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Abstract

The relationship between increase in faunal diversity and corresponding increase in habitat complexity was quantified using shrubland bird communities in western Africa. Vegetational characteristics were measured in circular plots around bird positions. Bird species were then arranged from grassy open habitats to dense shrubland and found to be separated into three distinct communities when subjected to Duncan's multiple range procedure in conjunction with discriminant functions analysis. Random samples classified with respect to bird species showed there were few species in the more abundant open habitats and a disproportionate number of species were packed into the less common but complex shrubby habitat. The species packing formula generated supports the concept that spacial heterogeneity is a factor promoting high biotic diversity.

Introduction

It is well known that in most situations there are more species in tropical areas than at other latitudes. One reason for this, proposed by Ricklefs (1973), related to the possible existence of greater habitat complexity, or spacial heterogeneity, in the tropics than elsewhere. This complexity could proliferate ecological niches thus promoting specialization among organisms thereby reducing competition and allowing increased numbers of species to coexist in tropical environs. Using a crude foliage measure with respect to terrestrial avian populations, MacArthur and MacArthur (1961) showed that the species packing phenomenon is indeed related to degree of vegetational complexity. My study presented here describes a precise way of measuring species packing by birds in association with increased environmental complexity through the range of early successional habitats existing at a study site in Ghana, western Africa. Also, a method for separating avian communities is delineated.

Materials and Methods

The study was conducted from 12 November 1970 to 13 July 1971 in a mixture of disturbed habitats on the campus of University College of Cape Coast (now Cape Coast University) at Cape Coast, Ghana, in western Africa. The natural vegetation of the area is tropical lowland forest (Moreau, 1966) but little remained on campus or in the surrounding areas due to agricultural and urban developments interspersed with the successional recovery of vegetation on abandoned land resulting from rotational agriculture. This produced a mosaic of early successional stages in vegetation ranging from grassy areas, to open grassy shrubland, to very dense tall shrubland, interspersed with small untidy farm plots of maize, cassava, tomatoes, yams, peppers, pineapples and eggplants plus scattered citrus, pawpaw, banana and oil palm trees. There were no large areas of any one vegetational type, but rather scattered mixtures of small units of all stages. All these stages and conditions existed on campus, which was very large in size (several square miles) and included the university buildings, faculty housing, and several villages with adjacent farm lands and fallow areas. Only birds in the various successional habitats and crops were studied, eliminating all early and mature forest stands and forest edge. Thus, dense shrubby thickets 3-6 m tall constituted the most advanced vegetational type investgated. The overall landscape was mostly flat with some slightly rolling topography.

The methods and analyses employed were initially used in the present study in 1970-1971. Later, at my recommendation, they were adopted by Posey (1974) in northwestern Arkansas in 1972 and subsequently applied by me to studies in Nepal in South Asia (1981-1982), Belize in Central America (1988-1989), and northern Michigan (1987-1997), all part of an ongoing global study. Consult James (1992) for a detailed description of the field methods, which are identical to those employed in the present African study. This involved measuring 11 vegetational characteristics in circular plots 14.6 m in radius centered on exact positions where birds were found. There were 20 such plots sampled for each bird species. The vegetational characteristics included, 1) counting leaves that touched 8 levels marked on tall poles placed vertically at 40 random positions in the plot, the random spots drawn from random numbers indicating steps along each of 4 orthogonal transects from the plot center to its edge (10 positions per transect), the first transect positioned from a random twist of a compass dial, 2) the height of the tallest tree or shrub, 3) average vegetational height across the 4 sectors of the plot, 4) and stem density determined by the total woody stems intercepted in a foot wide plane at waist high along each of the orthogonal transects. An additional five vegetational pattern characteristics (stem evenness and variability, foliage vertical evenness, and foliage coarse and fine grained horizontal evenness) were calculated from the 11 measured in the field for a total of 16 vegetational factors (Table 1) associated with each of the 20 plots for each avian species. (The sampling method and the definition of all vegetational factors are described in great detail in James, 1992.)

