

West African rivers as biogeographic islands: species richness of fish communities

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Summary. Some factors influencing the species richness of West African fish communities were studied in a sample of 26 rivers using four habitat and hydrologic variables. Analysis of a larger sample of 39 rivers showed that species richness was positively related to area. A power function with an exponent of 0.32 gave the best fit. As the surface area used was that of the catchment area and not that (unknown) of the river, the biological significance of this relationship and the possibilities of comparison were limited. Ridge regression analysis and forward stepwise selection indicated that a model that explained $\ln(\text{species richness})$ as a function of $\ln(\text{mean annual discharge})$ and $\ln(\text{catchment surface area})$ was best, accounting for 90% of the variance of the dependent variable. The combination of surface area and discharge was presumed to act through the volume of water available for the fishes and habitat productivity. Habitat diversity, measured by the diversity of the terrestrial vegetation covering the catchment area, had no significant positive effect when surface area was used in the regression. Rivers ("islands") should have fewer species than tributaries of similar size since, for fishes within a river system ("continent"), there is free circulation between all its branches. The model derived from the river data underestimated the species richness of a sample of 11 tributaries. This was compatible with the hypothesis of higher population extinction rates in insular biotopes. The residuals of the linear model did not show random geographical distribution; the rivers in some areas had more species than expected. The possibility that historical factors, especially Quaternary climatic variations, might cause this distribution is discussed.

Key words: Species richness – Insular biogeography – Freshwater fish communities – West Africa – Forest refuge hypothesis

Since the work of MacArthur and Wilson (1963, 1967), it has been customary in community ecology to consider environments surrounded by habitats unfavourable to the biological group studied as biogeographic islands. Some examples are mountaintops for boreal species (Brown 1971), caves for cave-dwelling species (Vuilleumier 1973) and forest woodlots for forest species (Martin 1980).

Insofar as rivers are separated from each other by barriers which strictly aquatic animals cannot pass, it is justifi-

able to consider them as biogeographic islands but, up to now, only a few attempts have been made (Daget and Ittis 1965; Daget 1968; Sepkoski and Rex 1974; Daget and Economidis 1975; Welcomme 1979; Livingstone et al. 1982; Eadie et al. 1986). Freshwater fish communities in Africa have been analysed three times in this context and species-area relationships have been emphasized. Daget and Ittis (1965) tried to check Preston's (1962) predictions of the value of the exponent of Arrhenius's law, where the species richness of a community increases in proportion to a power function of the surface area. As the water surface of a river cannot be measured, Daget and Ittis, like the following authors, used the catchment surface area. Their study included 13 rivers, mostly in the Ivory Coast. Welcomme (1979) described species-area relationships for 25 rivers throughout Africa. The most complete study was that of Livingstone et al. (1982): data on 26 rivers were analysed by multiple regression with species richness as the dependent variable and the surface area of the drainage, length of the main branch, and discharge at the mouth as predictor variables. The principal results of their study was that discharge was a better predictor of species richness than surface area.

For about 10 years, ichthyologists of ORSTOM (Institut Français de Recherche Scientifique pour le Développement en Coopération) have participated in a program studying water courses in West Africa to evaluate the impact on the fish communities of anti-simuliid insecticides used by the World Health Organisation in the prevention of onchocerciasis (Lévêque et al. 1988). This program has greatly enlarged our knowledge of West African ichthyofauna, and it appears that some species richness values used in the studies cited above are underestimated. In this study we analyse species richness of West African rivers again in the light of these new data. Species richness is compared in rivers and in a group of 11 tributaries that can be considered, for aquatic animals, as equivalent to "continental" situations since, within a river system, species circulate freely between all the branches. The aim of this comparison is to test whether insularity affects species richness of West African rivers.

Methods

Data

Of the 39 rivers studied, all except in Nile, which empties into the Mediterranean, discharge into the Atlantic ocean

along the West African coast from the mouth of the Senegal to that of the Zaïre. A sample of 11 tributaries was studied in the drainage areas of the Niger, Volta, Sassandra, and Bandama.

