

Biogeographical patterns of endemic terrestrial Afrotropical birds

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Abstract.

Biogeographical zones are described for terrestrial bird species endemic to the Afrotropics using up-to-date distributional data and multivariate statistical techniques. This provides an objective basis for a hierarchy of subregions, provinces and districts, based on a set of rules. Results are compared to previous studies at continental and regional scales. Biogeographical zones for passerines and non-passerines are compared and found to be similar. Peaks of species richness and narrow endemism are described for the six major subdivisions (subregions) identified by the cluster analysis. Coincidence of peaks of species richness and narrow endemism is found to be low, such that areas selected to represent high species richness tallies will often fail to represent narrow endemics. Strong regionalization of Afrotropical birds indicates the need to use a biogeographical framework in conservation priority setting exercises to ensure that unique, but species-poor, avifaunas are not neglected.

Key words. Afrotropical region, biogeography, birds, endemism, Ethiopian Region.

INTRODUCTION

The study of patterns of bird species distribution has a long history in Africa, ranging from the descriptive accounts by Chapin (1923, 1932) and Moreau (1966) to the use of multivariate techniques by Crowe and coworkers (terrestrial Afrotropical birds: Crowe & Crowe, 1982; Afrotropical waterbirds: Guillet & Crowe, 1985), Stuart et al. (montane forest birds, 1993), Diamond and coworkers (Afrotropical forest birds: Diamond & Hamilton, 1980; Diamond, 1985) and Williams et al. (1999). Using another approach FjeldsÅ and coworkers

(Fjeldså, 1993, 1994; Fjeldså & Lovett, 1997) used genetic distance based on the DNA/DNA hybridization data (Sibley & Ahlquist, 1990) to distinguish areas where ancient species persist from those where diversification is more intense or recent. Moreover, BirdLife International investigated areas where narrowly endemic birds congregate in Endemic Bird Areas (Stattersfield et al., 1998) and developed maps of avian biomes across all of Africa for their Important Bird Area project (Fishpool & Evans, 2001). The Crowe, Diamond, Fjeldså and Fishpool & Evans studies all used distributional data from the Atlas of speciation in African passerine birds (Hall & Moreau, 1970; Snow, 1978). The intervening two decades since the publication of these volumes have seen considerable improvement in knowledge of both the taxonomy and distribution of birds in subSaharan Africa. This paper aims to revisit the field of Afrotropical avifaunal biogeography through the use of a data base created through extensive literature searches on published distributional information.

A multivariate approach, similar to that of Crowe and coworkers, is used to describe geographical regions holding distinct and homogeneous avifaunas in the Afrotropics (sensu Chapin, 1923: 123). Comparisons are made with previous studies both at the continental (Chapin, 1932; Crowe & Crowe, 1982; Fishpool & Evans, 2001) and subregional (e.g. Benson & Irwin, 1966; Winterbottom, 1978; Diamond & Hamilton, 1980) scales. This analysis supplements the results of species turnover and biogeographical boundaries in Africa by Williams et al. (1999).

Peaks (or hotspots) of species richness and narrow endemism (as measured by indices of range-size rarity) are described and compared for avifaunal subregions in order to determine whether peaks of narrow endemism are due to mass effects (e.g. Gaston, 1994) or independent historical factors. Peaks are compared within subregions, which represent distinct avifaunas, in order to minimize the confounding effects that the large variation in species richness over the Afrotropical region could have on such comparisons. Description of overall patterns of species richness and narrow endemism for the Afrotropical Region are presented elsewhere (Brooks et al., 2001; de Klerk et al., 2002).

METHODS

The data base

Only the 1437 terrestrial bird species that are endemic to the Afrotropical mainland (continental Africa south of 20°N, termed subSaharan Africa) were included in the analyses as waterbirds, pelagic species and non-breeding migrants, and non-endemic species have been shown to have distributional patterns that differ from those of Afrotropical endemics (de Klerk et al., 2002). The full terrestrial species data base (including endemics, non-breeding migrants and nonendemics) was analysed, but the inclusion of non-breeding migrants and non-endemic residents were found to 'blur' fine-scale patterns in northern and eastern Africa where these two groups of species concentrate, as most of these species inhabit several biogeographical regions. Ideally, data would include abundance data, as few species may make up the majority of bird biomass in any community. However, these data are not currently available for all terrestrial bird species in the Afrotropics, and so analyses are based on presence-only data.

Although non-passerines do not form a monophyletic group, non-passerine (n = 427) and passerine (n = 1010) species are analysed as two subsets of the Afrotropical endemics, to facilitate comparison with results of Crowe & Crowe (1982). Distributional data for these

endemic terrestrial Afrotropical bird species were digitized as putative presence within 1 × 1 degree grid cells (c. 110 × 110 km) using Worldmap Software (Williams, 1997). The data base was developed by the FitzPatrick Institute of African Ornithology, University of Cape Town, and the Zoological Museum, University of Copenhagen between 1994 and 1997 from various published sources (see http://www.zmuc.dk/commonweb/research/biodata_sources_birds.htm for a full list of all reference material used to develop the data base). The January 1997 version was used for all the analyses performed here. Coastal grid cells are included if more than a quarter of their area is covered by land.

Taxonomy follows Sibley & Monroe (1990, 1993), which is based on the comprehensive molecular studies by Sibley & Ahlquist (1990) (henceforth referred to jointly as the 'Sibley compilations'). Another recent compilation covering all Afrotropical birds is that of Dowsett & Forbes-Watson (1993), which is based on the taxonomy presented in Dowsett & Dowsett-Lemaire (1993) (henceforth referred to jointly as the 'Dowsett compilations'). Specific taxonomic decisions in both the Sibley and the Dowsett compilations are contested (see Elgood, 1994; Stuart, 1995; references cited below), as will be the case with any new classification. The Sibley compilations were chosen despite numerous criticisms (e.g. Krajewski, 1991; O'Hara, 1991; Raikow, 1991; Peterson, 1992; for reviews of Sibley & Ahlquist, 1990; Siegel-Causey, 1992 for a review of Sibley & Monroe, 1990) since, overall, it agrees with lessons from more detailed molecular studies (numerous studies recently published or in progress). The Dowsett compilations, in contrast, represent a traditional application of the biological species concept, which tends to recognize fewer species (= 'lumping' sensu Hall & Moreau, 1970; see Brooke, 1994). Subsuming in one species multiple taxa, each with their own histories (Barrowclough, 1992), could camouflage informative patterns of speciation, and thereby reduce the precision of conservation priority analysis (Fjeldså, 2000).

