Avian endemism in northeastern tropical Africa

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The avian endemism of Ethiopia and the Horn of Africa was analyzed using a database where all bird distributions in Africa south of the Sahara are recorded in a one-degree grid. Applying a hierarchical classification algorithm, the tropical Northeastern Subregion of Africa stands out clearly and can be subdivided in an Ethiopian Highlands Province and the Somalia-Masai, Tana-Jubba and Turkana districts and a Danakil Province. The Horn of Africa Province is associated with the Northern Arid (Sahara) Subregion in this hierarchical classification, although this reflects the replacement of savanna with desert birds more than shared endemism. Although most of the Ethiopian Highland endemics are distributed all over the highland, a more complex pattern of local endemics can also be defined, using a complementarity algorithm. Local endemism is very pronounced among the larks, Alaudidae. The majority of endemics belongs to recently radiated groups, and is mainly related to the fauna of East Africa; however, the fauna of the Sidamo district contains relict elements, two of these of a significant evolutionary age. The pattern of endemism in the birds of northeastern tropical Africa has a number of features in common with patterns found in plants.

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Introduction

Being the largest highland area in Africa, well isolated from other Afromontane areas by the lowlands grass savannas of southern Sudan and by the desert of the Lake Turkana area (White 1983), it is not surprising that the Ethiopian highlands have a number of unique and endemic species of birds (Urban & Brown 1971; Stattersfield *et al.* 1998; BirdLife International 2000). Other smaller aggregates of endemic species have been defined in the adjacent foothills and for various parts of the Horn of Africa. However, a large proportion of the avifauna is comprised of widespread species, and other species are disjunctly distributed (Fig. 1), illustrating how endemism may arise as once-widespread species decline to form widely isolated populations.

In this paper we will analyse patterns of endemism and biogeographic relationships of birds in Ethiopia and adjacent areas using a database of bird distributions in Africa south of the Sahara. The Percy FitzPatrick Institute of Cape Town and the Zoological Museum of Copenhagen jointly developed this database. We used the Worldmap software (Williams 1998), which is a PC-based graphical tool designed for rapid and interactive digitisation

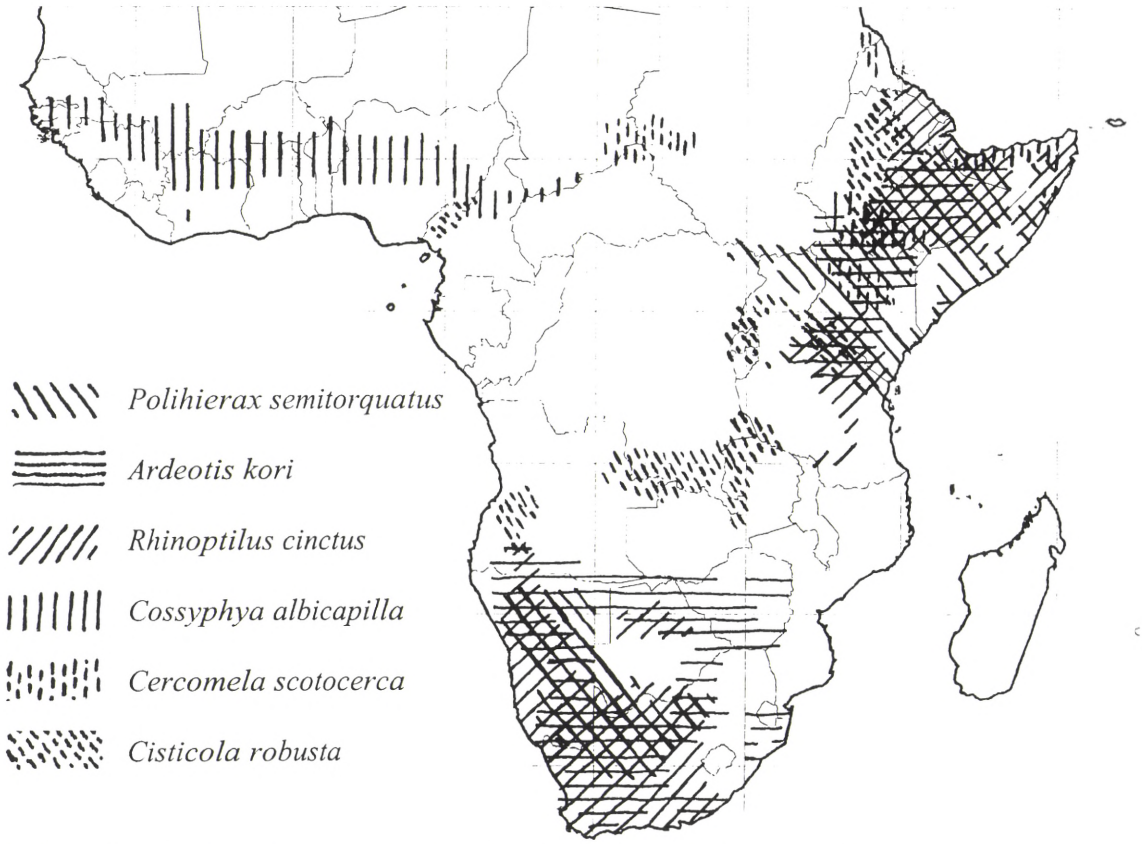


Fig. 1. Distribution of six species of non-migratory Afrotropical birds with disjunct distributions (note that some of the populations may already be recognizable as phylogenetic species).