Locating bird plots involved thorough and systematic searches of suitable areas having the diverse habitats mentioned above. Positions of both sexes, adults and subadults, of all species encountered were marked and plots were sampled later the same day. Birds were not marked individually, so sampling the same bird at different locations was possible. However, this repetition was minimized by sweeping through a given area only once and not repeating coverage. A total of about 61 hectares of suitable habitat was searched in the course of the study. Only local permanent resident birds were used, excluding the very rare species, also excluding those only seen flying over, seasonal migrants, and winter visitors from Europe. A total of 50 random plots without birds, nearly a plot per hectare of area covered, also was sampled in the study area to determine the nature of the actual vegetation present for comparison with habitats occupied by birds. Positions of random samples were located by drawing grids on maps of the various areas where bird plots were obtained and randomly selecting grid coordinates. Each segment of the overall study area was sampled in proportion to its relative size.

The data were analyzed with an IBM-360 Model 50 digital computer using statistical programs written by James E. Dunn, Mathematics Department, for the University of Arkansas mainframe system available in the 1970s. (All the routines mentioned below are examples of these programs.) The heterogeneous variance among the 16 vegetational variables was stabilized employing a program (Zodrow et al., 1988) developed from Box and Cox (1964) and Andrews et al. (1971) that transformed the original values. The arrangement of bird species in the vegetational complex and identification of important vegetational features were accomplished by subjecting the transformed data to multivariate analysis of variance (Morrison, 1967; Cooley and Lohnes, 1971) in conjunction with step-down analysis (Bargmann, 1962). Significance of separation of avian species along the first discriminant function axis was achieved by employing Duncan's multiple range procedure (Steel and Torrie, 1960). Each random sample plot was classified with respect to the various avian species habitats using quadratic discriminant function analysis (Anderson, 1958), and the regression relationship between habitat and avifauna was calculated using a program that performed a forward-selection polynomial fit.

Bird censuses were performed in the study area on a return to the campus in June 1978. Conditions looked remarkably unchanged then with some shifting of successional plots due to rotational agriculture. There were 4 census transects each 46 m wide and of variable length. The combined coverage totaled 16.56 hectares.

Results and Discussion

Twenty-three species of birds (Fig. 1) were common enough at the study site to obtain the 20 requisite sample plots. The resulting analysis showed that most the vegetational characteristics sampled in the avian plots were highly correlated with the first discriminant function, and most also were significant or nearly so (α=0.05) in separating the avian species along the discriminant axis (Table 1). Because all but one characteristic showed positive correlations, this indicates that vegetational density in nearly all strata varied from sparseness on one end of the axis to high density at the other end. The pattern is depicted in Fig. 1 showing an increasing shrubbiness progressing along the discriminant axis; open grassy areas on the left to tall dense shrubland on the right. The avian species are positioned along this progression (Fig. 1) determined by the mean discriminant scores for each. (The first discriminant function accounted for 54% of the overall variance, the second only 10% and decreasing from there, Wilks' Lambda $P<0.0001$.)

There was extensive habitat overlap in the plots for successive groupings of birds along the axis shown by results of Duncan's multiple range procedure (the various horizontal lines underscoring species groups in Fig. 1). For example, the lowest line at the lower right in the Figure extends under the tick marks for nine species positioned along the topmost line extending from *Lanius barbarus* to *Andropadus virens*. This shows that the vegetational plots for those species did not differ significantly (α=0.05). The next range line above that one drops the two right hand species and thereby picks up *Tockus fasciatus* to characterize a new group of eight birds that are essentially alike in habitat characteristics, and so on in stair step fashion to the left end of the Figure *Lanius collaris* on