Patterns of distribution

Distance index and cluster algorithm

The Bray–Curtis distance index (Bray & Curtis, 1957) is used as a measure of similarity (1 minus distance) to compare each grid cell to every other grid cell based on its species composition (e.g. Everitt, 1993). The Bray–Curtis measure is used as it does not consider conjoint absences (Sneath & Sokal, 1973; Krebs, 1989), which would have been inappropriate in this study as data are based on presence-only information and do not include confirmed absence information. A hierarchical classification algorithm is 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 (Gauch, 1982). Choice of appropriate algorithm is largely determined by the type of input data (Everitt, 1993). Hands & Everitt (1987) found that for binary data, with clusters of different sizes, centroid algorithms performed best. Hence an UPGMC (unweighted pair-group method using centroid) (Sneath & Sokal, 1973) algorithm was applied. BMDP-2 software (Dixon, 1990) was used to implement both the Bray–Curtis distance measure and the UPGMC classification algorithm.

Cluster validity — cluster size, number of clusters, similarity value

The decision as to which of the clusters identified by the classification algorithm constitute useful biogeographical entities can be reached in a number of ways. One

approach is to define 'stopping rules', such as 'minimum group size', where a cluster of the specified size will not actively be subdivided further (although smaller groups may be caused by the natural structure of the data), and 'maximum level of divisions' which specifies the number of groups to be formed (Hill, 1994: 33). These stopping rules have been applied to divisive algorithms, but the philosophy could also be applied to dendrograms generated by agglomerative methods. Another stopping rule is a 'set level of distance or similarity'. There are, however, no guidelines as to what minimum group size, maximum level of divisions, or particular distance or similarity level might be appropriate in any particular study, or what the effect of varying the values of the stopping rule may be. In addition, in a study region that shows great variation in species richness, such as the Afrotropics (de Klerk et al., 2002), such constant cut-off approaches may not be valid if the relationship between variation in species richness and these various cut-off approaches is not understood. For instance, the number of species present in an area can be expected to affect the strength of relationships between grid cells through determining the size of the available species pool from which such relations may be drawn.

Everitt (1993: 2) maintains that as any classification scheme simply represents a division of objects into groups based on a set of rules, such a classification is neither true nor false, and so should be judged on the usefulness of the results. Our purpose is to identify geographical regions of distinct and homogeneous avifaunas in the Afrotropics based on their complement of bird species. Consequently, this study assumes that there must be some number of bird species either restricted to, or strongly associated with, any particular biogeographical zone in order for it to be identified as a valid entity (*sensu* Crowe & Crowe, 1982). This study therefore defines zonerestricted species as those whose global distributions are largely restricted to a particular avifaunal zone. Zone-restricted species whose range edges coincide with a particular zone boundary are termed zone-associated. All calculations were performed using ARC/INFO GIS software (version 6.1.I., Environmental Systems Research Institute, Redlands, CA, USA).

The definition of zone-restricted or zoneassociated species necessitates the use of arbitrarily defined cut-off levels for which there are no hard and fast rules. Approaches vary from the 100% restrictedness in classic definitions of narrow endemism (Williams et al., 1996), to the 50% cutoff of the Braun–Blanquet floristic association method (e.g. Westhoff & van der Maarel, 1973). We investigated i) how the number of zonerestricted and zone-associated species defined were affected when the percentage cut-offs were varied at 5% intervals from 60% to 100%; ii) the relationship between the number of zonerestricted and zone-associated species per percentage cut-off, with zone size and zone species richness; and iii) how the number of zoneassociated species changed with the number of zone-restricted species defined. Large variations of grid cell species richness both within and between subregions confound these investigations. For example, there are some small zones with particularly high species richness (e.g. the Albertine Rift and East African Montane Provinces) and one or two very large zones with particularly low species richness (e.g. the Northern Arid Province). Therefore, no clear trends could be identified to guide cut-off definitions. The number of zone-restricted species identified dropped off sharply as the percentage cut-off was increased from 60 to 65 and from 65 to 70, whereafter it decreased more slowly. Consequently, the arbitrary cut-off of 70% was used. Due to biases in the data it is not appropriate to implement a cut-off in an absolute fashion, and definition was therefore guided by the distributions of the individual species. Biases result from the scale (each grid cell represents c. 110 × 110 km) of the data and mapping factors that cause a species to appear more widespread than it in fact is. These include errors of commission (that is,

species being represented as present where they do not occur) (e.g. Gelderblom & Bronner, 1995), which arise despite ranges being conservatively interpolated from point data, very narrowly distributed species' range evenly straddling a line of latitude or longitude (which would then be included as present in both grid cells either side of the line of latitude or longitude). An attempt to correct for this bias was made by plotting very restricted species from verified point records only.

We decided to recognize any zone that can be defined by the existence of a zone-restricted or zone-associated species. The reasoning is that if the species evolved in situ, then there may well be a biogeographical process of interest related to such a zone.

The broadest avifaunal grouping recognized is a subregion. These are subdivided into provinces, which in turn may be subdivided into districts. Usage of the terms subregion, province and district loosely follows Crowe & Crowe (1982). However, whereas their usage of these terms corresponded specifically to clusters identified by genera, species and subspecies, respectively, no such taxonomic approach to zone classification is inferred in the present study. 'Zone' is used as a generic term for any cluster of grid cells, whether it be a subregion, province or district.