of distributional data for large numbers of species. The records were allocated to grid cells corresponding to geographical degrees, for range-maps (made by conservative interpolation, and taking the distribution of suitable macrohabitats into account), or point localities for species that are considered genuinely rare or local. The distributional data were compiled from regional handbooks and distribution atlases (for northeastern tropical Africa especially Archer & Godman 1937; Cave & MacDonald 1955; Urban & Brown 1971; Nikolaus 1987; Solomon Tilahun *et al.* 1996; Ash & Miskell 1998) and published articles (*e.g.* Safford *et al.* 1995; Ash & Miskell 1988; Ash 1998; Ash & Gullick 1990) as well as information from a large number of persons, and from the databases of BirdLife International. Preliminary descriptions of the databases are given in Burgess *et al.* (1998, 2000) and in Brooks *et al.* (in press). The avifauna of Ethiopia and the Horn of Africa can therefore be analyzed in a continent-wide perspective.

Widespread and endemic species

The variation in species richness across Africa is illustrated in Fig. 2. This map clearly shows the importance for biodiversity of the highlands in eastern Africa, and especially of dis-

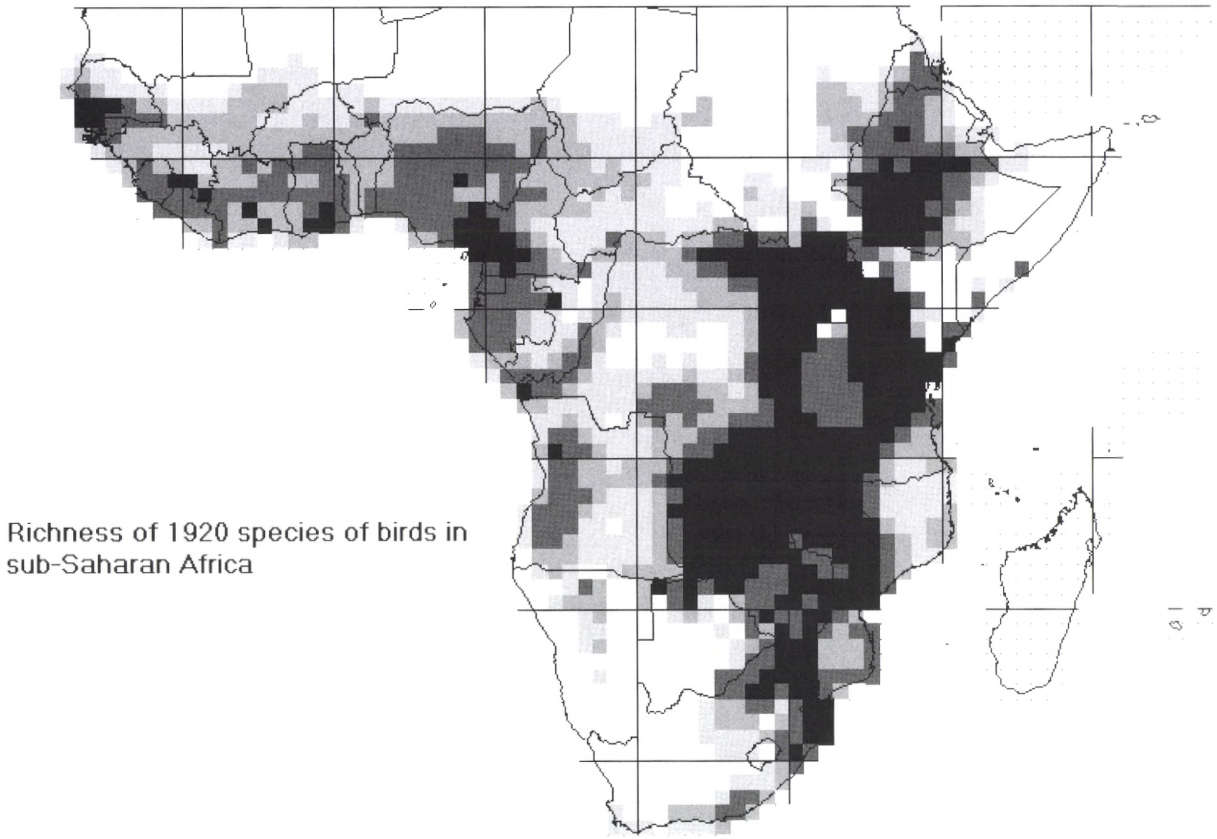


Fig. 2. Species richness of all species of birds in Africa south of the Sahara. The darkest areas have the highest relative species richness.

tricts with mosaics of savanna and forest and high topographic complexity. It also shows the relatively isolated position of the Ethiopia highland, and its somewhat impoverished fauna, compared with the highlands of Kenya and the Albertine Rift. The Ethiopia highland stands out more clearly if we consider endemism (sum of inverse range-sizes for all bird species represented in each grid-cell). Its importance is even more marked if we illustrate instead (Fig. 3) the distribution of threatened birds (critical, endangered and vulnerable categories, following the IUCN criteria, see Collar & Stuart 1985, Mace & Stuart 1994 and BirdLife International 2000). According to these criteria many species are classified as endangered because of their small distributions, so this map illustrates a combined effect of endemism and intensive human land conversion. According to Fig. 3 the entire Ethiopian mountain massif west of the Rift Valley is important from a conservation perspective, together with the Nechisar and Bale areas and foothills of the Sidamo area, and some highland sites around the Gulf of Aden.

