Environmental factors influencing bird species diversity in Kenya

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Abstract

Sustainable resource management requires understanding the factors that increase or decrease species richness. Regional species richness patterns may be predicted by analysing patterns of variation in the environment. A number of studies have shown that bird species richness at a regional scale is influenced by climatic variables. We examined environmental correlates of bird species richness at a quarter degree square scale (55 × 55 km). Mean annual potential evapotranspiration accounts for 46% of the observed variation in species richness, while mean annual temperature and range annual potential evapotranspiration are significantly correlated with species richness and together account for a further 5% of the observed variation. The results are consistent with the hypothesis that environmentally available energy limits regional species richness.

Key words: abiotic factors, birds, Kenya, species richness

Résumé

La gestion soutenable des ressources exige la compréhension des facteurs qui augmentent ou réduisent la richesse des espèces. On peut prédire les schémas régionaux de la richesse en espèces en analysant les schémas de variation dans l'environnement. De nombreuses études ont montré que la richesse en espèces d'oiseaux est, à l'échelle d'une région, influencée par les variables climatiques. Nous avons étudié les corrélations environnementales de la richesse en oiseaux à l'échelle d'un carré de 55 × 55 km. Le potentiel annuel moyen d'évapotranspiration compte pour 46% de la variation observée dans la richesse en espèces, tandis que la température annuelle moyenne et la variation annuelle du potentiel d'évapotranspiration sont significativement liées à la richesse en espèces et ensemble, comptent pour 5% supplémentaires de la variation observée. Les résultats concordent avec l'hypothèse selon laquelle l'énergie environnementale disponible limite la richesse régionale en espèces.

Introduction

Biological diversity is the variety and variability among living organisms, the ecological complexes in which they live, encompassing genetic, species and ecosystems in a region (Stoms & Estes, 1993). Maintenance of biodiversity has become one of the principal goals of conservation (Williams & Gaston, 1994). Currently, there is a huge interest in conserving biological diversity due to a sharp increase of species extinctions, as habitats are becoming more fragmented and degraded world-wide (Walker *et al.*, 1992). The search for factors determining the number of species in diverse habitats or regions is an important step toward understanding the spatial distribution of species richness and its ecological determinants (Stoms & Estes, 1993) as well as predicting the response of ecosystem functions to global change. As a practical measure of biodiversity, conservationists use species richness, which is the number of species in a site or habitat (McIntosh, 1967).

Species diversity is not determined in all cases by the same single factor but is the outcome of many contributing factors (Diamond, 1988). Associated with almost every pattern of variation in species diversity are patterns of variation in many different biophysical factors, as well as anthropogenic processes that could conceivably influence biological diversity (Huston, 1994). Ecologists have searched for environmental factors that may limit biological diversity (Currie & Paquin, 1987; Currie, 1991).

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However, physical environmental factors may predict biodiversity and are potentially attractive, as they are already available or may be relatively inexpensive to acquire (Williams & Gaston, 1994). Patterns and processes are strongly scale dependent (Levin, 1992). In other words, patterns in species diversity are influenced by the spatial and temporal scale at which both a group of organisms and the factors that possibly determine the species richness of this group operate (Bohning-Gaese, 1997). Research on factors influencing avian biodiversity has been conducted mainly at within-habitat (alpha) diversity and regional (epsilon) diversity. Studies about within-habitat diversity, traditionally conducted by ecologists, have revealed the importance of foliage-height diversity and horizontal habitat heterogeneity in predicting species richness (Karr & Roth, 1971; Roth, 1976). Conversely, regional studies have pointed to the importance of climatic variables such as potential evapotranspiration, mean annual temperature and solar radiation in predicting species richness of birds (Rabinovich & Rapoport, 1975; Wright, 1983; Turner *et al.*, 1988; Currie, 1991). These variables are highly correlated among themselves and reflect the availability of energy to be partitioned among different species (Currie, 1991).