Patterns and peaks

Patterns and peaks of species richness and narrow endemism highlight areas that support relatively more species in total or more rangerestricted species, which may indicate unique combinations of current environmental conditions, or may indicate historical forces. Either causal force will need to be considered when proactive conservation strategies are developed. Maps of peaks of species richness and narrow endemism are produced for species associated with a subregion using Worldmap software (Williams, 1997). Narrow endemism can be measured as a discontinuous or continuous variable (see Gaston, 1994 for discussion). The rare-quartile is used as a discontinuous measure (Gaston, 1994) and range-size rarity, calculated here as weighted richness by inverse range-size rarity (Csuti et al., 1997), is used as a continuous measure. Results for range-size rarity and the rare-quartile gave similar results and so only results for the more frequently used range-size rarity are presented here. Peaks, or hotspots, are usually defined as a certain percentage of cells that score highest according to a particular biodiversity measure (e.g. Burgess et al., 2000). The 5% criterion is an arbitrary, but frequently used, cut-off level (e.g. Myers, 1988, 1990; Prendergast et al., 1993; Lombard, 1995; Williams et al., 1996), and is the percentage used in this study to define peaks.

Peaks of species richness and narrow endemism are compared by calculating the Phi (or Cramer) coefficient (Zar, 1984) to test the magnitude of coincidence of the relationships, and the significance of the relationship is assessed by the χ^2 with Yates's correction for continuity (or Fisher's exact test depending on frequency size) (Zar, 1984).

RESULTS

Six subregions containing a total of 36 zones (20 districts and 16 provinces) are identified for terrestrial birds endemic to the Afrotropical mainland by the cluster analysis and supported by zonerestricted and zone-associated species (Fig. 1a). Complete lists of zone-

associated and zonerestricted species are appended to this reference in <http://www.zmuc.dk/VerWeb/STAFF/jf2.htm>.

Most subregions are defined at a Bray–Curtis distance (BC) of between 0.4 and 0.5 (Fig. 1b), with the exception of the Northern Arid subregion, which forms a cluster at 0.75. Note that because Bray–Curtis is a distance measure, the smaller the figure, the greater the similarity. The North-eastern and Northern Savanna subregions are the most closely related, clustering at BC = 0.53. The North-eastern subregion is identified at BC = 0.50, and the Northern Savanna subregion at BC = 0.52. The Southern Savanna subregion (BC = 0.46) joins the North-eastern and Northern Savanna grouping at BC = 0.57, followed by the Guinea–Congolian subregion (BC = 0.45) at BC = 0.60, South-western subregion (BC = 0.43) at BC = 0.65, and finally the Northern Arid subregion (BC = 0.84) at BC = 0.88.

Passerines and non-passerines both identify 29 zones. Passerine (p) zones are not, on average, defined more strongly than non-passerine (np) zones (average BC = 0.34 vs. 0.31; compare Fig. 2a,b). Passerines define the South-western (BC(p) = 0.45; BC(np) = 0.55) and North-eastern subregions (BC(p) = c. 0.35; BC(np) = 0.55) more strongly, while non-passerines define the Southern Savanna (BC(p) = c. 0.55; BC(np) = 0.45) and Northern Arid subregions (BC(p) = c. 0.82; BC(np) = 0.75) more strongly. Some differences are seen between the zones defined for non-passerines from those defined for passerines, and from either of these with the full data base. Classification results of the full data base are determined largely by the numerically dominant passerines (1010 passerine species vs. 427 non-passerine species).

Subregions are subdivided into two (Northern Arid subregion) to 10 (Southern Savanna subregion) zones. The most speciose zone is the Albertine Rift Province with 835 species (58.2% of all species in the data base in 44 grid cells; Table 1), and it also contains the greatest total number of zone-restricted species (48). The East African Montane Province follows with 36 zone-restricted species, and the Ethiopian Highlands Province with 25 zone-restricted species. However, the Mt Cameroon District contains the highest species numbers in relation to area, namely an average of 69.5 species per grid cell, vs. 19 species per grid cell in the Albertine Rift Province (Table 1).

In the North-eastern subregion, peaks of species richness are concentrated in the Somali–Masai lowlands, whereas narrow endemism is concentrated in the north-western Ethiopian Highlands (Fig. 3a).

In the Northern Savanna subregion, the Bamenda Highlands and the Obudu Plateau (which extend inland from the Cameroon Mountains) are highlighted as a peak of narrow endemism (Fig. 3b). Other narrow endemism peaks occur in the mountains of West Africa, the lowlands around the Niger Inundation, Lake Chad and the Sudd (Bahr el Jebel), as well as in the forest–savanna transitions in the Upper Guinea and in the Ubangi–Uelle savanna. Species richness is concentrated in the broad band of Sudanian woodland which runs north-west to south-east, with an isolated peak occurring in the region of the Sudd and woodland-savanna transition to the south thereof.

Narrow endemism in the Southern Savanna subregion is concentrated on the mountains from southern Kenya through Tanzania and Malawi and south to the Chimanimani Mountains, and west on the Manika Plateau in the south-east of the Democratic Republic of Congo and the Angolan Escarpment (Fig. 3c). There is also a peak in the coastal forest of South Africa.

The Guinea–Congolian subregion comprises the main tracts of African lowland rain forest together with adjacent montane complexes of the Albertine Rift and Mt Cameroon–Bamenda Highlands complex (Fig. 3d). The Disjunct District is identified by the cluster analysis because of the similar avifaunas in the northwestern and north-eastern parts of the Congolian rain forest. The Ituri–Albertine area forms the eastern border of the Guinea–Congolian subregion and falls within an area of complex topography, which represents a ‘melting pot’ where a number of avifaunas meet (Fanshawe & Bennun, 1991), including those of lowland, northern savannas and montane forest, with many species shared with the mountains of the Southern Savannah subregion.

Narrow endemism in the South-western subregion is concentrated in this district in the Cape Fold Mountains, extending east to Drakensberg– Lesotho Highland system and north into the Namib coast and adjacent hills and plateau (Fig. 3e). Species richness is concentrated in the Karoo and an area of high species replacement (see Williams et al., 1999) in the transition zone between winter and summer rains.

The species-poor Northern Arid subregion has seven zone-restricted species, all of which occur in the Horn of Africa Province, which stretches from the Somali coast inland to the Haud Plateau. Noteworthy species richness peaks occur in the This is somewhat to be expected due to its extremely arid character, and it is defined by default as it has no characteristic or zonerestricted species, and so is defined by the boundaries of neighbouring zones which do have characteristic or zone-restricted species. The similarity between the Horn of Africa and Northern Arid Provinces is due mainly to the depauperate faunas but also a few shared species. Interestingly, a number of ‘arid corridor plant species’ extend into both these zones (Thulin, 1994).