The entire tropical northeastern region of Africa (Ethiopia, Eritrea, Somalia and the Turkana district of Kenya) has some 672 resident species of birds, of which some 80 (12%) species are endemic and near-endemic. Of

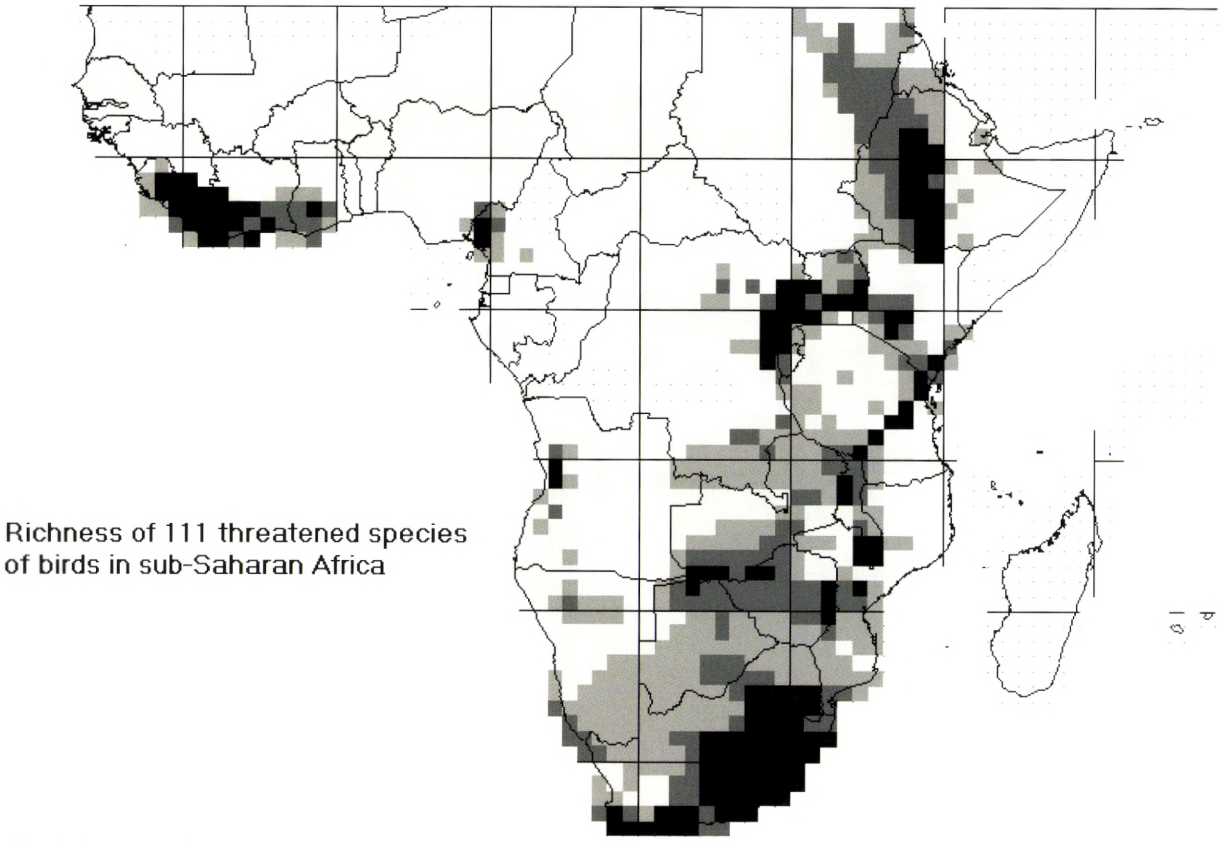


Fig. 3. Species richness of threatened species (*i.e.* critical, endangered and vulnerable categories, in this case including northern migrants). The darkest areas have the highest relative species richness.

these only 22 are forest or woodland birds. Among the remaining open-land birds, the most remarkable group is the larks (*Alaudidae*) with 31 species of which 12 are endemic. Some of these have very small ranges (single sites in some cases) and are associated with very specific kinds of semi-desert terrain, characterised by different soils (rocks to barren red soil) and specific kinds of vegetation, presumably of restricted distribution. Most African larks are resident, and recent molecular studies indicate that the pattern of differentiation may be much more complex than suggested by the currently accepted species level classification (Ryan & Bloomer 1999).

Hamilton (1989) considered Ethiopia to be a minor core area for endemism and biodiversity, while Brenan (1978) suggested the plant endemism of Ethiopia to be over 20%. Friis *et al.* (2001) judges the plant endemism of Ethiopia to be between 10 and 20 per cent, and Lye (2001) considers the endemism (of Cyperaceae) to be even higher in Somalia. Compared with plants, the avian endemism is modest, with much fewer examples of very narrow distributions, although the larks represent exceptional cases, which almost parallel the endemism in geophytes (Nordal *et al.* 2001).

Definition of avifaunistic regions

Our Africa Bird Database is well suited for objectively defining large-scale biogeographic regions, as the data are recorded in 1° cells rather than for predefined eco-regions of variable size. The ideal method for defining patterns of endemism would be to use a Parsimony Analysis of Endemism (see Morrone 1994). However, the existing software and computers unfortunately cannot handle datasets of >1700 species and 2169 area units according to this algorithm.