This study aims to identify environmental variables that correlate with species richness of birds. The relationships between species richness and climatic variables, range and mean annual rainfall, percentage moisture availability, range and mean elevation, range and mean annual temperature, as well as range and mean annual potential evapotranspiration, were examined. The study sought to establish the factors that are generally most important at a regional scale. As a consequence, the study was performed at a quarter degree scale (55 × 55 km), which matches the scale of the distribution maps in the bird atlas of Kenya (Lewis & Pomeroy, 1989).

Methods

The study area

Kenya is situated between latitudes 5°40′ N and 4°4′ S and between longitudes 33°50′ and 41°45′ E. Kenya has diverse landforms ranging from the coastal plains through the dry Nyika Plateau to the savanna grasslands and the highlands on both sides of the Rift Valley. The region at the east of the Rift Valley lies at about 2000 m above sea level and is dominated by Mount Kenya (5230 m) and Aberdare Range, reaching almost 4000 m.

In the west, the country slopes toward Lake Victoria, but also has mountainous areas (the Mau Range and Mount Elgon (4320 m) on the border with Uganda). The highlands, forming most of the south-west and central parts of the country, have an elevation varying from 1400 m to 2800 m above sea level. Altitude exerts the greatest influence on temperature in Kenya. There is a wide range between the maximum and minimum temperatures; from below freezing point on the snow-capped Mount Kenya to over 40 °C in some parts of the north and north-eastern parts of the country. Generally, the low-lying northern plains are the hottest areas, with maximum temperatures commonly exceeding 35 °C. Annual rainfall follows a strong seasonal pattern. These seasonal variations are most pronounced in the dry lowlands and the north as well as east, but weakest in the humid highlands of the Central and Rift areas. There are three main regions of heavy rainfall. A relatively wet belt extends along the Indian Ocean coast. A second area of high rainfall covers western Kenya just east of Lake Victoria. A third type of region receiving heavy rainfall coincides with the main mountain ranges. Valley barriers tend to stand out as dry areas (UNEP, 1987).

Bird species data

The *Bird Atlas of Kenya* (Lewis & Pomeroy, 1989) mapped the distribution of 871 species in Kenya (there are about 200 more, but they had too few records to be worth mapping). However, at the time of publication, it was estimated that only 40% of the possible records had been obtained, despite the rather large size of the mapping units used (quarters of degree squares). Since then, additional records (Oyugi, 1994) have increased this to about 42% (Pomeroy & Dranzoa, 1997). The atlas maps (Lewis & Pomeroy, 1989) use symbols to indicate the nine categories of record. However, only species of birds recorded in Kenya since 1970 were included in this analysis. Vagrant species and those represented only by anecdotal records were excluded.

The distribution maps (Lewis & Pomeroy, 1989) for 871 of the 1065 species of Kenyan birds were photocopied and scanned in 256 grey scales and then saved as Tagged Image File Format (TIFF). An algorithm was developed for extracting the mapping symbols for the following status of birds from the scanned TIFF maps: (1) confirmed breeding after 1/1/1970, (2) present and probable breeding after 1/1/1970, and (3) records after 1/1/1970 (but no confirmation of breeding).

The algorithm rectified the images to obtain standard northing by identifying the location of two pixel patterns that appear in all images, and from their positions computed the orientation of the map. Finally, the algorithm translated and rotated the image to obtain a rectified image. For each status, the maps use a specific pattern. After rectification, the position of each block (55 × 55 km) was approximately known. For each block position, the algorithm computed a slightly wider buffer and then tried to find the best match for all three patterns. For some block positions, we found that lake and country boundaries obscured the recognition of patterns. We corrected for this at specific block positions by cross-checking the pattern against the original map in the bird atlas. In addition, we looked at trends in histograms per pattern that helped to identify problems where the algorithm erroneously identified patterns. Thus, all errors caused by translating the analogue database to a digital database were removed by operator intervention.

Analysis of data

The calculation of species richness was based on combination of the status of birds recorded since 1970, namely, confirmed breeding after 1/1/1970, present and probable breeding after 1/1/1970 and records after 1/1/1970 (but no confirmation of breeding). In each grid cell (55 × 55 km), the number of species present was counted to give a value for total species richness. The climatic variables for the 55 × 55 km grid cells were estimated from the agro-climatic zone map of Kenya 1980 (Sombroek *et al.*, 1982). The calculations of the environmental parameters are presented in Table 1.

