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Natural and man-made biogeography in Africa: a comparison between birds and phytopathogens

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ABSTRACT. The geographical patterns of 979 species of passerine birds and of 180 viruses, bacteria and fungi attacking cultivated plants in Africa south of the Sahara were analysed. On average, the geographical range of birds is 3.0 million km^2 (SD 1.7) whilst that of phytopathogens is 4.2 million km^2 (SD 4.0). The difference is significant for $P < 0.001$. Maps of percentage isolines for species richness are presented, showing rather uniform characteristics in the case of birds and pronounced clumping in the case of phytopathogens. Eight pairs of maps of equiprobabilistic lines centred in different points of the continent are also presented, picturing the percentage of species shared between the different areas and a given centre of observation. The 50% isoline is utilized for calculating 'resistance' (R) and 'anisotropy' (A), that is, a way to measure the dispersibility of sets of species and the topographical irregularity of barriers and corridors, respectively: $R = 1 - (a_{50}/a_t)$ and $A = (p_{50}/\sqrt{a_{50}}) - 3.54$, being a_{50} the area covered by the 50% equiprobability line, a_t total area of the region (Ethiopian Africa), p_{50} the perimeter of a_{50} line and 3.54 the ratio $p/\sqrt{a}$ for the circle, which has anisotropy zero. The average value of R is 0.82 for birds and 0.59 for phytopathogens, the difference being significant at $P < 0.01$. The average value of A is 2.99 for birds and 2.71 for phytopathogens, the difference not being significant. By means of a computer program of numerical classification, and based on a sample of 150 bird and eighty phytopathogen species, the region was divided into six zones of maximum compactedness. Two maps illustrating the geographical patterns of species are included, the birds showing a certain degree of concordance with natural biomes, and the phytopathogens showing a rather strong relation with agricultural practices.

Introduction

Invading species in agricultural lands are strongly associated with the human activity and show particular features in their biogeography (Rapoport, Ezcurra & Drausal, 1976; Ezcurra, Rapoport & Marino, 1978). In the present paper we intend to study this problem in more detail by analysing the geographical distribution of 180 species of phytopathogens (viruses, bacteria and fungi) and 979 species of passerine birds of Africa. The purpose is to compare the geographical patterns of species associated with human activities (phytopathogens) with those of wild species (passerine birds).

In order to avoid the influence of Palaearctic species as much as possible we restricted our attention to the Ethiopian Region, taking the parallel 20° N as the northern limit, that is, we took into account the species inhabiting Africa south of the Sahara. The information on phytopathogens was obtained from the Commonwealth Mycological Institute maps

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on plant diseases. In the case of birds, our information came from Hall & Moreau (1970).

Methods

A grid was superimposed over each map to quantify numerically the geographical ranges of species. Since the original maps are at different scales, we also used two different grid sizes. In the case of phytopathogens we used a 30 × 35 divisions grid, each square having *c.* 70 500 km^2. The bird maps were worked with a 47 × 50 grid, each square having *c.* 25 900 km^2. In each map, the squares where the species was present were annotated, delimiting its geographical distribution. These data were stored on a magnetic disc and arranged into two matrices of binary information, one for the birds and the other for the phytopathogens. If the element a_{ij} of a matrix is zero it means the species i is absent in the square j. If the element has value 1 it means the species is present in that square.

With these data at hand we were able to calculate, for each group: (1) mean range of species; (2) number of species per square; (3) number of species shared by each square with a given square considered as 'centre of observation'; (4) delimitation of biogeographic areas by numerical taxonomy.

The number of shared species (item 3) was obtained by counting and individualizing the species present in a given square, and by calculating the percentage of these species present in each square of the matrix. The results are presented in the form of topographic maps. Each line is a demarcation of the spreading of a given percentage of species from the centre of observation, which has the value 100%. It is a simple pictorial way of showing a very complex Venn graph, in some cases with more than a hundred superimposed range maps. Each map depicts the 'cloud of probabilities' around a given point and the curves may be called equiprobabilistic lines. More details on the method are reported in Rapoport (1975). The determination of areas by numerical taxonomy was performed by the method of Lance & Williams (1968) of 'information analysis', already used for biogeographical problems (Kikkawa & Pearse, 1969; Rapoport *et al.*, 1976; Ezcurra *et al.*, 1978).