We therefore used a Bray-Curtis distance index (*e.g.* Everitt 1993) to measure the dissimilarity, cell by cell, for the endemic terrestrial Afrotropical birds (de Klerk, unpublished thesis, and see Williams *et al.* 1999 for Twinspan and Decorama ordination using the same dataset). We use the Bray-Curtis index here since it does not consider conjoint absences (*e.g.* Sneath & Sokal 1973; Krebs 1989). A hierarchical classification algorithm was applied to the resultant distance matrix in order to indicate groupings, or clusters, of grid cells that comprise similar avifaunas, and to indicate how these clusters relate to each other. A UPGMC (unweighted pair-group method using centroid) algorithm (Sneath & Sokal 1973) was applies using BMDP-2M software (Dixon 1990). It needs to be born in mind that this is a divisive cluster analysis, which simply represents a joining of objects into groups based on a set of rules. So the result is neither true nor false, and should be judged on the usefulness of the results (Everitt 1993) for the practical subdivision of faunas.

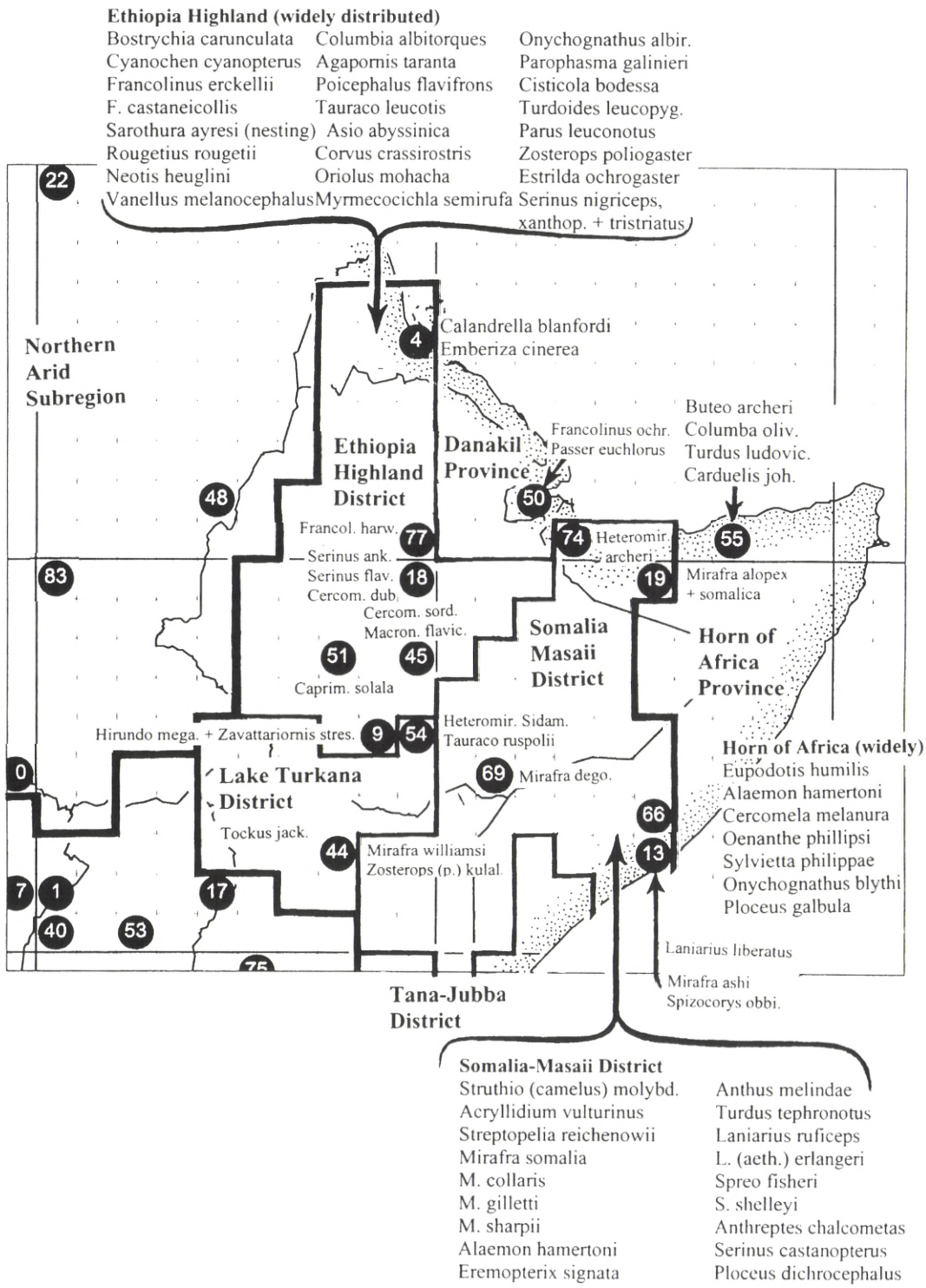
The boundaries of biogeographic provinces and districts in tropical northeastern Africa are drawn in Fig. 4. On this illustration is also listed all species which are endemic (or near-endemic) to the respective regions. For detecting the finer patterns of differentiation we used a complementarity algorithm: here all species distributions are compared and a minimum number of areas is identified which covers all endemic African birds (see legend to Fig. 4 for explanation). The software also has functions for identifying species, which are exclusively represented in the particular cells of the minimum set (as indicated in Fig. 4). It also has functions for displaying the combined (superimposed) distributions of these particular species as well as information about the total array of species represented in a particular cell (Fig. 5).