Coincidence of peaks of narrow endemism and species richness, as measured by ϕ^2 , range from 0.04 to 0.25 (Table 2). These results show that peaks of narrow endemism are not strongly coincident with peaks of species richness.

DISCUSSION

The present analysis confirms that distributional patterns of birds in the Afrotropics demonstrate discrete groupings of homogeneous avifaunas, which are separated by transition zones with high turnover of species (i.e. replacement of one avifauna by another, *sensu* Whittaker, 1960). These transitional zones are characterized by both high scores of species range-edges and species replacement (Williams et al., 1999). The major subregional divisions suggested by the cluster analysis agree well with the results from a divisive classification technique (Williams et al., 1999), indicating that results presented in this study are robust to different hierarchical algorithm techniques. These results are also well supported by fieldbased studies conducted at localized scale, such as those for Ethiopia (Urban & Brown, 1971), Kenya (Muriuki et al., 1997), the Brachystegia belt (Benson & Irwin, 1966), Angola (Hall, 1960; Traylor, 1963), the Guinea–Congolian subregion (Diamond & Hamilton, 1980) and the Southwestern subregion (Winterbottom, 1978). Specific differences are outlined in de Klerk (1998).

Differences in the results obtained by this study and previous studies conducted at a continental extent are largely due to the differences in scale at which the studies were conducted, as well as differences in methods and goals. For instance, the coarser scale of the Crowe & Crowe (1982) study, which used a 4-degree grid can explain why their non-

passerine scheme did not distinguish the Namib District, which this study identified as only three 1-degree grid cells. Again, the identification of the Dahomey gap merely as a 'dip' by the Crowe & Crowe (1982) scheme rather than a discrete break, as was identified by our study, is probably also due to the coarser scale of their study.

The fact that our scheme identifies twice as many divisions as did Chapin (1932), as well as the marked differences in subdivision of subregions and affinities among zones, is probably an effect of scale combined with methodology and more detailed knowledge of bird distributions. Chapin's work was published before the Atlases of Speciation (Hall & Moreau, 1970; Snow, 1978) were available, and his methodology 'attempted to follow [avifaunal divisions of the Congo] into adjacent countries and improve upon the maps of Wallace, Reichenow, and Sharpe' (Chapin, 1932: 89). His methodology specifically explains the case of the inclusion of the northern forestsavanna transition into the forest subregion (Chapin's West African subregion or our Guinea–Congolian subregion), rather than into a savanna subregion (his East and South African subregion or our Northern Savanna subregion), as suggested in this study.

Differences between the African IBA biome map (Fishpool & Evans, 2001) and our study simply reflect the different approaches and aims of these two studies: Fishpool & Evans (2001) apply criteria at a continental or global scale to develop broad-scale biome restricted species lists, whereas our study aimed to identify unique avifaunas at a finer scale. The African IBA biome map identified montane avifaunal components explicitly as one Afrotropical Highlands biome, whereas our study is not always able to distinguish between distinct avifaunas that may occur at different altitudes within the same grid cells, or within riverine forest habitat. For instance, the avifaunas of the Eastern Arc Mountains were not distinguished from that of the surrounding Somali–Masai lowland steppe and Zambezi vegetation. Whether these grid cells are classified as containing an Eastern Arc or Somali–Masai avifauna depends largely on which taxa are analysed. Passerines emphasize the Eastern Arc montane elements while non-passerines emphasize the Somali–Masai lowland elements. However, those montane avifaunas that cover larger areas are identified as distinct from lowland avifaunas such as, e.g. the Angolan Highlands District and the Mt Cameroon, Albertine Rift and Ethiopian Highlands Provinces.

The primary divisions of the dendrogram are between the more mesic subregions (Northeastern, Southern Savanna, Northern Savanna and Guinea–Congolian) and the more arid subregions (South-western and Northern Arid). This has also been noted by Moreau (1935), Crowe & Crowe (1982), and Williams et al. (1999) and may be due largely to a number of species that occur widely in the Afrotropics except in the driest parts (e.g. *Ispidina picta*, *Halcyon senegalensis*, *Oxylophus levaillantii*, *Myioparus plumbeus* and *Ploceus cucullatus*), which increase the similarity of the mesic subregions, while simultaneously resulting in species 'drop outs' (i.e. species reaching the end of their ranges without being replaced by other species — see Williams et al., 1999) and hence lower species richness values of the more arid subregions. These trends of decreasing species richness result in low species richness of the South-western and Northern Arid subregions (total species richness = 477 and 206, respectively) compared to the more mesic subregions (e.g. total species richness of the Southern Savanna subregion = 1057 and of the Guinea Congolian subregion = 982). Low species richness acts to decrease the effective species pool from which relationships between zones can be formed. This reduces the strength of relationships between species-poor and species-rich subregions, and of relations among zones within species poor subregions, explaining why the arid subregion can be defined at such large Bray–Curtis distances and still represent valid avifaunal entities.

Passerines do not show finer-scale zonation than non-passerines (or stronger definition of zones on average), despite there being more than twice as many passerine as non-passerine species in the Afrotropics. Recent molecular evidence shows that passerines are as old as the major non-passerine groups and probably date well back in the Cretaceous, in the Gondwanan region (e.g. Ericson et al., 2002), and so both groups may well have been subjected to similar forces, as suggested by Crowe & Crowe (1982). In addition, it would appear that, especially in the rain forests, both non-passerines and passerine species are generally much older than was previously thought (Roy et al., 2000).

Differences between the passerine and nonpasserine schemes can be explained by specific species patterns. For example, the non-passerines include the Ethiopian Highlands in the Southern Savanna subregion, due to a number of nonpasserine *Acacia* savanna species, which have extended from the Southern Savanna subregion to the Ethiopian Rift (e.g. *Ardeotis kori* and *Pterocles gutteralis*). Non-passerines identify the Gabon District as part of the western portion of the Disjunct District. This is partly due to the lack of non-passerines restricted to the Gabon area, but also due to a number of non-passerine species that are restricted to the humid coastline of West Africa, from the Congo River north to the Guinea forests (e.g. *Centropus leucogaster*), which increase the similarity of the avifaunas in this area. The passerines, however, identify the Gabon District as a distinct entity, due partly to the presence of the zone-restricted *Ploceus subpersonatus*.