The parameters resistance (R) and anisotropy (A) were calculated according to the method proposed by Rapoport (1973), that is

$$R = 1 - (a_{50}/a_t)$$

and

$$A = p_{50}/\sqrt{a_{50}} - 3.54$$

where a_{50} is the area covered by the 50% equiprobability line, a_t is the total area of the region considered (Africa south of the Sahara), p_{50} is the perimeter of the 50% curve and 3.54 is the ratio $p_{50}/\sqrt{a_{50}}$ for the circle, which has anisotropy zero. From the centre of observation, R is a measurement of the effectiveness of barriers to the free dispersal, and A provides information on the irregularity of the distribution of these barriers. The underlying idea is the following: we can imagine a container – or a continent – which is perfectly flat and horizontal (isotropous), and perfectly smooth (without resistance). If we spill a glass of water in the centre, the liquid will spread radially until reaching the borders of the container. Suppose we cover the bottom of the container with a sheet of absorbent paper, and repeat the same experiment. At the end we will have a circular spot of water. In this case, we say that the container is isotropous but resistant to the spreading of water. If the spot is irregular, with sinuous borders, we will suspect that the medium is not homogeneous, that is, anisotropous. Sinuses or bays will indicate the presence of barriers, and peninsulas the presence of corridors.

The spreading of pests or invading species is generally circular at the beginning. After a time, the form of their geographical ranges is not circular any more; they show a perimeter/area ratio very far from that of the circle, similar to the ratios observed by chorological studies of natural species.

In other words, if continents oppose no resistance to the spreading of species, all of them should occupy the complete surface up to the sea coast. This rarely occurs. If continents were completely isotropous, the species ranges would be circular. This, also, rarely occurs.

Each map represents the 'topography' of the spreading from a central sample where the highest peak was situated. This 'radar-view' is, in a way, a means of seeing 'how the species feels' the landscape of barriers and corridors. It is interesting to note that although different points of Africa produce different patterns of maps, there is some 'agreement' among the various species on the location of barriers. A map of equiprobabilistic lines centred in the Sahara desert is quite different from a map centred in the equatorial rainforest. Both of them, however, show a tightening of isodensity lines along the ecotone between the rainforest and the savanna. For the desert species a forest represents a strong barrier, and vice versa for the silvicolous species.

In fact, it is possible to measure resistance and anisotropy for each equiprobabilistic curve. We selected the 50% curve by analogy to the mean life-time used for measuring the disintegration of radioactive elements. These curves, in some way, show a 'runoff' pattern, and were used by Rapoport (1973) as a tool for the prediction of pests' spread.

Results

(1) *Mean range of species*

The average geographical area of the bird species studied is 2 978 500 km^2 (SD 1 665 500 km^2), while the figure for the phytopathogens is 4 228 500 km^2 (SD 3 979 500 km^2). The difference is highly significant ($P < 0.001$), indicating that phytopathogens are more widespread in their ranges than birds. Expressed as a percentage, if birds have a mean area of 100%, the phytopathogens have one of 142%.

(2) *Number of species per square*

It is already known that species richness varies in different parts of a continent. The results are expressed in the maps in Fig. 1 in the form of percentages of the total sample. We had to convert the absolute values to percentages in order to make both maps comparable, due to the fact that 180 species of phytopathogens only represent a sample from their total number. Conversely, the 979 species of passerine birds represent the complete 'population', i.e. the status of faunistic knowledge of this taxon in 1970, according to Hall & Moreau.

If the reader is interested in getting the approximate number of passerine birds at a given point, he has to interpolate between the two contiguous equiprobabilistic lines, multiply this value per 9.79 and round the decimals to get an entire number.