Each grid cell was georeferenced onto a geographical-coordinate system, which served as the baseline reference map for both the Kenya environmental data and bird species richness data. The environmental data were stored as many individual layers of grid cells. For each layer, the grid cells contained single values representing each variable class. The series of environmental variable grids conformed to the same geographical coordinate system as the grid cells representing bird species richness. Thus, each grid cell finally contained nine climatic variables (Table 1) and bird species richness. Forward stepwise multiple regression and regression lines between the dependent variables (bird species richness) and the independent variables (environmental) were calculated, as well as 95% confidence intervals. In addition, the Pearson correlations between environmental variables were calculated.

Table 1 Measures of grid cell environmental variation used in correlation and regression analyses of bird species richness and environmental variables

Climatic variable	Calculation
Mean annual rainfall (mm)	The mean of mean annual rainfall for agroclimatic zones found in the grid cell
Range annual rainfall (mm)	The highest minus the lowest value extracted for mean annual rainfall
Mean annual temperature (°C)	The mean of mean annual temperature for agroclimatic zones found in the grid cell
Range annual temperature (°C)	The highest minus the lowest value extracted for mean annual temperature
Mean annual potential evapotranspiration (mm)	The mean of mean annual potential evapotranspiration for agroclimatic zones found in the grid cell
Range annual potential evapotranspiration (mm)	The highest minus the lowest value extracted for mean annual potential evapotranspiration
Mean elevation (m)	The mean of elevation classes
Range elevation (m)	The highest minus the lowest elevation
Moisture availability (%)	The ratio of mean annual rainfall to mean annual potential evapotranspiration expressed as percentage (Sombroek *et al.*, 1982)

Table 2 Results of regression analyses and bootstrap estimates of standard error of Kenyan bird species richness against measures of mean annual rainfall (MAR), range annual rainfall (RAR), mean annual temperature (MAT), range annual temperature (RAT), mean annual potential evapotranspiration (PET), range annual potential evapotranspiration (RPE), mean elevation (ME), range elevation (RE) and percentage moisture availability (MO). SE = standard error, BSD = bootstrap standard deviation. Sample size = 220

Climatic variables	r	r^2	SE	BSD
MAR	0.655	0.429	0.018	0.018
RAR	0.604	0.364	0.023	0.021
MAT	−0.649	0.421	1.759	1.744
RAT	0.388	0.151	2.557	2.353
PET	−0.680	0.463	0.036	0.034
RPE	0.496	0.246	0.062	0.063
ME	0.642	0.413	0.012	0.012
RE	0.463	0.215	0.016	0.015
MO	0.667	0.445	0.322	0.327

Results

The results (Table 2) show that the highest positive correlation is observed with percentage moisture availability, which accounts for 45% of the variability in bird species richness in Kenya. However, bird species diversity-declines in areas with the highest percentage moisture availability. Figure 1(b) shows that the map of bird species richness predicted by the regression model that includes percentage moisture availability (Fig. 2a) roughly matches the map of observed species richness (Fig. 1a). Moreover, climatic variables related to moisture availability, such as mean annual rainfall and mean elevation, also have strong positive correlation with bird species richness (Table 2).

However, measures of environmental variation such as range annual rainfall, range annual temperature, range annual potential evapotranspiration and range elevation have a relatively weak positive correlation with species richness. Conversely, mean annual potential evapotranspiration and mean annual temperature are negatively correlated with bird species richness (Table 2). The least squares fit for the relationship between bird species richness and mean annual potential evapotranspiration (Fig. 2b) shows that higher potential evapotranspiration depresses bird species richness.