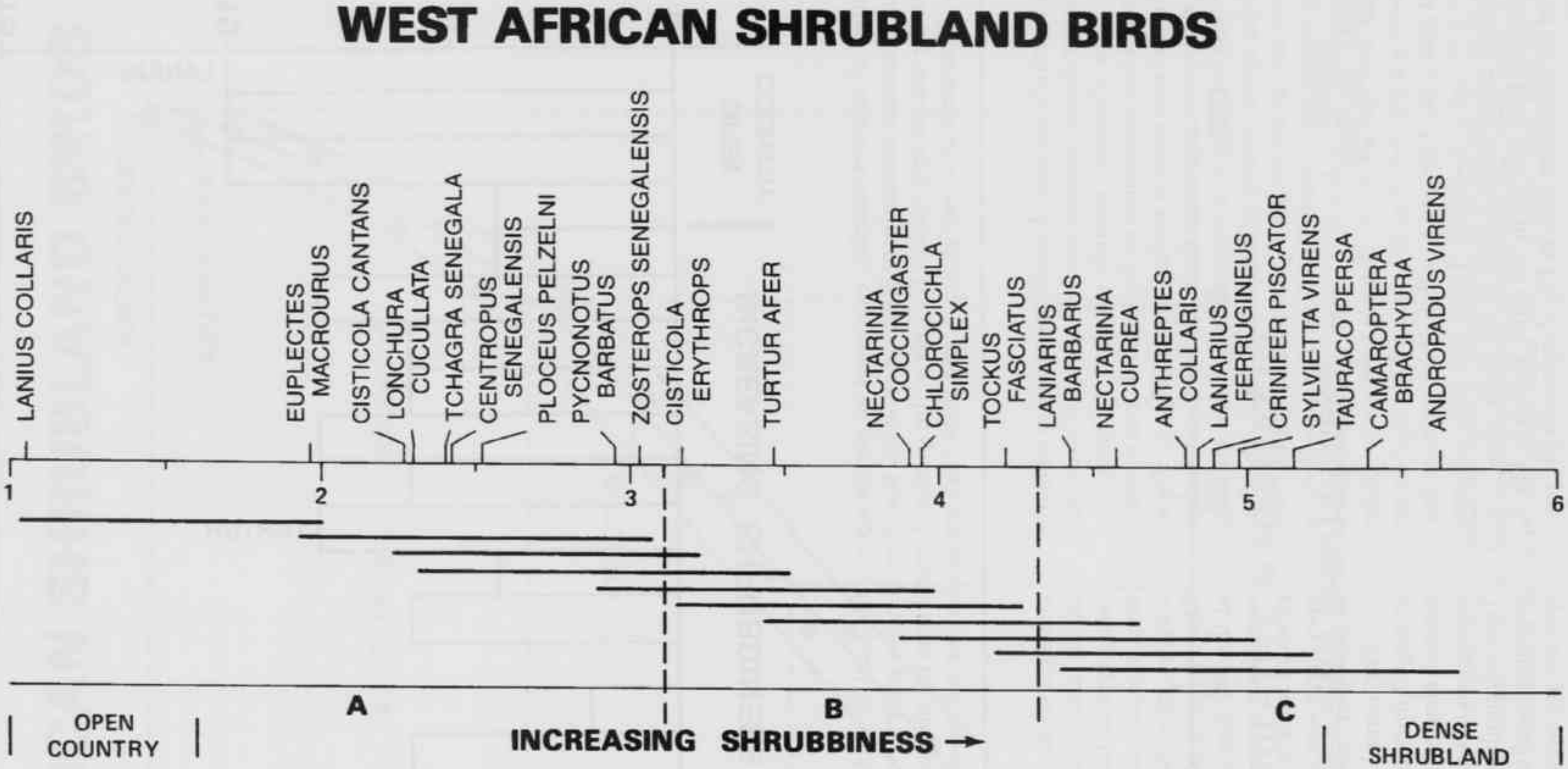

Fig. 1. Arrangement of bird species from open country to dense shrubland along the first axis produced by discriminant function analysis. The horizontal lines underscore groups of species that were not significantly different in habitat usage based on Duncan's multiple range procedure (α=0.05). The vertical dashed lines separate the three distinct avian communities that have nonoverlapping horizontal lines and thus occupy different habitats (explained in text). (English names of birds associated with scientific names are given in the Appendix.)