Species richness in passerine birds is rather uniform in its distribution, with only one peak exceeding 30% in the zone of Lake Victoria, where the confluence of several biomes occurs. The number of species in deserts, however, decreases more pro-

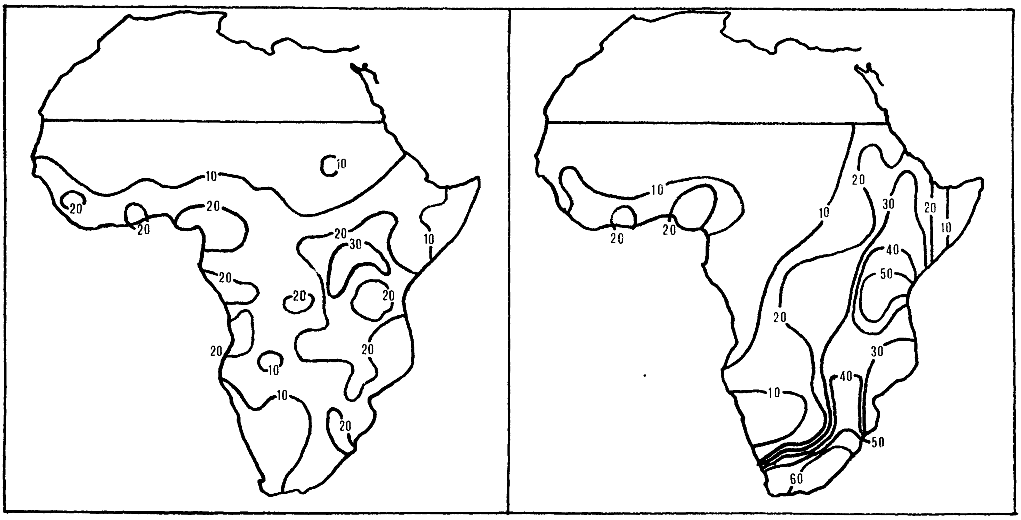

FIG. 1. Species isodensity lines. Figures represent percentages of the total number of considered species. Left, passerine birds (978 species considered). Right, phytopathogens (180 species considered).

nouncedly. By contrast, phytopathogens show sharp differences, with high concentrations in agricultural lands. The south-eastern fringe of Africa, from Lake Victoria to Cape Town, concentrates the maximum number of agricultural pests, with decreasing numbers over the rest of the Ethiopian Region. Outside this 'contagion', a tendency for the number to increase is encountered only on the northern coast of the Guinea Gulf where centres of intensive agriculture also exist. Some points in South Africa concentrate more than 67% of the agricultural pests considered by us.

(3) *Number of shared species*

Fig. 2 shows eight pairs of maps of equiprobabilistic curves centred in 'points of observation' selected from different biomes. The 50% curves, on the basis of which resistance and anisotropy are measured, appear thicker on the maps.