As standard error is the most common way of indicating statistical accuracy (Efron & Tibshirani, 1998), the standard error of the correlation coefficients (Table 2) was estimated by bootstrapping standard deviation. The bootstrap is a recently developed technique for making certain kinds of statistical inferences. It is a computer-based method for estimating the standard error, confidence intervals and distributions for any statistic (Efron & Tibshirani, 1998). Bootstrap samples consisted of 2500 points selected at random and with replacement from the actual sample points in every climatic variable. Table 2 shows that the bootstrap performed fairly well in estimating the standard error of the correlation coefficients. Note that the standard errors for the correlations are fairly close to bootstrap standard deviations in all climatic variables. This implies that the empirical standard deviation approaches the population standard deviation with large number of bootstrap replications.

In the stepwise multiple regression analysis of bird species richness versus all climatic variables, only mean annual potential evapotranspiration, mean annual temperature and range annual potential evapotranspiration were significant independent variables in the model (Table 3). Mean annual potential evapotranspiration

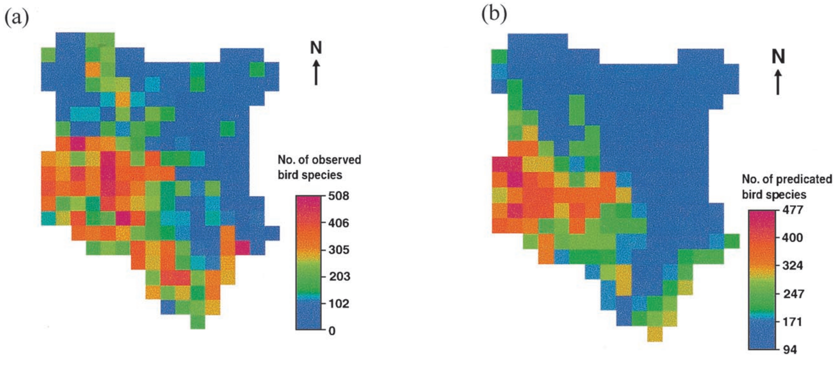

Fig 1 The spatial distribution of bird species richness. (a) Number of bird species recorded in Kenya since 1970 (Lewis & Pomeroy, 1989). (b) Number of bird species as predicted by percentage moisture availability

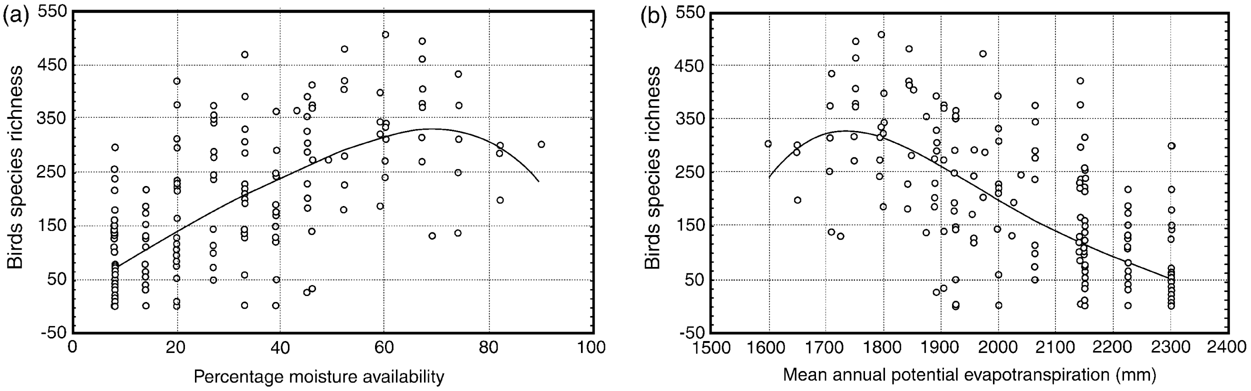

Fig 2 (a) Relation between species richness (S) and percentage moisture availability (M), fitted with 4th order polynomial function, $S = 9.56 + 8.62\,\mathrm{M} - 0.15\mathrm{M}^2 + 0.003\mathrm{M}^3 + 2.04\mathrm{M}^4$. (b) Mean annual potential evapotranspiration (P) versus species richness, fitted with 4th order polynomial function, $S = -1.02 + 200.3\mathrm{P} - 0.15\mathrm{P}^2 + 4.66\mathrm{P}^3 - 5.58\mathrm{P}^4$