The following variables were measured for each river:

SR: species richness. The species lists were compiled from existing publications, unpublished reports, and collections of the Museum National d'Histoire Naturelle de Paris (Paris, France), the Musée Royal de l'Afrique Centrale (Tervuren, Belgium) and the British Museum (London, UK). Species capable of covering long distances in the sea were

Table 1. Untransformed data for the 39 rivers studied

Rivers	Species richness	Surface (km) ²	Mean annual discharge (m ³ ·s ⁻¹)	Vegetation diversity	Forest (%)
Nile	127	3349000	2640	2.62	8
Senegal	110	441000	687	0.97	3
Gambia	89	77000	170	0.50	20
Tomine	55	23200	—	—	—
Konkouré	74	16470	353	0.00	100
Kolenté	58	7540	—	—	—

Table 2. Species-area relationships

Variables	Intercept	Slope	<i>r</i>	<i>I</i>	<i>Z</i>
SR-S	60.58	1.07×10^{-4}	0.764**	0.047	-5.19**
SR-lnS	-302.46	38.07	0.683**	0.032	-2.05*
lnSR-S	4.03	5.63×10^{-7}	0.619**	0.264*	-5.18*
lnSR-lnS	0.84	0.32	0.899**	0.044	0.65

SR = species richness; S = surface area; *r* = correlation coefficient; *I* = Moran's *I*; *Z* = sign test of the residuals

* $P < 0.05$, ** $P < 0.001$

and Smith (1966). The aim of this test is to detect whether, once the residuals are arranged as a function of dependent variable value, those of the same sign tend to be grouped more than would occur at random; if they do group together, it may be assumed that there is no linearity.

To evaluate to what degree the multiple regression models we used would account for possible geographic trends, we tested for spatial autocorrelation of the residuals using Moran's *I* (Sokal and Oden 1978a, b), which tests whether the value of a variable at one locality is independent of values of the variable at neighbouring localities. Positive autocorrelation shows that high values tend to be spatially grouped; in our case, this indicated that we might have failed to include a factor related to geography in our model. To use Moran's *I* it was necessary to construct a proximity matrix for the drainage areas. We decided to consider two drainage areas as connected if they were contiguous at at least one point. As only one positive spatial autocorrelation could be interpreted, a one-tailed test was used (*I*-test for small samples; Sokal and Oden 1978a, b).

Results

Species-area relationships

Table 2 summarizes the different species-area relationships tested in the sample of 39 rivers.

In terms of the coefficient of determination, the best fit was obtained by the power relation (after double transformation of the data by Napierian logarithms) with an exponent of 0.32 (Fig. 1). This also gave the most satisfactory distribution of the residuals, since residual sign was distributed at random in relation to the dependent variable.

There was no spatial autocorrelation of the residuals, indicating that the geographic factor in the variation in species richness as a function of surface area was well described by the model.

Multiple regressions

Knowing that discharge was proportional to drainage surface area multiplied by precipitation in the drainage area, the surface area and discharge variables were integrated into the analysis after transformation to Napierian logarithms to ensure a linear relationship between them. The relationship between species richness and each of the two transformed variables was also more linear when species richness was replaced by its logarithm. Logarithmic transformation of the percentage of forests and vegetation diversity index did not significantly change the results, so these two variables were retained untransformed in the analysis.