Analyses of large-scale patterns of variation in biodiversity indicate that a large amount of the variation in species richness can be explained by climate and coarse-scale topographic heterogeneity (see e.g. Balmford et al., 2001; Rahbek & Graves, 2001) constrained by physical boundaries (e.g. Jetz & Rahbek, 2001). However, if all patterns are due to current environment and topography, a neutral model of distribution would apply, and we would expect the range-restricted species to be nested within areas of high species richness due to mass effects (Prendergast et al., 1993; Gaston, 1994). In subSaharan Africa this only holds true at a coarse scale, and then only for a limited number of areas (de Klerk et al., 2002). The Guinea–Congolian subregion provides an example of where hotspots are nested at a broad scale in montane–lowland complexes which are characterized by localized areas of stability (Fjeldså et al. in press). However, even here exact coincidence of peaks of narrow endemism with peaks of species richness is low, with peaks of species richness being concentrated in areas characterized by higher total annual and mean monthly productivity values than rangerestrictedness hotspots. Range-restrictedness hotspots, in turn, have significantly higher topographical complexity (coefficient of variation of altitude) than do species richness hotspots (de Klerk, unpublished data). The idea that narrow endemism is concentrated in areas of topographical complexity, which is likely to confer localized climatic stability over short, medium and longterm climatic cycles, has been highlighted in other studies (e.g. Fjeldså, 1994; Fjeldså et al., 1997). In many areas, the mismatch between localities of peaks of species richness and narrow endemism are marked. For instance, in the North-eastern subregion narrow endemics are dispersed throughout the Ethiopian Highlands and adjacent Somalia–Masai lowlands, whereas species richness is concentrated only in the lowlands.

The strong regionalization of the Afrotropical avifauna means that conservation priorities cannot be focused only on species rich areas. Such an approach will neglect the unique and highly distinct avifaunas of the less species rich arid environments, such as those of the North-eastern and South-western subregions. Conservation priorities for Afrotropical birds must be set within a biogeographical framework, as has often been recommended by various studies (e.g. Udvardy, 1975; Emanuel et al., 1992; Turpie & Crowe, 1994; Turpie,

1995; Olson & Dinerstein, 1998). Setting conservation priorities for Afrotropical birds is additionally complicated by the lack of co-occurrence of narrow endemics (for example in the Ethiopian Highlands), such that many areas will be required to adequately represent narrow endemics (see Brooks et al., 2001). The low coincidence of peaks narrow of endemism with peaks of species richness, means that it is often not possible to identify areas that simultaneously cater for rare species as well as many widespread ones.

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Table 1 Zone area (no. cells/zone), absolute (spp. rich), percentage (% spp. rich) and relative species richness (rel spp. rich), and number (no. ends), percentage (% ends) and relative number of endemics (rel end), and number of characteristics species (no. chars) per avifaunal zone. Percentage species richness (% spp. rich) and zone-restricted species richness (% end) are the proportion of all species in the data base (1437). Relative species richness (rel spp. rich = no. spp./zone size) and relative zone-restricted species richness (rel end = no. ends/zone size) are the proportion of the respective avifaunal zone size (no. cells/zone).

<i>zone name</i>	<i>no. cells/ zone</i>	<i>spp rich</i>	<i>% spp rich</i>	<i>rel spp rich</i>	<i>no. ends</i>	<i>% end</i>	<i>rel end</i>	<i>no. char s</i>
<i>Northeastern Subregion</i>	162	629	43.8	3.9	41	-	-	4
Somalia-Masai	53	344	23.96	6.49	7	0.49	0.13	0
Tana-Jubba	19	391	27.23	20.58	3	0.21	0.16	0
Lake Turkana	22	480	33.43	21.82	5	0.28	0.18	1
Ethiopian Highlands	51	411	28.62	8.06	25	1.74	0.49	3
Danakil	17	199	13.86	11.71	1	0.07	0.06	0
<i>Northern Savanna Subregion</i>	552	689	47.9	1.2	14	-	-	3
West Central	191	395	27.51	2.07	4	0	0	3
East Central	112	354	24.65	3.16	1	0.07	0.01	0
Southeastern	57	432	30.08	7.58	3	0.14	0.04	0
Southwestern	51	541	37.67	10.61	5	0.35	0.10	0
Northern	141	227	15.81	1.61	1	0.07	0.01	0
<i>Southern Savanna Subregion</i>	467	1057	73.6	2.3	70	-	-	1
Drier Zambezi Woodland	87	535	37.26	6.15	9	0.35	0.06	0
Wetter Zambezi Woodland	75	483	33.64	6.44	4	0.28	0.05	0
Zanzibar-Inhambane	70	433	30.15	6.19	2	0.14	0.03	1
Angolan Highlands	48	420	29.25	8.75	3	0.07	0.02	0
Central Tanzanian	30	503	35.03	16.77	4	0.21	0.10	0
Zambezi Woodland-Savanna Transition	40	350	24.37	8.75	0	0	0	0
East African Montane	37	664	46.24	17.95	36	2.16	0.84	0
Outer Southern Congo Savanna	48	550	38.30	11.46	7	0.35	0.10	0
Tongaland-Pondoland	29	393	27.37	13.55	4	0.14	0.07	0
Benguela	3	207	14.42	69.00	1	0	0	0
<i>Guinea-Congolian Subregion</i>	319	982	68.3	3.1	69	-	-	3
Central	96	438	30.50	4.56	3	0.28	0.04	0
Disjunct	36	473	32.94	13.14	3	0	0	0
Gabon	27	376	26.18	13.93	1	0.07	0.04	0
Mt Cameroon	6	417	29.04	69.50	4	0.28	0.67	0
Inner Southern Congo Savanna	40	456	31.75	11.40	0	0	0	0
Lower Guinea	11	319	22.21	29.00	0	0	0	0
Upper Guinea	47	414	28.83	8.81	10	0.70	0.21	3
Ubangi-Uelle Savanna	12	345	24.03	28.75	0	0	0	0
Albertine Rift	44	835	58.15	18.98	48	3.13	1.02	0
<i>Southwestern Subregion</i>	228	477	33.2	2.1	17	-	-	8
Highveld	24	296	20.61	12.33	2	0.07	0.04	0
Karoo	53	211	14.69	3.98	2	0.14	0.04	2
Fynbos	19	215	14.97	11.32	2	0.14	0.11	5
Kalahari	112	420	29.25	3.75	9	0.35	0.04	1
Namib	20	174	12.12	8.70	2	0.07	0.05	0
<i>Northern Arid Subregion</i>	211	206	14.3	1.0	6	-	-	1
Northern Arid	171	94	6.55	0.55	0	0	0	0
Horn of Africa	40	148	10.31	3.70	6	0.42	0.15	1

