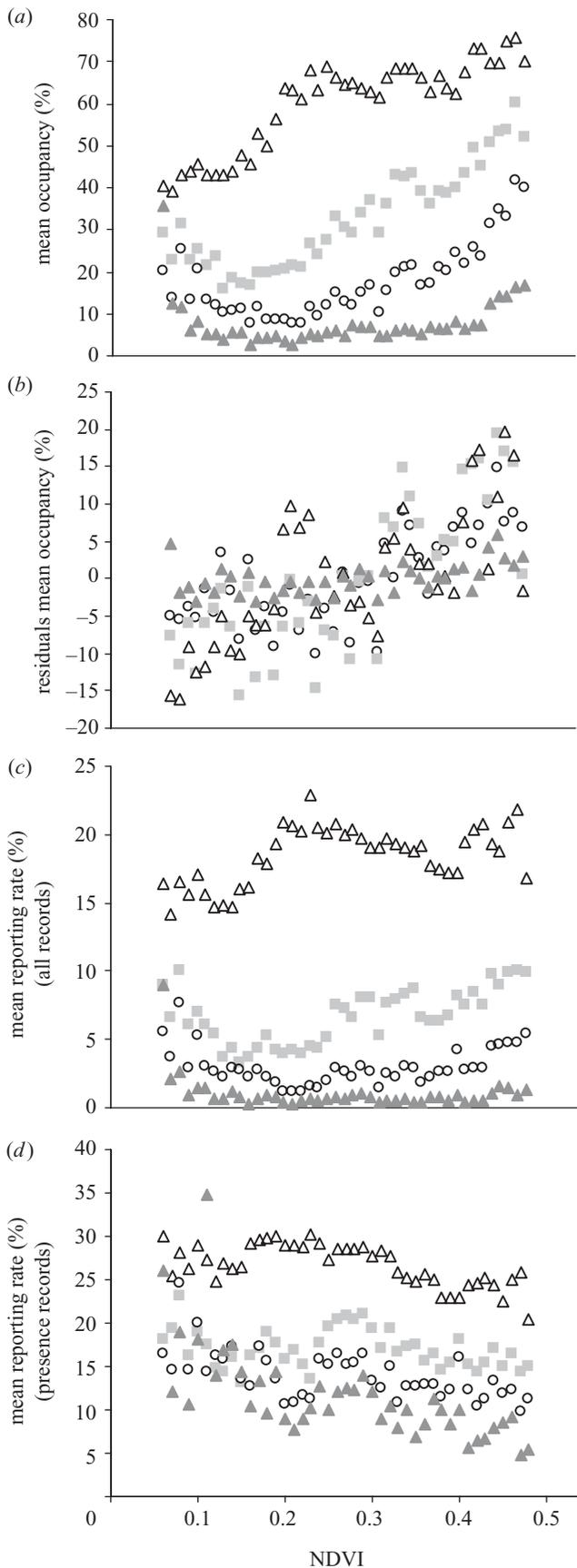

Figure 4. (*a*) Mean energy range and (*b*) mean geographical range of species present in NDVI classes along the productivity gradient (squares; error bars indicate s.d.). In (*a*,*b*) the overall NDVI class species-richness curve is given for comparison (diamonds). (*c*) Variation of patterns of NDVI class species richness for geographical RSQs along the NDVI gradient (RSQ: first, grey triangles; second, circles; third, squares; fourth, open triangles).

grid cells ($r^2 = 0.49$, $n = 1858$, $p < 0.001$), and for those occurring in individual NDVI classes ($r^2 = 0.96$, $n = 47$, $p < 0.001$; figure 4*b*). Therefore, species present at higher levels of energy tend to be more restricted in both their distribution across energy levels and their distribution across space. Most rare species actually occur only at high NDVI levels (figure 4*c*).

(d) *Energy–occupancy relationship*

The mean percentage occupancy of species within an NDVI class increases along the energy gradient (figure 5*a*). That is, on average, species occupy a greater percentage of grid cells at high energy levels than at low energy

(a) mean occupancy (%)

(b) residuals mean occupancy (%)

(c) mean reporting rate (%) (all records)

(d) mean reporting rate (%) (presence records)

NDVI

Figure 5. (*a*) Mean percentage occupancy of species along the productivity gradient; (*b*) controlled for log geographical extent and log surface area (unstandardized residuals plotted). Average mean species reporting rate for: (*c*) all grid cells within NDVI classes; and (*d*) only occupied grid cells within NDVI classes along the NDVI gradient (RSQ: first, grey triangles; second, circles; third, squares; fourth, open triangles).