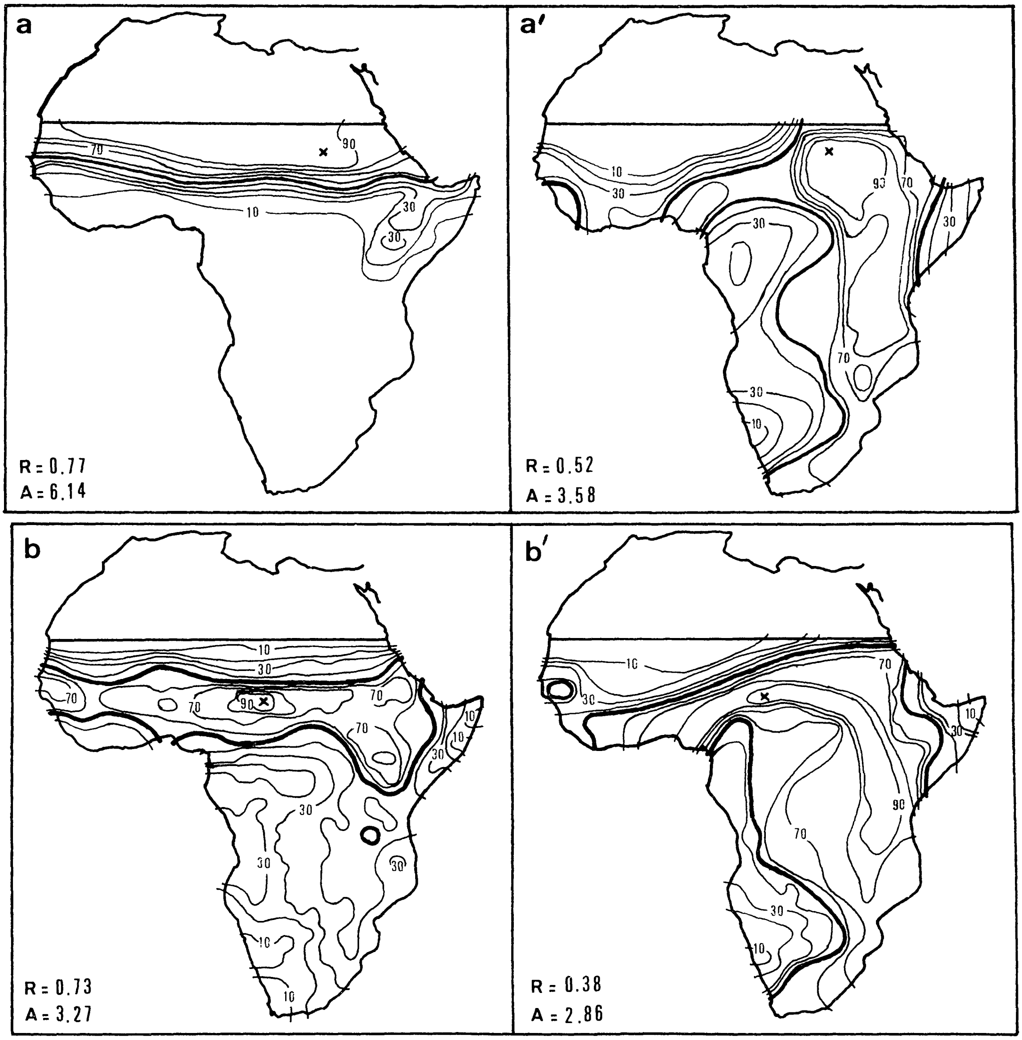

FIG. 2. Isoprobability lines centred in four selected sites, representing different biomes. The lines represent the loss of species from a central sample (100%) marked by a cross. Each couple of maps is centred in the same geographical site, left: passerine birds; right: phytopathogens. a–a′, Saharan desert; b–b′, northern dry woodland; c–c′, rainforest; d–d′, montane vegetation; e–e′, moist woodland; f–f′, southern dry woodland; g–g′, desert, h–h′, macchia.