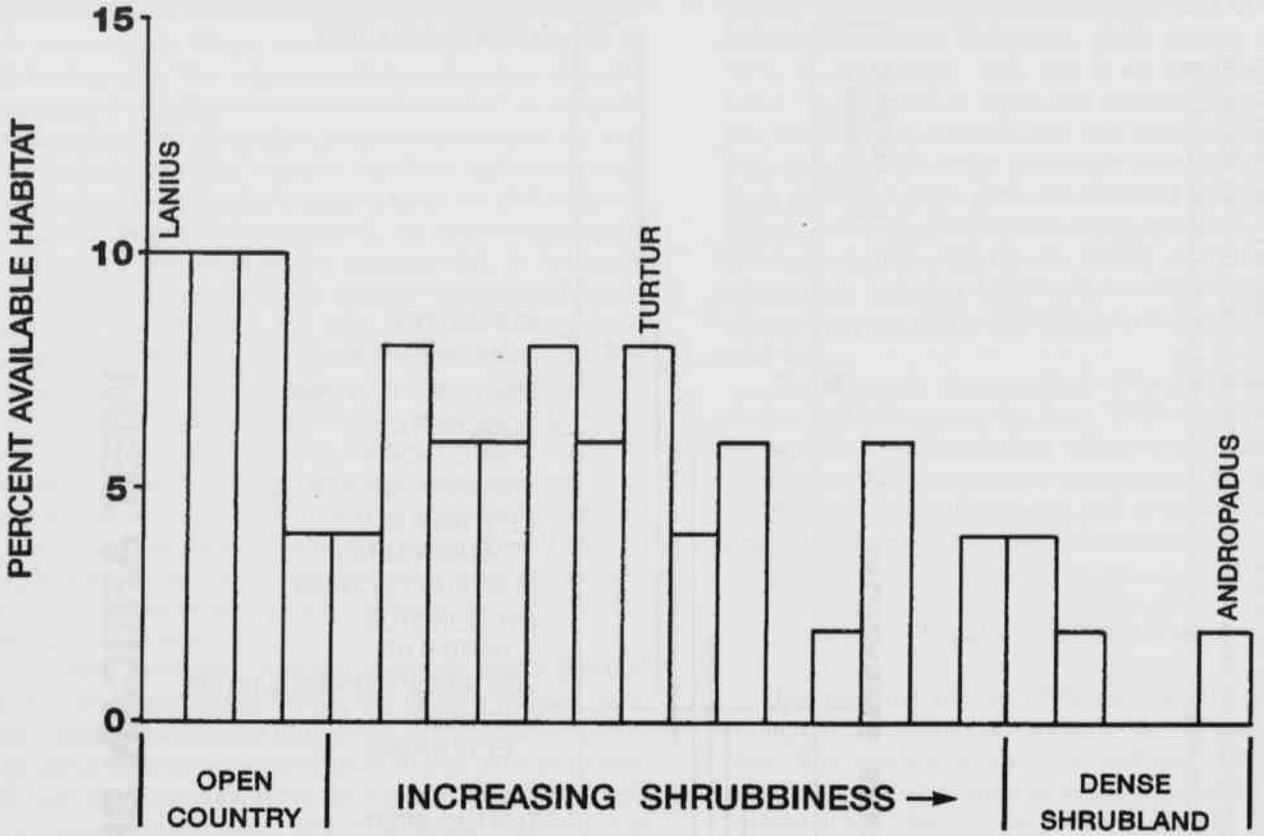

Fig. 2. Number of random samples, expressed as percentages of the total 50 such samples, that were classified for each bird species using quadratic discriminant function analysis. Random samples represent available habitat in the area, and there was no habitat in the sample appropriate for four of the species. Vertical bars for the species are arranged in order from open country to dense shrubland as shown in Fig. 1, and three bars are labeled for reference.

the far left just barely includes *Euplectes macrourus* in its habitat and these two barely overlap the next group of birds. All these range lines obviously broadly overlap, but there are three groups of birds subtended by lines that do not overlap (separated by the two vertical dashed lines in Fig. 1). These avian groups therefore represent three distinct communities of birds ($P<0.05$) existing in a vegetational mosaic showing transition from open country to dense shrubland. The first group of birds are on the far left represented by the top two overlapping range lines extending from *Lanius collaris to Zosterops senegalensis.* Now notice the sixth range line down that subtends five species from *Cisticola erythrops* to *Tockus fasciatus.* There is a gap between this one and the top two on the left, and also a gap between it and the bottom most line on the right previously described. These two gaps separate the three distinct avian communities in the study area.

Arranging the bird species in the order shown in Fig. 1, the heights of the histogram bars in Fig. 2 represent the percentages of the random sample habitat plots that were classified, using quadratic discriminant function analysis, as being typical habitat for each of the avian species. The random samples provide a representation of the proportions of various microhabitats actually present in the study area. More random plots fell in the open country end of the graph at the left than at the shrubland end to the right, and there were four species in the right half for which there was no random sample fit (Fig. 2). All this suggests that in the study area there was a greater percentage of available habitat that suited open country birds than shrubland ones.