Table 3 Stepwise multiple regression analysis of Kenyan bird species richness against measures of mean annual rainfall, range annual rainfall, mean annual temperature (MAT), range annual temperature, mean annual potential evapotranspiration (PET), range annual potential evapotranspiration (RPE), mean elevation, range elevation and percentage moisture availability. Sample size = 220

Step no.	Variable entered	r	r^2	Change in r^2
1	PET	0.680	0.463	0.46
2	MAT	0.704	0.496	0.03
3	RPE	0.715	0.511	0.02

accounted for 46% of the observed variation of bird species richness in Kenya. In addition, mean annual temperature and range annual potential evapotranspiration were also significantly independently correlated with bird species richness, and together accounted for a further 5% of the observed variation.

Many environmental properties are highly correlated with each other (Huston, 1994; Bohning-Gaese, 1997). Table 4 shows that the variables related to available energy, such as mean annual potential evapotranspiration and mean annual temperature, are strongly correlated ($r = 0.788$). However, variables related to available energy are negatively correlated with measures of climatic variation as well as moisture related variables. As for energy related variables, variables related to available moisture (percentage moisture availability, mean annual rainfall and mean elevation) and measures of climatic variation (range annual rainfall, range annual temperature, range annual potential evapotranspiration and range elevation) are highly correlated among themselves.

Table 4 The coefficient of correlation (r) between independent variables, mean annual rainfall (MAR), range annual rainfall (RAR), mean annual temperature (MAT), range annual temperature (RAT), mean annual potential evapotranspiration (PET), range annual potential evapotranspiration (RPE), mean elevation (ME), range elevation (RE), percentage moisture availability (MO). All correlations are significant at the $P < 0.05$ level. Sample size = 220

	MAR	RAR	MAT	RAT	PET	RPE	ME	RE
RAR	0.803							
MAT	−0.823	−0.773						
RAT	0.468	0.617	−0.612					
PET	−0.950	−0.756	0.788	−0.463				
RPE	0.542	0.845	−0.568	0.601	−0.514			
ME	0.817	0.765	−0.991	0.617	−0.785	0.570		
RE	0.526	0.652	−0.674	0.937	−0.522	0.621	0.676	
MO	0.998	0.812	−0.828	0.480	−0.955	0.566	0.822	0.539

Discussion

Bird species richness is strongly correlated with mean annual rainfall, percentage moisture availability and mean elevation. Mean annual rainfall and percentage moisture availability account for 43% and 45% of the observed variation of bird species richness, respectively. These results are consistent with the hypothesis that benign conditions permit more species (Currie, 1991). In Kenya such areas have abundant trees, which are important as sources of food, or for nesting or perching for bird species (Lewis & Pomeroy, 1989). The high rainfall areas are mainly situated in high altitudes (highlands) with greater topographic and habitat diversity that support several bird species endemic to forests and grasslands (Muriuki *et al.*, 1997).

Our results agree with this finding because mean elevation accounts for 41% of the variability in bird species. On the other hand, altitudinal range accounts for only 22% of the observed variation of species richness, as many bird species, both aquatic and terrestrial, are restricted to certain altitude ranges (Lewis & Pomeroy, 1989).

Some studies indicate that species richness increases as climatic variation decreases (MacArthur, 1975). However, our results show that bird species richness increases with measures of climatic variation such as range annual rainfall, range annual temperature and range annual potential evapotranspiration. What could be the reason? The effects of climatic variation on species richness depend on whether the variation is predictable or unpredictable. In a predictable, seasonally changing environment, different species may be suited to conditions at different times of the year. Hence, more species might be expected to coexist in a seasonal environment than in a completely constant one. By contrast, unpredictable climatic variation is a form of disturbance, and species richness may be highest at intermediate levels, i.e. species richness may increase or decrease with climatic instability (Begon *et al.*, 1990).