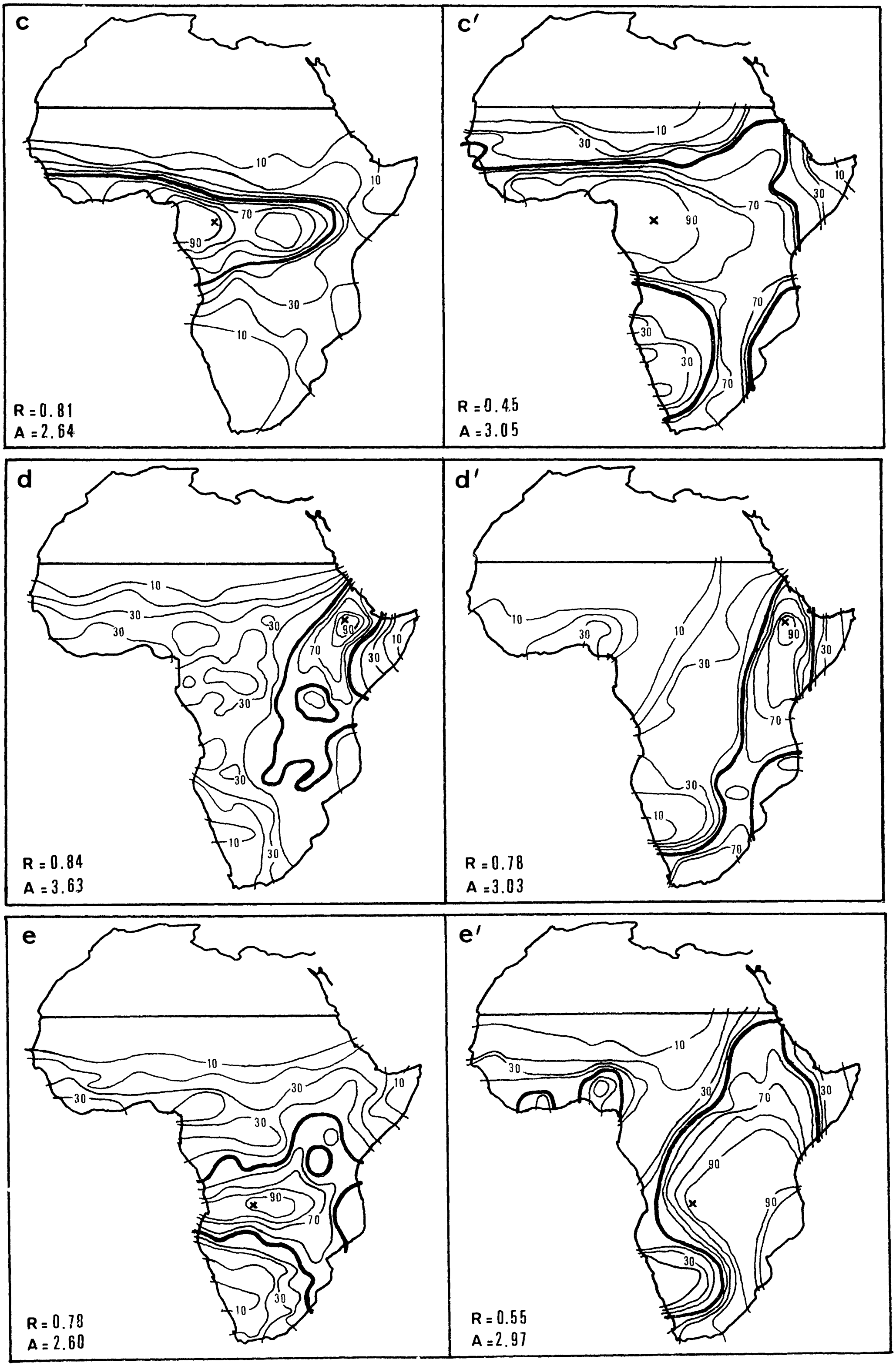

FIG. 2 (*continued*)