The Northeastern Subregion

In the hierarchical classification of areas, the area we deal with in this paper, the tropical *Northeastern Subregion* of Africa, stands out as a distinctive cluster with altogether 58 zone-restricted bird species. The subregion can in turn be divided into an *Ethiopian Highlands Province* and several lowland districts, namely the *Somalia-Masai*, *Tana-Jubba* and *Turkana Districts* and the *Danakil Province*. The strong affinity of the lowland districts to each other is attributable to a number of species that are distributed more or less throughout the dry and arid *Acacia-Commiphora* thorn scrub and savanna that sweeps from the Gulf of Aden to Lake Turkana. However, it should be noted that some of the narrowly endemic species (including the distinctive *Hirundo megaensis*, *Zavattariornis stresemanni* and *Tauraco ruspolii*, covered in cells 9 and 54 in Fig. 4) inhabit different habitats in the foothills of the Borana district, which span the borderline to the Ethiopian Highland Province (Syvertsen & Dellelegn 1991). This means that the data are not sufficiently fine-grained to identify minor areas of endemism and describe the pattern with precision.

The Ethiopian Highlands Province

The *Ethiopian Highlands Province* is the most important avifaunal zone in terms of numbers of endemics. However, most of the endemic


Ethiopia Highland (widely distributed)
Bostrychia carunculata
Cyanochen cyanopterus
Francolinus erckellii
F. castaneicollis
Sarothura ayresi (nesting)
Rougetius rougetii
Neotis heuglini
Vanellus melanocephalus
Columbia albitorques
Agapornis taranta
Poicephalus flavifrons
Tauraco leucotis
Asio abyssinica
Corvus crassirostris
Oriolus mohacha
Myrmecocichla semirufa
Onychognathus albir.
Parophasma galinieri
Cisticola bodessa
Turdoides leucopyg.
Parus leuconotus
Zosterops poliogaster
Estrilda ochrogaster
Serinus nigriceps, xanthop. + tristriatus
22
Northern Arid Subregion
4
Calandrella blanfordi
Emberiza cinerea
Buteo archeri
Columba oliv.
Turdus ludovic.
Carduelis joh.
Francolinus ochr.
Passer euchlorus
Ethiopia Highland District
Danakil Province
50
48
Francol. harw.
77
74
Heteromir archeri
55
Serinus ank.
Serinus flav.
18
19
Mirafra alopex + somalica
83
Cercom. dub.
Cercom. sord.
Macron. flavic.
Somalia Masaii District
Horn of Africa Province
51
45
Caprim. solala
Hirundo mega. + Zavattariornis stres.
9
54
Heteromir. Sidam.
Tauraco ruspolii
Horn of Africa (widely)
Eupodotis humilis
Alaemon hamertoni
Cercomela melanura
Oenanthe phillipsi
Sylvietta philippae
Onychognathus blythi
Ploceus galbula
0
Lake Turkana District
69
Mirafra dego.
66
Tockus jack.
44
13
Mirafra williamsi
Zosterops (p.) kulal.
7
1
17
40
53
Laniarius liberatus
Mirafra ashi
Spizocorys obbi.
Tana-Jubba District
Somalia-Masaii District
Struthio (camelus) molybd.
Acryllidium vulturinus
Streptopelia reichenowii
Mirafra somalia
M. collaris
M. gilletti
M. sharpii
Alaemon hamertoni
Eremopterix signata
Anthus melindae
Turdus tephronotus
Laniarius ruficeps
L. (aeth.) erlangeri
Spreo fisheri
S. shelleyi
Anthreptes chalcometas
Serinus castanopterus
Ploceus dichrocephalus

species occur widely distributed in the highland, although often segregated in different habitats of forest and montane grassland. The majority of the endemic highland species are associated with forest (*Francolinus castaneicollis, Tauraco leucotis, Zosterops poliogaster, Agapornis taranta*; *Poicephalus flavifrons* and *Asio abyssinicus* in *Podocarpus* forest, *Parophasma galinieri* in bamboo forest and *Cisticola bodessa, Dendropicos abyssinicus* and *Oriolus monacha* in *Juniperus procera* forest). Others occupy woodland (*Parus leuconotus*), grassland (*Cyanochen cyanopterus, Vanellus melanocephalus, Rougetius rougetii, Macronyx flavicollis, Estrilda ochrogaster*), or moor- and heathlands (*Serinus nigriceps*). *Sarothura ayresi* depends on seasonally inundated montane grassland, and its known breeding population is restricted to Berga and Weservi. Associated with cliffs are *Columba albitorques, Corvus crassirostris, Myrmecocichla melaena, Onychognathus albirostris, Passer swaynsoni* and *Serinus ankoberensis*.

The most narrowly endemic species do not show a particularly clustered (nested) pattern, but occur single or a few together. As examples, *Francolinus harwoodi* has a tiny range in thornscrub around the upper Blue Nile (cell 77 of the minimum set, with parts of the Abbai [Blue Nile] River Basin, see Robertson *et al.* 1997, and possibly in Gore). The entire distribution area of *Cercomela dubia* and *Serinus flavigula* is covered by the adjacent cell 18. In addition, *Myrmecocichla melaena* and *Serinus ankoberensis* inhabit rocky terrain in both these cells. *C. dubia* is known from scattered records also elsewhere in the province. The single specimen of *Caprimulgus solala* is from the Rift Valley at Nechisar (cell 51). No bird species is narrowly endemic to the eastern highland (unlike *Tachyoryctes macrocephalus* and *Megadendromus nikolausi* among rodents).