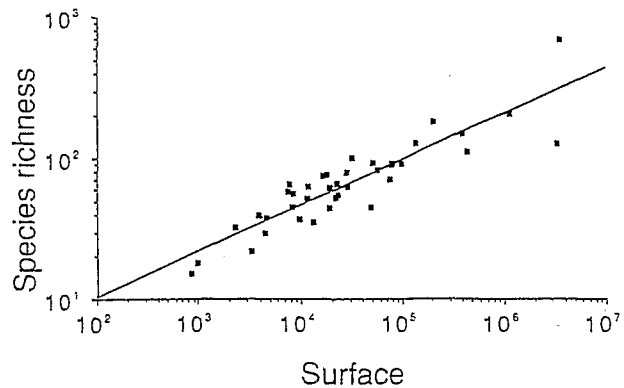


Fig. 1. The relationship between species richness and catchment surface area (km^2) in 39 West African rivers

Table 3. Correlation matrix of the variables used in regression analysis

	ln S	ln AD	DV	PF
ln SR	0.91	0.93	0.73	-0.43
ln S		0.90	0.90	-0.63
ln AD			0.75	-0.31
DV				-0.64

SR = species richness; S = surface area; AD = annual mean discharge; DV = diversity of terrestrial vegetation types; PF = percentage forest cover (see text)

Table 4. Multiple regression of ln(species richness) versus the four predictor variables. Coefficients are estimated by the least-squares method

Coefficients						
ln S	ln AD	DV	PF	Intercept	VIF	<i>R</i>
0.229	0.229	-0.305	-0.001	0.771	23.53	0.955
<i>P</i> = 0.048	<i>P</i> = 0.017	<i>P</i> = 0.065	<i>P</i> = 0.778			<i>P</i> < 0.001

VIF = maximum variance inflation factor; *R* = multiple correlation coefficient; variable abbreviations as in Table 3

Table 3 shows the correlation matrix between variables. Some predictor variables were highly intercorrelated, such as ln(surface area) with ln(discharge) and with the vegetation diversity index. The result of multiple regression with all the predictor variables is presented in Table 4. The maximum variance inflation factor was 23, indicating high collinearity between the predictive variables and suggesting prudence when examining the results obtained by classic multiple regression. These indicated that two variables had positive coefficients. ln(surface area) and ln(discharge), the coefficients being significantly different from zero in both cases. The two other variables had negative coefficients, one of which (vegetation diversity) approached statistical significance.

The multiple correlation coefficient was high (0.955); this value was highly significant.

The results obtained after ridge regression for *k* values from 0 to 1 are summarized in Fig. 2, which shows changes in the coefficients of the regression equation as a function of *k*. Since the variables were standardized beforehand, co-

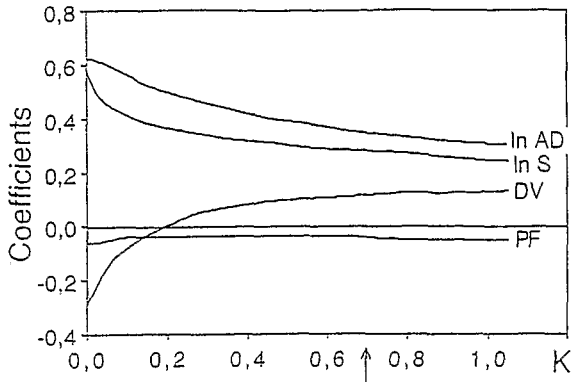


Fig. 2. The ridge trace for the rivers data. Arrow shows the value of k for which $VIF=1$. See text for abbreviations

efficient amplitude could be compared directly. The maximum variance inflation factor was 1 at about $k=0.7$. It is interesting to note that the sign of one of the coefficients changed after coefficient value stabilized at about $k=0.5$. The standardized coefficient of vegetation diversity index increased from -0.29 to 0.10 . A positive value agreed better with the effect of habitat diversity on species richness usually found, but it could not be determined whether this was statistically significant, since the tests usually employed cannot be applied in the case of ridge regression (Hocking 1976). No matter what the k value was, the forest percentage coefficient remained near to zero, while the coefficients of surface area and discharge remained high.

If this curve is used to select model predictor variables, Hocking (1976), following Hoerl and Kennard (1970 a, b), proposes that variables with a coefficient near zero or varying rapidly with k should be eliminated. This led us to eliminate forest percentage and the vegetation diversity index, keeping only surface area and discharge.