Table 2 Phi comparisons of peaks of species richness and peaks of narrow endemism. Only those species which have more than 50% of their distribution restricted to a subregion are included in the analysis for that subregion

Subregion	Phi	p
Northeastern Subregion	0.12	<<0.05
Northern Savanna Subregion	0.09	<<0.05
Southern Savanna Subregion	0.12	<<0.05
Guinea-Congolian Subregion	0.25	<<0.05
Southwestern Subregion	0.04	<<0.05
Northern Arid Subregion	0.25	<<0.05

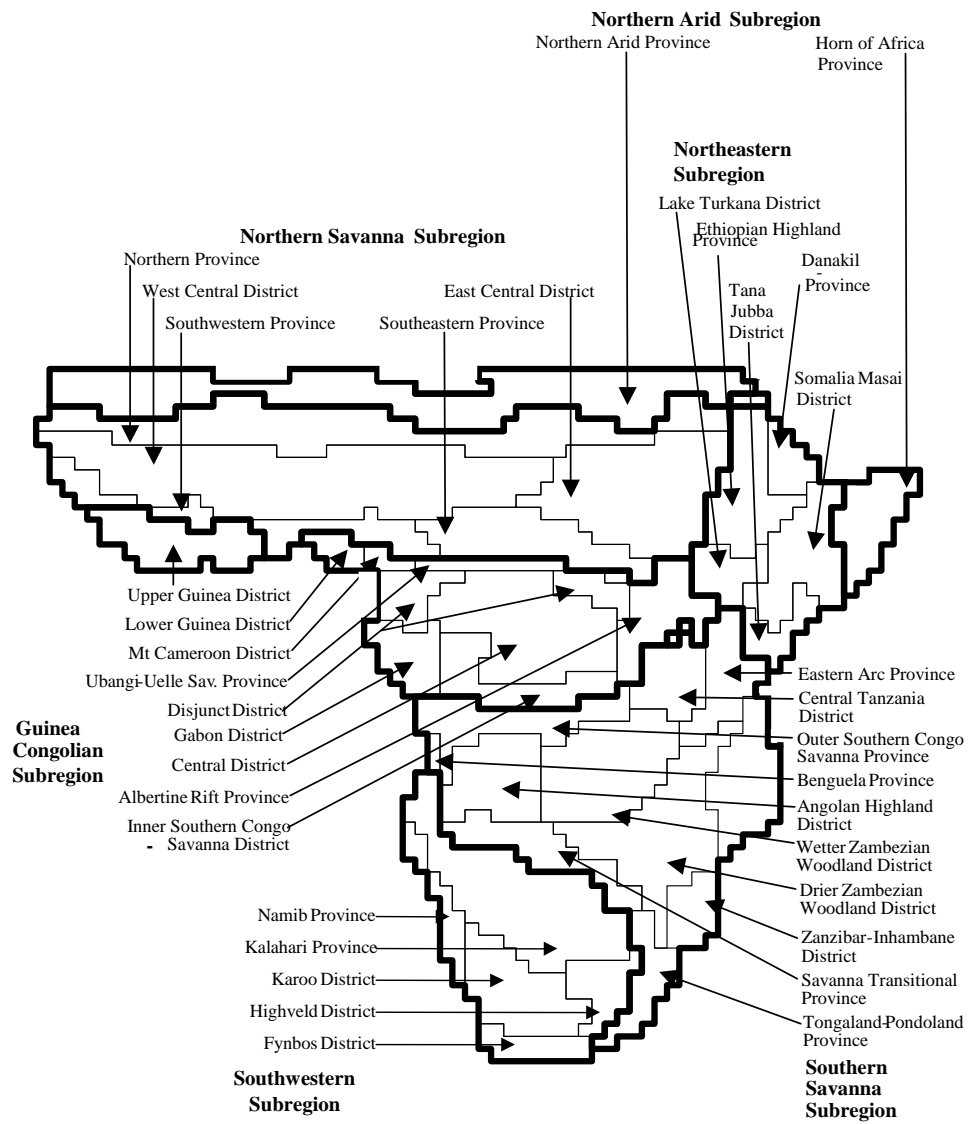


Fig 1(a)