The cumulative percentage of species (y axis, Fig. 3) arranged from open habitat to dense shrubland (Fig. 1) was plotted against (x axis) the corresponding cumulative percentage of open to dense habitat available shown in Fig. 2. This relationhip (Fig. 3) indicates that when 50% of the available habitat is accounted for only about 30% of the species are accommodated, and that the final 40% of the

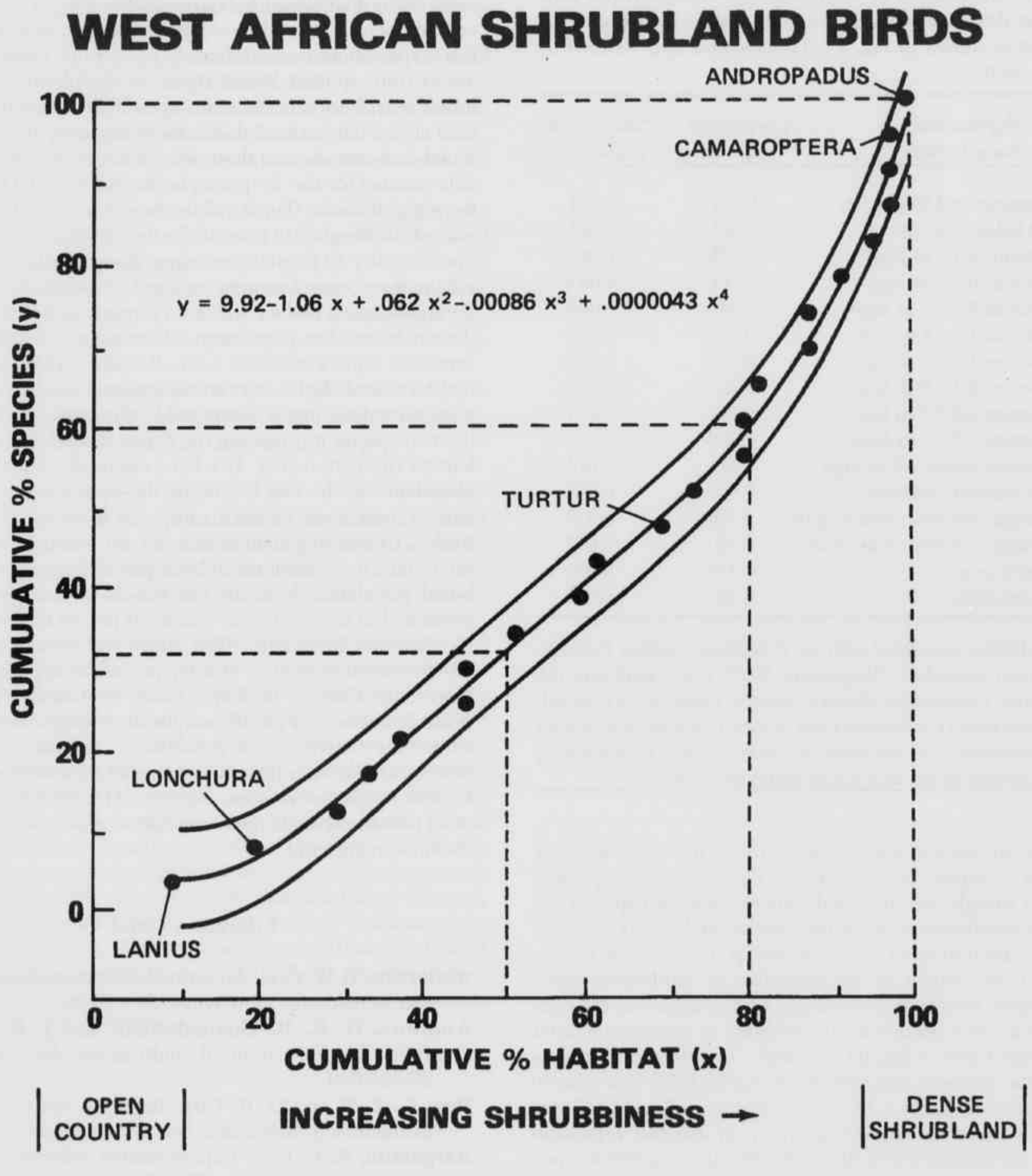

Fig. 3. Relationship between the accumulation of available habitat (abscissa) and accumulation of avian species present (ordinate) from open country to dense shrubland. The closed circles are bird species positions arranged in the same order as in Fig. 1. The formula given describes the best fit to the avian points shown by the center solid line. The outer solid lines are the 95% confidence limits. Dashed lines are described in the text.

Table 1. Correlations of 16 vegetational characteristics with the first discriminant axis, the axis that formed the avian ordination shown in Fig. 1 (characteristics fully defined in James, 1992).