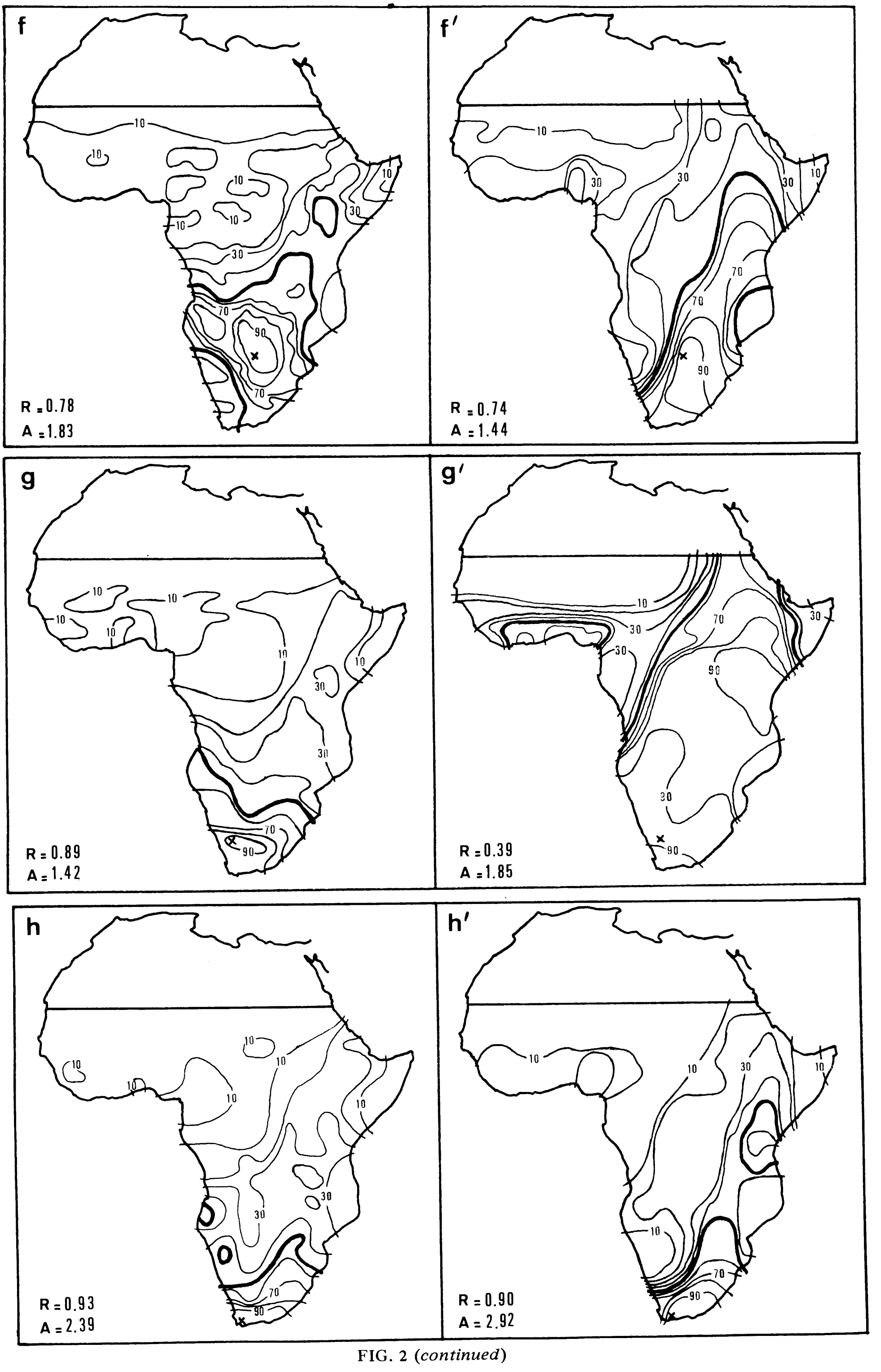

FIG. 2 (*continued*)

The curves, in the case of passerine birds, seem to follow loosely the contour of biomes. The phytopathogens, however, show slight influence from the biomes and tend to spread over the zones of intensive agriculture and highest human activities. On average, resistance (R) values are 0.82 ± 0.07 for birds and 0.59 ± 0.19 for phytopathogens. A '*t*'-test as well as a sign test tell that the differences are significant for $P < 0.01$. The opposite case occurs with anisotropy which shows quite similar values for birds ($A = 2.99 \pm 1.46$) and phytopathogens (2.71 ± 0.70). The differences are non-significant. These values somewhat differ from a similar calculus of resistance and anisotropy in passerine birds performed by Rapoport (1973) for the whole continent: $R = 0.87$ and $A = 4.05$, based on seventy-eight equiprobabilistic maps.

It is interesting to point out that the highest values of resistance, in both groups, correspond to the maps centred on the South African macchia (Fig. 2h,h$'$). This would indicate the existence of conditions conducive to the reduction of the geographical range of species. Floristically speaking, the macchia show strong endemisms and this phenomenon may be extensible to birds also. But this seems not to be the case for phytopathogens, because the species considered in our study are rather widespread, cosmopolitan or semicosmopolitan taxa. Possibly, their reduced areas may be related to the geographical patterns and spatial distribution of agricultural lands in that region.

The map in Fig. 2(a) shows the highest value of anisotropy ($A = 6.14$). With regard to this point, it should be emphasized that in cases like this, where the contour of the 50% line is not completely defined (it lacks its northern border), the values may change when considering the complete continent.

Delimitation of biogeographic areas

Due to computer-time limitations we were obliged to reduce the number of species to be processed. In the case of passerine birds, the map in Fig. 3(left) was obtained through a sample of 150 species, phytopathogens had to be reduced to eighty species. The process of classification was interrupted at the fifth division, that is, a six-zones map. The dendrograms indicate the way in which the computer performed the divisions; they should be followed from top to bottom in order to get two, three, etc., zone divisions. The numbers at the bottom of the dendrogram correspond to the zone represented by that branch, and the height of the black columns indicates the remaining heterogeneity for that zone.