Forward stepwise selection led us to integrate \ln (discharge), then \ln (surface area) and to stop there. We thus kept the same variables by this method as those retained after a study of the coefficient changes as a function of k .

We therefore kept the model integrating \ln (discharge) and \ln (surface area) as a predictor of \ln (species richness). The results are given in Table 5. The maximum variance inflation factor was not more than 5 and coefficient estimation using the least-squares method was acceptable. The multiple correlation coefficient (0.947) was highly significant.

The sign test showed that the residuals were distributed at random as a function of dependent variable value. However, the spatial autocorrelation of the residuals was significant. Residual positive values were grouped in three areas: (1) Gambia and Guinea (the Gambia and the Konkouré rivers); (2) a region including coastal rivers between the Boubo (eastern Ivory Coast) and the Oueme (Benin); (3) Cameroon, Gaboon and Zaïre (the Nyong, Ntem, Ogowe, and Zaïre).

Species richness in tributaries

The characteristics of the 11 tributaries used in this study are shown in Table 6. Figure 3 compares the observed values of species richness in tributaries with those calculated from the predictive model for rivers. The predicted values

Table 5. Multiple regression of \ln (species richness) versus \ln (catchment surface area) and \ln (mean annual discharge). Coefficients are estimated by the least-squares method

Coefficients						
$\ln S$	$\ln AD$	Intercept	VIF	I	Z	R
0.135	0.245	1.504	5.15	0.239	-0.811	0.947
$P=$	$P=$			$P<$	$P>$	$P<$
0.021	0.001			0.05	0.05	0.001

Abbreviations as in Tables 3 and 4

Table 6. Untransformed data for the 11 tributaries studied

Tributaries	Farthest down-stream locality	Species richness	Surface (km ²)	Mean annual discharge (m ³ ·s ⁻¹)
Niandan (Niger)	Baro	81	12770	252
Bénoué (Niger)	Lokoja	120	64000	382
Black Volta (Volta)	Bamboi	96	134200	247
Nasia (Volta)	Nasia	36	5175	30
Daka (Volta)	Yendi	28	1214	7
Yani (Bandama)	Seguela	39	3000	18
Marahoué (Bandama)	Mankono	65	6700	27
N'Zi (Bandama)	Dimbokro	68	24100	64
Kan (Bandama)	Tiebissou	36	1200	3
N'Zo (Sassandra)	Guiglo	40	6410	84
Sassandra (Sassandra)	Guessabo	62	35000	308

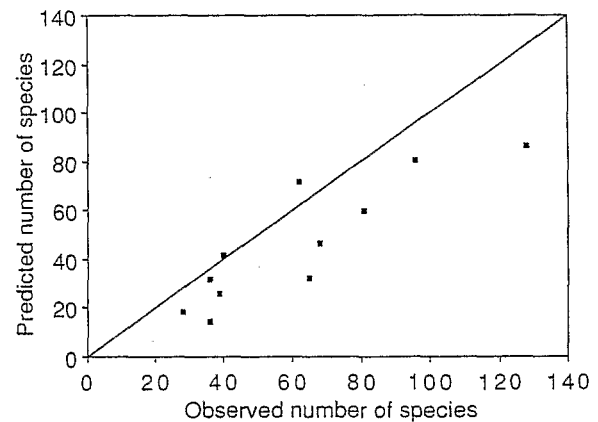


Fig. 3. The relationship between the number of species observed in 11 tributaries and the number of species predicted by the following model: \ln (species richness) = $(\ln$ (mean annual discharge) \times 0.245) + $(\ln$ (catchment surface area) \times 0.135) + 1.504. The straight line represents points for which predicted value equals observed value

tended to be lower than the observed ones, as shown in 9 out of the 11 tributaries. This proportion was statistically different from that expected using the null hypothesis of 50% of the observed values lower than the predicted ones ($\chi^2=4.45$, $P<0.05$).