$p < 0.001$) to a significantly negative hump-shaped pattern with an initial decrease for all other species (first to third RSQ: $r^2_{first} = 0.50$, $r^2_{second} = 0.88$, $r^2_{third} = 0.88$; all $n = 43$, $p < 0.001$). As intermediate levels of NDVI are more widely scattered (figure 2), mean percentage occupancy is expected to be lower in these areas, assuming approximately contiguous geographical ranges of species. Indeed, controlling simultaneously for geographical extent and surface area by partial correlations reveals strong linear relationships between NDVI and residuals of mean percentage occupancy for all species (figure 5*b*; $r^2_{first} = 0.10$, $p < 0.05$; $r^2_{second} = 0.69$, $p < 0.001$; $r^2_{third} = 0.83$, $p < 0.001$; $r^2_{fourth} = 0.66$, $p < 0.001$; all $n = 43$).

In fact, on a single species evaluation, the majority (80%) of species show increasing occupancies along the energy gradient, with significantly positive correlations between NDVI and occupancy for 64% of all species.

(e) *Energy–abundance relationship*

The increase in species occupancy is parallelled by an overall increase in species average reporting rates within NDVI classes, a proxy measure for abundance (figure 5*c*). The pattern mimics that of occupancy (monotonic increase fourth RSQ: $r^2_{fourth} = 0.28$; negative hump-shaped relationship for first to third RSQ: $r^2_{first} = 0.37$, $r^2_{second} = 0.62$, $r^2_{third} = 0.55$; all $n = 43$, $p < 0.001$) as there are strong linear correlations between mean percentage occupancy and average reporting rate (first to fourth RSQ: $r^2_{first} = 0.59$, $r^2_{second} = 0.52$, $r^2_{third} = 0.65$, $r^2_{fourth} = 0.30$; all $n = 43$, $p < 0.001$).

By contrast, when analysing only those grid cells with presence records within NDVI classes, the average reporting rate per species actually decreases along the NDVI gradient (figure 5*d*; first to fourth RSQ, all $n = 43$: $r^2_{first} = 0.46$, $p < 0.001$; $r^2_{second} = 0.35$, $p < 0.001$; $r^2_{third} = 0.08$, n.s.; $r^2_{fourth} = 0.40$, $p < 0.001$). Also for single species evaluations, significant correlations between the mean reporting rate per occurrence record within NDVI classes and NDVI are negative for 34% of all species and positive for only 19%. The ratio of negative to positive correlations is similar for all quartiles with a slightly higher proportion of negative correlations for narrow ranging species (percentage of negative versus percentage of positive correlations at $p > 0.05$, first to fourth RSQ: 20/4, 35/18, 36/25, 41/30).

(f) *Species turnover*

Overall species turnover between adjacent grid cells within individual NDVI classes decreases linearly along the energy gradient (figure 6; $r^2 = 0.35$, $n = 43$, $p < 0.001$). Partitioning species into geographical range size quartiles shows variation of the pattern. As expected, species turnover is higher for more narrowly distributed species, as they are rare, i.e. more scattered, everywhere.
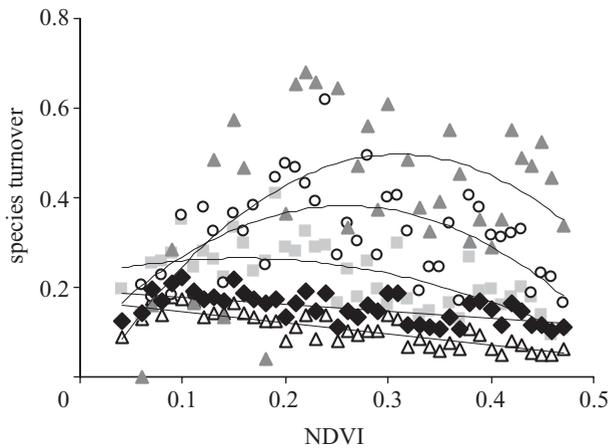
levels. This pattern holds for all geographical range size quartiles, but is weaker for narrowly distributed species (figure 5*a*). Also, the pattern changes from a monotonic increase for common species ($r^2_{fourth} = 0.80$, $n = 43$,

Figure 6. Relative species turnover (β_{sim}) between adjacent grid cells within NDVI classes along the productivity gradient (all species, diamonds; RSQ: first, grey triangles; second, circles; third, squares; fourth, open triangles; regression lines follow the sequence RSQ first, second, third, all species, fourth from top to bottom).