Stepwise multiple regression shows that bird species richness is most closely related to mean annual potential evapotranspiration, mean annual temperature and range annual potential evapotranspiration. The common element is that they all reflect aspects of the regional energy balance (Currie, 1991). This is in agreement with the studies at large areas (generally 400–50 000 km^2), which have emphasized the importance of variables related to available energy in predicting species richness (Bohning-Gaese, 1997). The best predictor of bird species richness is mean annual potential evapotranspiration, which accounts for 46% of the variability of bird species richness. Potential evapotranspiration (PET) is estimated from air temperature and solar radiation, and represents the maximum amount of water that would be lost by evaporation from surfaces and transpiration of plant leaves when evapotranspiration is not limited by water availability (Huston, 1994). It is highly correlated with terrestrial primary productivity and is thus a measure of community energy use (Currie & Paquin, 1987). This observation is consistent with the hypothesis that energy is partitioned among species such that the total available energy limits species richness (Currie, 1991).

Other factors induce variability around the limits determined by energy: for example, physically complex environments such as mountains may favour more equal energy partitioning among species, and thus permit relatively more species to occur together (Currie & Paquin, 1987). Thus, for a given level of PET in Kenya, bird species richness is greater in moist mountainous areas that can support the growth of trees, thereby providing nesting habitat and food for bird populations.

The authenticity of the regional data layers needs to be confirmed. Often coarse scale data coverages are useful for visual demonstration purposes but are worthless for scientific analysis (Miller *et al.*, 1989). The high correlations between mean annual rainfall and mean annual potential evapotranspiration, mean annual temperature as well as mean elevation provide strong evidence for the ecological validity of these data. The strong negative correlation between mean elevation and mean annual temperature ($r = -0.991$) reflects the notion that the higher you go the cooler it becomes. However, predicting bird species richness requires precise environmental data. Thus, the regional perspective requires the sacrifice of ecological precision for the sake of the generality, as well as the provision of more data, thereby allowing statistical predictions. Environmental and species diversity relationships, documented by regression statistics, can be used to identify areas more likely to be characterized by high species diversity. These areas will be recognizable only on the regional scale, and field observations will be required for precise boundary determination (Miller *et al.*, 1989).

The results provide strong evidence that environmental factors do influence species richness. However, bird species richness is undoubtedly influenced by many other factors not considered in this study. Generally, it is the interaction of many factors that leads to extinction and thus to a decrease in species richness (Stoms & Estes, 1993). Phylogenetic analysis of montane African greenbuls identified speciation events due to isolation in different montane areas in eastern Africa (Roy *et al.*, 1998). Moreover, regional bird populations are affected by human activities such as clearing forests, removing mangroves, draining swamps, and the increased use of agricultural chemicals, which destroy or pollute the habitat of both resident and migrant birds. Habitat loss caused by deforestation and replacing natural woody vegetation with plantations of exotic trees lead to loss of bird species diversity (Pomeroy & Dranzoa, 1997).

Conclusions

The study shows that bird species richness increases with moisture availability, hence the most moist regions in Kenya – the central and western highlands – support the highest species richness. However, most of Kenya's agriculture and populace are also concentrated in this region, and most of the existing protected areas are small. The small size of these protected areas, their scattered location, their progressive isolation through the loss of connecting habitat and increasing edge to area ratios, are cause for concern (Muriuki *et al.*, 1997). Therefore, management plans are needed to prevent a confrontation between conservation and human interests. Planning of conservation priorities does not only require detailed knowledge of patterns of species richness but also an understanding of interactions between historical and ecological processes (Fjeldså, 1994).

Biodiversity indicators such as species richness are only one of several criteria used for conservation evaluation (Margules & Usher, 1981). Of particular importance are questions such as, is the species there in viable numbers, and how many of the species are rare. Furthermore, different taxonomic groups may show different patterns – even within groups patterns of species richness may be different for different guilds of species. The challenge is to develop predictive statistical models for many groups of species, establishing patterns in their distributions in such a way as to indicate clearly the conservation potential of different localities (Braithwaite *et al.*, 1989).

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