Vegetational characteristic	Correlation coefficient	*Step-down probability
Avg. vegetational height (m)	0.667	0.001
Height tallest tree (m)	0.361	0.015
Total stems at 1.2 m high	0.743	<0.001
Total leaves 0-0.6 m high	-0.344	0.044
Total leaves 0.6-1.2 m high	0.380	0.003
Total leaves 1.2-1.8 m high	0.612	0.061
Total leaves 1.8-2.4 m high	0.629	0.605
Total leaves 2.4-3.0 m high	0.725	<0.001
Total leaves 3.0-3.7 m high	0.716	0.024
Total leaves 3.7-4.3 m high	0.588	0.012
Total leaves above 4.3 m high	0.473	0.012
Foliage vertical evenness	0.630	0.061
Horizontal evenness (coarse grain)	0.156	0.036
Horizontal evenness (fine grain)	0.276	0.037
Stem evenness	0.432	0.379
Stem variability	0.464	0.008

*Probabilities associated with the F statistics resulting from the step-down procedure (Bargmann, 1962) when analyzing the successive vegetational characteristics in order of corresponding correlations coefficients from highest to lowest, thus testing the significance of vegetational characteristics in separating avian species on the first discriminant function axis.

species are packed into the final 20% of the dense shrubby habitat (compare dashed lines in Fig. 3). If this regression were a straight line it would indicate that bird species are evenly distributed through the vegetational matrix, as is the case in the middle of this relationship (Fig. 3). This middle part of the habitat is representative of moderately open shrubland. However, the strongly curved upturn at the right end of the line documents the addition of species at a faster rate than there is habitat available. This relationship supports the concept proposed by Ricklefs (1973) that general increase in diversity is in part an outcome of increased spatial (two dimensional) heterogeneity, in this case represented by the complexity of dense shrubland compared to open grassland. The regression formula shown on Fig. 3 for the overall curve is a fourth degree polynomial that mathematically describes the species packing process, which is a rather tight relationship considering the narrow confidence limits shown.

Avian population data from the bird censuses in the study area gave contradictory results. Because there was more open than closed habitat available (Fig. 2) it is expected that open country birds would be the most abundant, and this expectation was confirmed by census results. Using *Turtur* (Blue-spotted Wood Dove) as the obvious dividing line (Fig. 2) between abundant open habitat and less abundant closed habitat available in the study area, the four combined censuses showed there was a total of only 64 individuals counted for the 12 species in the more closed habitat to the right of *Turtur* (Fig. 2) while there were nearly twice as many individuals (119 in total) for the 11 species in the more open country to the left (including *Turtur*). In fact, as noted above, there were four species (the four blanks in Fig. 2) in the more closed half for which no random samples matched their habitats. The population difference was highly significant (Chi Square = 16.52, 1 d.f., $P<0.001$). This conclusion that birds seeking the commoner habitats where indeed the more abundant ones is countered by the census findings that the two species terminating the dense shrubland end of the habitat ordination (Fig. 1) where essentially equal in high abundance to the two beginning the open country end (15 and 10 individuals counted compared to 13 and 13 respectively). Converting total counts for all censuses across all microhabitats to numbers of birds per 40 hectares, the combined population level for just the 23 commoner species examined in this study was 432 birds per 40 hectares.

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Appendix. English names associated with scientific names used in text and Fig.s, listed in alphabetic order of scientific names (names according to Grimes, 1987).

Andropadus virens (Little Greenbul), *Anthreptes collaris* (Collared Sunbird), *Camaroptera brachyura* (Grey-backed Camaroptera), *Centropus senegalensis* (Senegal Coucal), *Chlorocichla simplex* (Simple Greenbul), *Cisticola cantans* (Singing Cisticola), *Cisticola erythrops* (Red-faced Cisticola), *Crinifer piscator* (Grey Plantain-eater), *Euplectes macrourus* (Yellow-mantled Widow-bird), *Laniarius barbarus* (Barbary Shrike), *Laniarius ferrugineus* (Bell Shrike), *Lanius collaris* (Fiscal Shrike), *Lonchura cucullata* (Bronze Mannikin), *Nectarinia coccinigaster* (Splendid Sunbird), *Nectarinia cuprea* (Copper Sunbird), *Ploceus pelzelni* (Slender-billed Weaver), *Pycnonotus barbatus* (White-vented Bulbul), *Sylvietta virens* (Green Crombec), *Tauraco persa* (Guinea Turaco), *Tchagra senegala* (Black-headed Bush-Shrike), *Tockus fasciatus* (Allied Hornbill), *Turtur afer* (Blue-spotted Wood-Dove), *Zosterops senegalensis* (Yellow White-eye).