It is remarkable that the division obtained

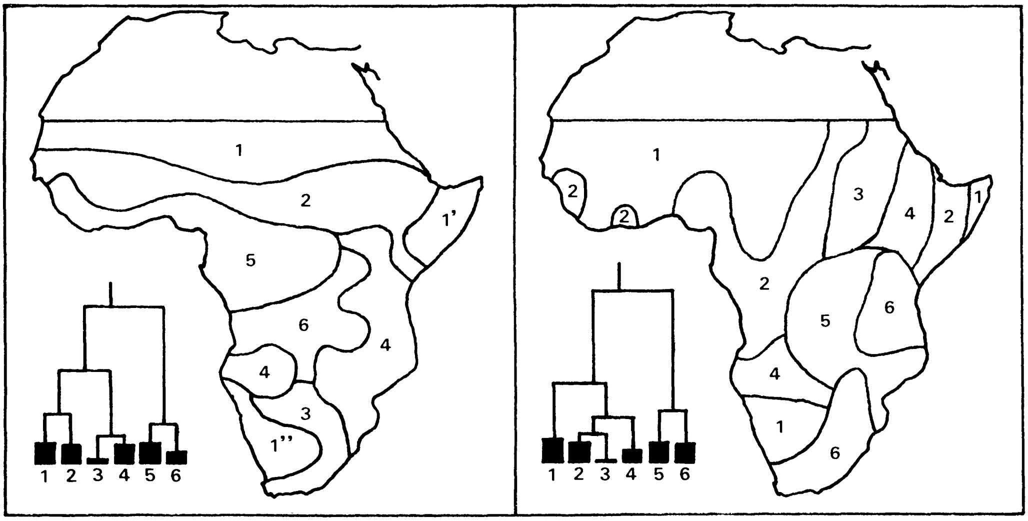

FIG. 3. Left: six-zones division based on the distribution of 150 passerine bird species. Right: six-zones division for crop phytopathogens based on the distribution of eighty viruses, bacteria and fungi species. Dendrograms indicate the way in which the computer program proceeds in the numerical classification of quadrats. Zones 1 are the poorest and zones 6 are the richest in the number of species.

for passerine birds (Fig. 3, left) only agrees with Wallace's (1876) zoogeographic division with respect to zone 5 (tropical rainforest). Excepting Madagascar and S. Arabia which we do not take into account here, Wallace divided the Ethiopian Region into three subregions which correspond, very roughly, to our zones $1 + 1' + 2$ + West 4 + East 4 (central and northern) + 6 = (Wallace's East African Sub-region), zones $1'' + 3$ + East 4 (southern portion) = (Wallace's South African Sub-Region), and zone 5 = (Wallace's West African Sub-Region). Our dendrogram, however, produces a different grouping at a three divisions level: 1 + 2, 3 + 4 and 5 + 6 zones. It may be useful to point out that, although we identify the Saharan, Somalian and Namibian deserts with numbers 1, $1'$ and $1''$, respectively, the computer program considers them as the same thing. Their similarities do not lie in the fact that they share the same species but, rather, in the fact that they have few species. In the case of birds, further divisions will certainly produce their separation as different units.

Our map has some correspondence, though, with the ecological division of Africa made by Devred (reproduced by de Voos, 1975).

Our Division (Fig. 3, left)	*Devred's Division*
Zones	Zones
1	Saharan–Sahelian
2	Soudanian (our zone 2 extends more widely to the East)
3	Kalaharian–Basutolian
4	No correspondence
5	Guinean
6	No correspondence

Discussion

Phytopathogens, when compared with passerine birds, clearly show the geographic patterns of species associated with human activities, in this case, agriculture. They have larger areas of distribution, are more widespread than the geography of biomes; they are able to invade different biomes provided agriculture is established there. This particular characteristic is especially noticeable on the map in Fig. 3. On the contrary, passerine birds seem to follow sometimes more or less accurately, and sometimes more or less loosely the distribution of biomes. Very roughly: zone 1, Saharan desert and semi-desert; zone $1'$, Somalian desert and semi-desert; zone $1''$, Namibian desert and semi-desert; zone 2, northern dry and moist woodland; zone 3, southern dry woodlands, bushveld and macchia; zone 4, complex combination of plant associations; zone 5, rainforest; zone 6, southern moist woodlands.

These data confirm our previous observations (Rapoport *et al.*, 1976; Ezcurra *et al.*, 1978) on the distribution of crop pests, which are more influenced by the types of agriculture than by the natural biogeography of the region.

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