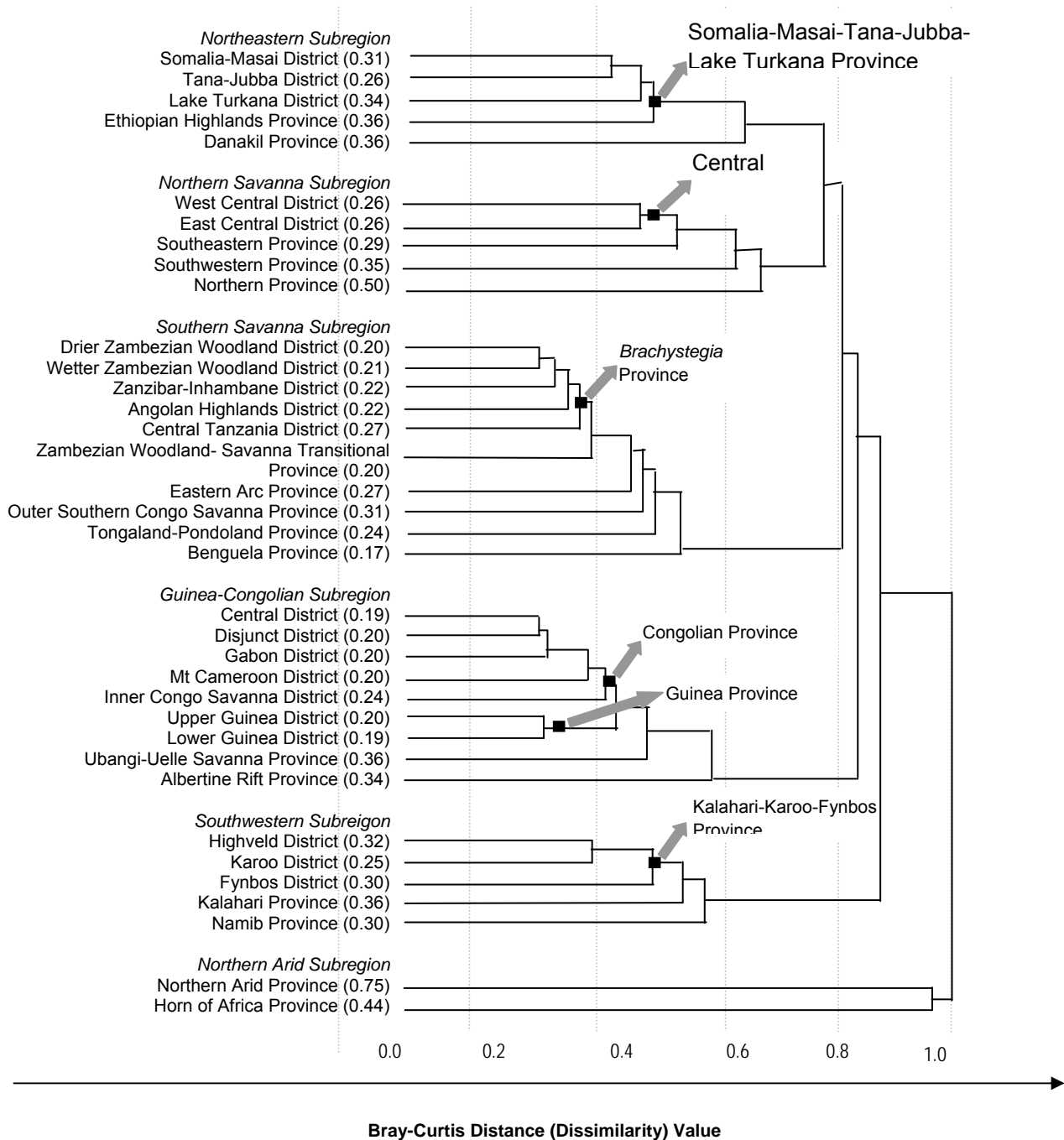


Fig 1(b)

Fig. 1 (a) Biogeographical zones and (b) dendrogram of relations between zones, defined for terrestrial species endemic to the Afrotropics using the Bray–Curtis distance index and the UPGMC (unweighted pairwise group method using Centroid) clustering algorithm.

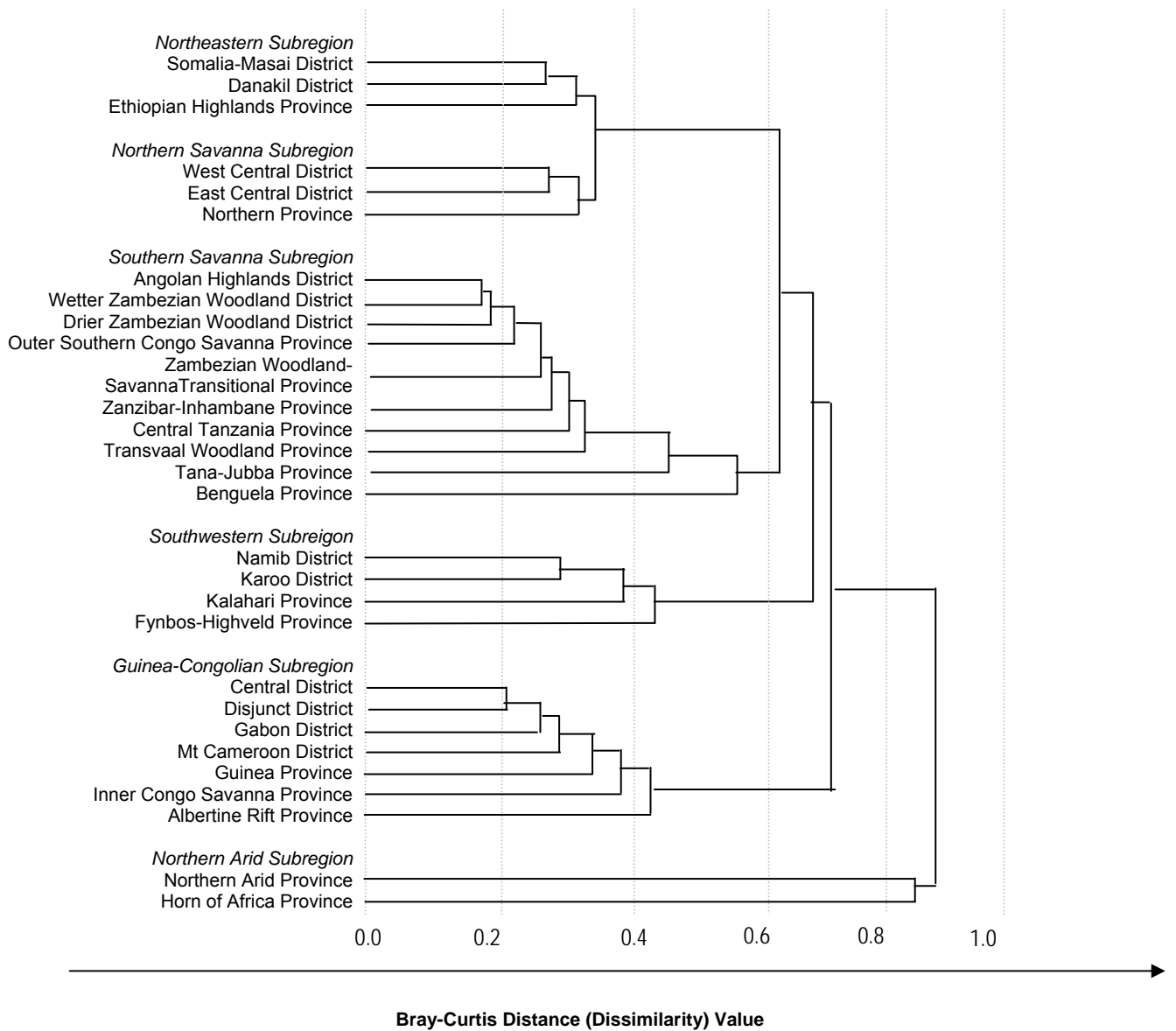


Fig. 2 (a)