Lake Turkana District

A remarkable aggregate of very narrow endemics is found on the transition from the Ethiopian Highland towards the Turkana desert, in the Borana district. This includes red soil desert with *Mirafra somalica, Acacia* forests with *Zavattariornis stresemanni* and *Hirundo megaensis* near Yabello and Mega, montane grassland with *Heteromirafra sidamoensis* near Negele, and evergreen forests with *Tauraco ruspolii* near Arero and Negele). The Turkana desert is species poor, characterised by *Tockus jacksoni*, and by two narrowly endemic species in the Kenyan part (*Mirafra williamsi* at Marsabit and Isiolo, and *Zosterops (poliogaster) kulalensis* in a montane forest 'island').

The Somalia-Masai District

The *Somalia-Masai District* covers the foothills and plains east and southeast of the Ethiopian highland, as far as and including the Haud Plateau, from the Gulf of Aden to northeastern Kenya. The district is dominated by *Acacia-Commiphora* thickets, and its endemic species occur single or a few together in a quite complex pat-

← **Fig. 4.** Areas of avian endemism in northeastern tropical Africa, as determined using the distributions of endemic African landbirds. Thus we excluded for this analysis waterbirds and northern migrants and species shared with the Palearctic region. The lines separate the biogeographic regions as determined by the cluster analysis, while numbered dots represent the near-minimum set of areas needed to cover all species, using a complementary analysis. In the latter analysis the most species rich cell is first chosen (1; a cell on the Congo/Uganda border), then the cell is chosen which provides most new species which were not represented in the first cell (2; a cell on Mt. Cameroon not shown), then the cell with the second highest number of new species (3; a cell with the East Usambara Mts of Tanzania), and then the cell with the third highest number (4; a cell at the Red Sea coast of Erithrea), and so onwards untill all species are chosen; this is followed by a redundancy back-check. The endemic and near-endemic species are listed for each Province or District, with species represented only by one cell in the minimum set mentioned in connection with this cell.

tern. The endemic species inhabit riparian woodland in Somalia (*Streptopelia reichenowi, Laniarius liberatus, Anthus melindae*), riverine marshland (*Ploceus dichrocephalus*), highland grassland (*Heteromirafra archeri*), dry bush and *Acacia* scrub (*Mirafra aloplex*) and more open and rocky habitat (*Mirafra sharpii* and *M. degodensis* (the latter only at Bogol Mayo). Finally, two species are known from the coastal dune grassland, *Mirafra ashi* in one red-soil site, *Spizocorys obbiensis* more widely and up towards the Horn.

The Danakil Province

The *Danakil Province* resembles the Somalia-Masai semi-desert grassland and shrubland and regs, hamadas and wadis of the Danakil depression and the Red Sea coast and neighbouring hills, and the norhern limits of the Chercher Highlands with *Juniperus procera* forests. *Francolinus ochropectus* is the only strictly endemic species (in Djibouti), as other characteristic species are non-endemics which extent along the Red Sea coast or into adjacent parts of the Arabic peninsula. There is also a considerable overlap with the Ethiopian highland fauna.

The Horn of Africa Province

The portion of the Haud (Ogaden) Plateau of the Somali peninsula that does not fall into the Somali-Masai District is identified by the cluster analysis as the *Horn of Africa Province*. This province does not form part of the tropical Northeastern Subregion, but is rather part of the *Northern Arid Subregion*. This is not due to shared endemic species, but more accurately due to the loss of savanna species, and the fact that these savanna species are replaced with desert birds, as we pass into the Sahara and towards the Horn. The Twinspan and Decorana analysis (Williams *et al.* 1999) associates the avifauna of the Horn of Africa with that of the *Northeastern Subregion*, and demonstrates that the transition is characterised mainly by a high index for range edges and a decline in species richness.