Discussion

The most striking results of this study can be summarized as follows. The sample of 39 African rivers studied shows a positive species-area relationship described by a power

function of the type $N=cS^z$ (N =number of species; S =drainage surface area); $z=0.32$. In a sample of 26 rivers, ridge regression and forward stepwise selection led us to use a predictive model of $\ln(\text{species richness})$ as a function of $\ln(\text{surface area})$ and $\ln(\text{discharge})$. The residuals obtained by this model showed positive spatial autocorrelation. The

0.19, Daget 1968) than those found in Africa or South America (0.552, Welcomme 1979). These results indicate that species richness tends to increase more rapidly with surface area in tropics than in temperate regions. This is usually interpreted as due to greater inter-habitat diversity in the tropics (Welcomme 1979). This conclusion, however,

to be constant. To improve already-existent hypotheses, attempts have been made to determine factors which might cause density to vary from one island to another. Wright (1983) proposed considering the total primary productivity of an island instead of its surface area because he noted better fit of the data with this single variable.

hypothesis on the basis of a positive species-area relationship (Gilbert 1980). However, area-dependent extinction rates are one reason why islands should have fewer species than comparable continental areas. On continents, local extinction can be compensated quickly by the immigration of new individuals from neighbouring populations, while

regions river discharges were not so greatly reduced and that, today, the rivers should harbour a greater number of fish species than those with similar characteristics but located outside the forest refuge zones. To what extent does the pattern of residual distribution conform to the location of the refuge areas generally admitted to be in West and Central Africa? The Cameroon-Gaboon-Zaire region is, on the whole, a zone where the species richness of the rivers exceeds that of model predictions, this agrees with the supposed location of refuge zones 2 and 3. The Gambia and the Konkoure, which are the only rivers in our study close to refuge zone 1, also have more species than expected. To discuss this further, we would need data on river discharges in Liberia and Sierra Leone. The third area of high species richness shown by our analysis, between eastern Ivory Coast and Benin, cannot be explained by the data now available on the climatic history of West Africa, and it is not evident what factor could act in the east of the Ivory Coast and not in the west. This pattern is probably artificial and results from a poor knowledge of the fauna of some small rivers to the west. Our data can thus only confirm the presence of refuge areas in Central Africa. There is also the possibility that non-random spatial distribution of residuals is due to the fact that a varying geographical factor has not been integrated into the model. Moreover, the fact that no spatial autocorrelation is perceptible when only surface area is considered should invite caution. The validity of the Pleistocene forest-refuge hypothesis, when applied to fish communities of Africa, should be evaluated considering the phylogeny of related groups, distribution, and endemism, and not only the species richness of the rivers.

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Appendix 1

bias. The coefficient of determination also decreases as k increases but for small k values it is hoped to obtain a more predictive model (Marquardt and Snee 1975; Snee 1977).

The main difficulty with this method is to select the optimal k value; there are several numerical ways of doing this but the simplest is to use a curve, called the ridge trace (Hoerl and Kennard 1970b; Marquardt and Snee 1975). If the evolution of the standardized coefficients is analysed as a function of k , it is seen that, after considerable change for the low k values, the coefficients stabilize rapidly and that k must be selected in that range. Finally, it is preferable not to choose $k > 1$, and the maximum variance inflation factor should be near 1.

Appendix 2

Variance inflation factor

The diagonal elements of the following matrix are called variance inflation factors:

$$(X'X)^{-1}$$

or, in ridge regression, diagonal elements of the following matrix (Marquardt 1970):

$$(X'X + kI)^{-1} (X'X) (X'X + kI)^{-1}$$

In both cases, $X'X$ must be a correlation matrix.

The variance inflation factor gives an estimate of the increase of regression coefficient variance of one of the predictor variables due to near collinearity with the other variables. If all the variables are orthogonal among themselves, all the variance inflation factors will be 1. If the maximum variance inflation factor is higher than 10, the estimation of coefficients by the least-squares method can be expected to be inaccurate.

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