Along the energy gradient, for the first, second and third RSQ species, turnover shows a hump-shaped pattern (first to third RSQ: $r^2_{first} = 0.30$, $n = 35$; $r^2_{second} = 0.33$, $n = 42$; $r^2_{third} = 0.44$, $n = 43$; all $p < 0.001$). The wider the distribution of species, the earlier the decrease phase in turnover along the energy gradient. In the extreme, the turnover of common species decreases monotonically along the whole gradient ($r^2 = 0.63$, $n = 43$, $p < 0.001$), as all species are present in most NDVI classes and percentage occupancy rises continuously (figures 4*c* and 5*a,b*).

4. DISCUSSION

At a quarter-degree resolution, the species richness of South African birds increases monotonically with energy availability across a considerable range of NDVI values (figure 3*a,b*). This is in accord with the findings of Van Rensburg *et al.* (2002), and those of similar studies of several other assemblages (Waide *et al.* 1999; Mittelbach *et al.* 2001). Within South Africa, the monotonic increase of avian species richness with energy at a quarter-degree resolution is not a by-product of more productive areas having a greater geographical extent (cf. Rosenzweig 1995), because the most productive and species-rich regions are less extensive than those of intermediate productivity, and the effect of productivity is even stronger after controlling for the variation in area.

The marked increase in species occupancy along the energy gradient indicates that factors affecting the presence or maintenance of populations of individual species influence the observed patterns of species richness. This conclusion is supported by the fact that most species can be found in very productive areas, and species occurring in areas of low productivity are mostly those that occur everywhere, as indicated by the relationship between productivity and range size (figure 4*a,b*). This supports the importance of ecological factors independently affecting each species, rather than evolutionary processes responsible for the evolution of whole assemblages (see § 1). Although there are also rare species that only occupy less

productive areas, they do not form a separate species pool, and energy levels seem to affect most species in a similar way.

The increase of species occupancy with increasing energy (figure 5*a*) is probably responsible for the generally decreasing trend of species turnover along the productivity gradient (figure 6), as grid cells become more and more similar to each other. The concept of elevated species turnover accounting for increased species richness at larger scales (Whittaker 1960; Gaston & Williams 1996; Brown & Lomolino 1998) is therefore not appropriate here. Previous findings of positive relationships between species richness and turnover might have been confused by using traditional measures of beta diversity confounded by species richness itself (Koleff *et al.* 2003). Using the β_{sim} index, a similar decrease in overall species turnover along species-richness gradients was also observed by Lennon *et al.* (2001), who attributed it to more random mixtures of rarer species within areas of low species richness.

All of these findings can be considered as providing support for the 'more individuals' hypothesis. However, this hypothesis also predicts higher densities of all species in grid cells of higher available energy, which we did not observe. On the contrary, we documented a decrease of mean species abundance with increasing productivity, as measured by mean reporting rate within occupied grid cells (figure 5*d*). Although results for RSQs must be interpreted with caution, as reporting rates are not fully comparable among species, the trends are similar for all species of differing range sizes. This decrease in local population density along the productivity gradient could result from reductions in niche breadth and/or higher diversity or heterogeneity of resources within grid cells (figure 1*d*; i.e. lower amounts of each individual resource). If this is the case, then both the 'more individuals' and the 'specialization' hypotheses may be relevant, but on different spatial scales. It seems that rather than simple increases in the amounts of all resources, increases in energy availability increase the probability of occurrence of different resources necessary for the occurrence of different species.

Our findings therefore indicate that ecological processes responsible for establishment and maintenance of local populations are also responsible for the observed species–energy relationship on this spatial scale. It is probable that evolutionary processes of speciation, diversification and differential extinction are more important on larger spatial scales, and that hump-shaped species–energy relationships as documented for the whole of Africa (Balmford *et al.* 2001) may concern different species pools with different rates of evolution. But we predict that whenever the species–energy relationship concerns essentially one common species pool, ecological factors related to population probability of occurrence and maintenance will be important and species richness will therefore increase monotonically with productivity.

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