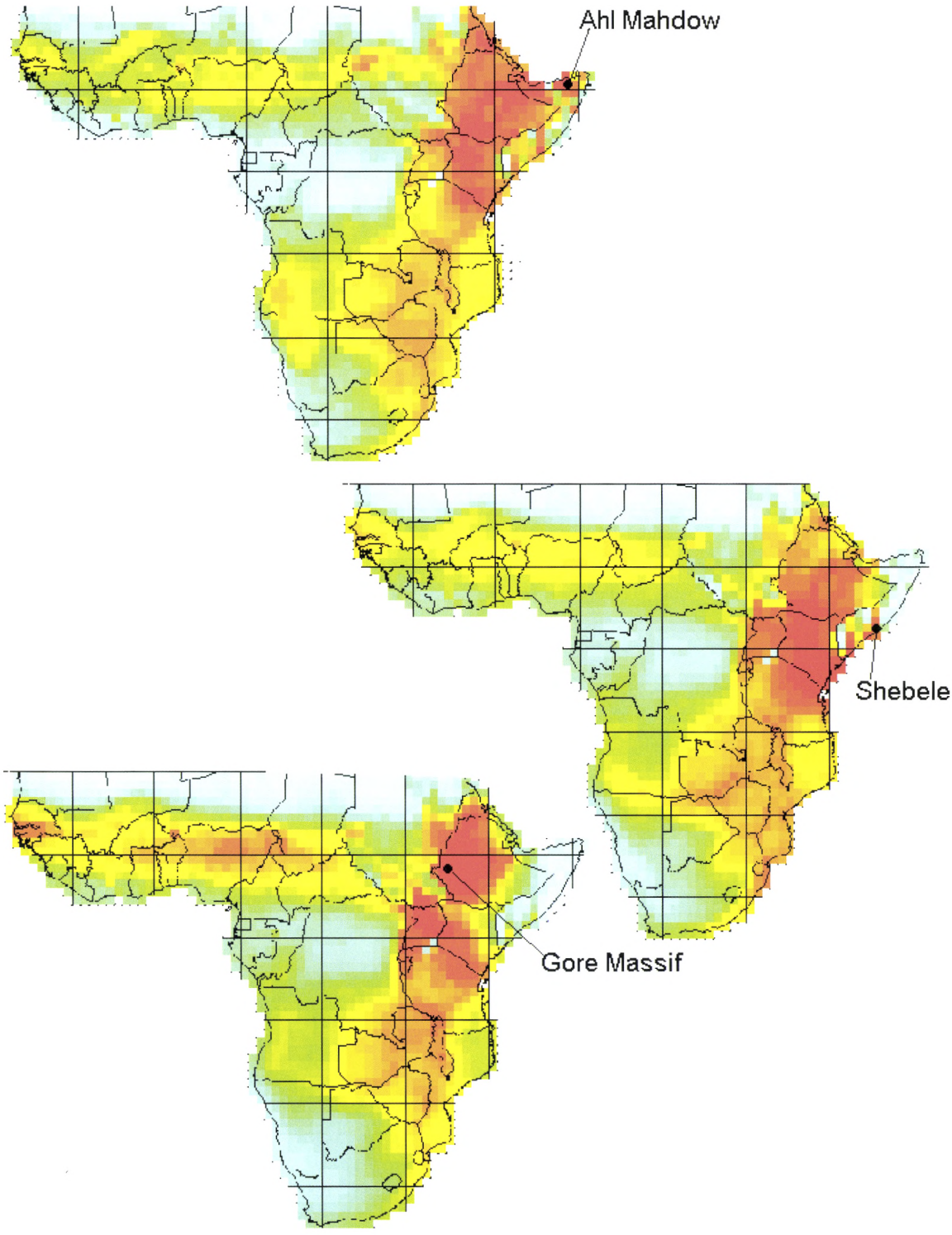
Endemic species for the Horn are *Sylvietta philippae, Eupodotis humilis and Oenanthe phillipsi*, and in the Nugal depression and Obbia coastline the larks *Mirafra somalica, Alaemon hamertoni* and *Spizocorys obbiensis*. The Warsengelia Highland and Ahl Madow scarp (previously Ahl Mado) has *Buteo archeri, Columba oliviae, Turdus (olivaceus) ludoviciae, Carduelis iohannes* (the two latter of these associated with the Daloh *Juniperus procera* forest).

Socotra Island, which has six endemic bird species, was not included in our dataset. The avifauna here is more closely associated with that of Africa than with the Arabian Peninsula. The avian endemism is quite modest compared with what is found in some other groups such as lizards.

The Tana-Jubba District

This is a mosaic area of coastal and riverine forests, evergreen and deciduous bushland and savannas, and extends southwards into Kenya, as a transition between the African Horn and the habitat mosaics of eastern Africa. The majority of species are shared with the coastal zone of Tanzania and Mozambique, but a few species are more narrowly endemic (*Tauraco fischeri, Macronyx aurantiigula, Phyllastrephus terrestris, Erythrocercus holochlorus, Cinnyris nectarinoides, Ploceus castaneiceps* and *P. boieri*).

Fig. 5. Biogeographic affinities of the bird fauna in northeastern tropical Africa, illustrated as the geographical distribution (richness) of species represented in three areas of endemism. Top: the distribution of the species of birds occurring on the northern scarp of the Horn of Africa at Ahl Madow. Right: the distribution of the species of birds occurring on the lower Shebele River in Somalia. Bottom: the distribution of the species of birds occurring at the Gore Massif, on the western slope of the Ethiopian Highlands. →


Ahl Mahdow
Shebele
Gore Massif

Evolution and biogeographic affinities

Two different approaches were used to determine the biogeographic affinities of the avifauna of tropical northeastern Africa: (1) Superimposing the current distributions of all species which are found in the different cells of the minimum set, and (2) reviewing the literature regarding relationships of the narrowly endemic species.

Superimposing distributions of widespread species
Some examples of the first approach are shown in Fig. 5. The resident birds of Gore, of the western slope of the Ethiopia Highland (Fig. 4, bottom) are well distributed all over the Ethiopia highland, with the majority of the species also present south of the Sudd and the Turkana Desert, in Kenya and Uganda. Many species are widely distributed in the savanna regions of eastern Africa, or they are found in the northern woodland savannas. However, the map illustrates a large amount of range disjunctions in southern Sudan, corresponding to the Sudd swamps and adjacent grass savannas. Birds from Addis Ababa, and those of other parts of the Ethiopia Highland, show very similar patterns, although with slightly fewer species represented in the western savannas. The birds of the lower Shebele River of Somalia (Fig. 5, right) are more uniformly distributed across Kenya to northeastern Tanzania, and are much less represented in the western savannas.

The birds of the fairly species-rich Ahl Madow scarp (on the northern edge of the Horn, Fig. 5, top) are rather locally distributed elsewhere on the Horn, but are generally well represented in the drylands and uplands of Ethiopia and East Africa, and fairly well represented along the Red Sea (many species also in Yemen). Many species are also represented in the Jebel Marrah highland of Darfur in central western Sudan and locally in the Sahel, and also locally in the southern savannas and drylands. The strong connection westwards over Darfur is also clearly demonstrated by the Danakil avifauna (Djibouti cell).

The general pattern that emerges from this is that the majority of birds in the tropical Northeastern Subregion of Africa are quite widely distributed in the African savannas, except for a poor representation in the grassland savannas of southern Sudan. This seems, overall, to be a more efficient barrier than the Turkana desert, except of course for the forest birds, where also the gap between the Boran foothills and the Kulal and Marsabit highlands represent a significant isolating barrier. In many cases, the faunal connection with the western savannas apparently was over the hills of central Sudan and Darfur, which in the past may have had a richer vegetation cover than today, maybe with some woodland.

Evolutionary relationship of endemics
The majority of endemic species of the tropical Northeastern Subregion have their closest relatives in eastern Africa south of the Turkana desert. In some cases, however, a considerable distribution gap exists (especially for some Somali endemics, some of which have their nearest relatives in southern Africa, as illustrated in Fig. 1). While the Danakil Province has a strong influence from the Palaearctic fauna, this is much less the case with the endemic fauna of the Ethiopia highland. Examples comprise populations of the northern *Tadorna ferruginea* and *Pyrrhocorax pyrrhocorax* and possibly *Aquila chrysaetos*, and two endemics: *Serinus ankoberensis*, which is related to *S. menachensis* of southwestern Arabia, and *Asio abyssinicus*, which is related to a widespread Palaearctic form. Overall, the affinities between the endemic Ethiopian avifauna and that of Arabia and Eurasia appear to be weak (in contrast to for instance mammals and plants).

Overall, speciation in birds seems to involve geographic isolation, either after chance dispersal across a habitat gap, or because of a disruption (by vicariance or relictuation) of a once-continuous range (Fig. 1). Recent analyses using DNA data suggest that, during the most recent geological past, the most intensive diversification in Africa was in the savanna regions, and mainly in mountainous areas. In contrast, the lowland rainforests seem largely to act as 'museums' retaining the species of the biologically much richer Tertiary rainforests (Fjeldså & Lovett 1997; Roy et al. 1997; contrary to earlier ideas about speciation caused by isolation in Pleistocene forest refuges, see Diamond & Hamilton 1980).

Patterns of local endemism

Within the montane areas, the narrow endemism is often locally aggregated in places with predictable ecoclimatic conditions, probably due to local orographic moderation of extreme weather conditions (Fjeldså *et al.* 1997). This implies that much of the endemism in the Afrotropical avifauna is relictual, and that the emergence of new species in the African avifauna is often related to stable local conditions.

The Ethiopia Highland seems to differ from this picture as most endemics live all over the highland, and do not show marked local aggregates. The highland is climatically unstable, with high vulnerability to drought and high inter-annual variability in the vegetation index (Fjeldså *et al.* 1997). Over a longer time perspective, the rifting and volcanism meant an enormous environmental disturbance (Sayer *et al.* 1992). In this case, the endemism seems to reflect the isolation of the highland as a whole, more than special local conditions. An exception may be the scarp near Addis Ababa, which has more stable local conditions, the foothills south of the Bale highland towards the Borana district (see below), and the Ahl Madow scarp on the north side of The Horn.

Molecular data and species ages

The distinctive appearance of many Ethiopian highland birds may reflect strong directional selection caused by the unstable and harsh climate (Dorst & Roux 1972). A molecular study of the large genus *Serinus* (Arnaiz-Villena *et al.* 1999) suggested that this group radiated since the end of the Miocene. Unfortunately the study did not include any of the endemic species of the tropical Northeastern Subregion of Africa, but judging from phenetics, all the endemic species seem to cluster fairly closely with species which were studied, and therefore seem to represent recently derived branches. However, a few highland endemics may represent much deeper branches. This applies to the distinctive highland rail *Rougetius rougetti*, which, according to preliminary DNA analysis, is a deep split (together with the East African *Crecopsis egreria*) within the cosmopolitan *Rallus* clade (B. Slikas, pers. comm). The highland goose *Cyanochen cyanopterus* is assumed to be related to the Andean and Patagonian geese of the genus *Chloephaga* (Johnsgaard 1965).

Stable local conditions, which may have allowed persistence of relict taxa, possibly exist in the Boran foothills. This area is characterised by a low inter-annual variability in ground conditions compared with most parts of the Ethiopia highland (Fjeldså *et al.* 1997). Furthermore, this area falls between the biotic influence of the ecoclimatically unstable western savannas and the Somali desert, and it is isolated towards the south by the Turkana desert. Three of the five narrowly endemic birds of this area may be relicts. The lark *Heteromirafra sidamoensis* belongs to the *H. ruddi* superspecies, which has a relict/disjunct distribution in Africa. The very aberrant 'crow' *Zavattariornis* is usually assumed to be related to the *Podoces* groundjays of the Asiatic highlands, and this is also indicated by a preliminary analysis of mitochondrial DNA data (P. Ericson, pers. com.). According to a phylogen-

etic analysis of tauracos (Veron 1999), *Tauraco ruspolii* is basal to all the typical green tauracos, which suggests that it may represent an ancient relict population, maybe of Miocene age (rather than being sister to *T. leucotis*, which inhabits adjacent geographical areas, as suggested by Borghesi 1997).

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