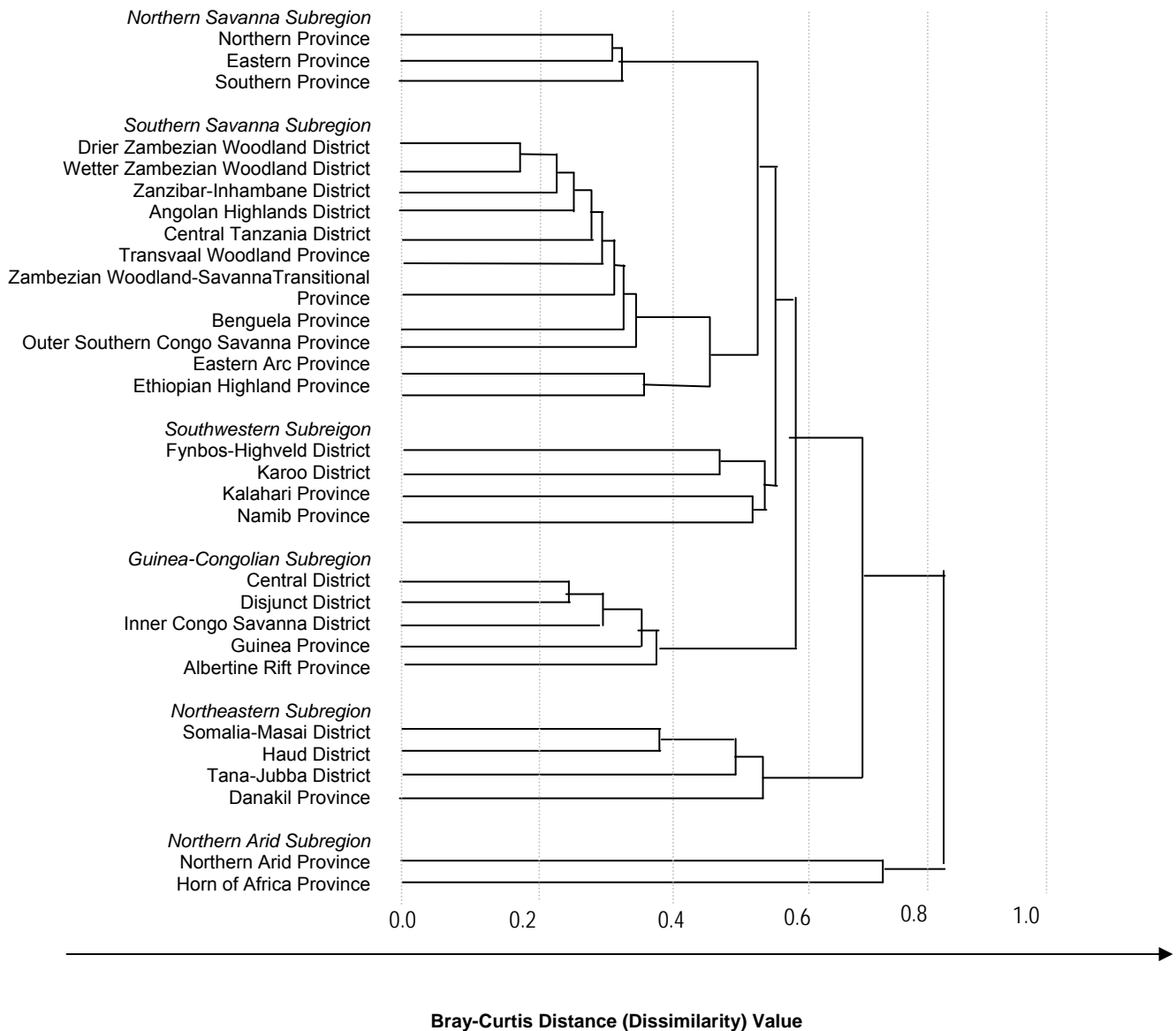
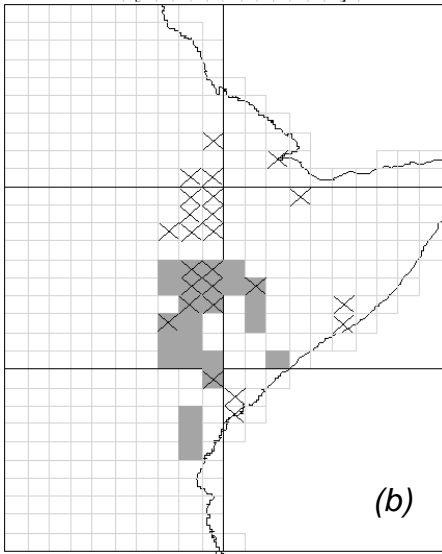
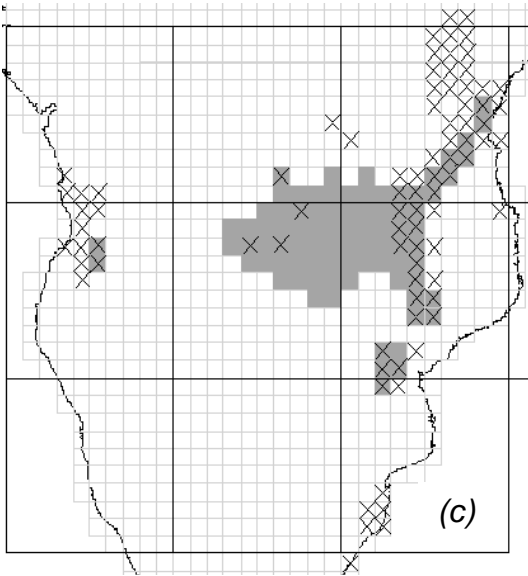
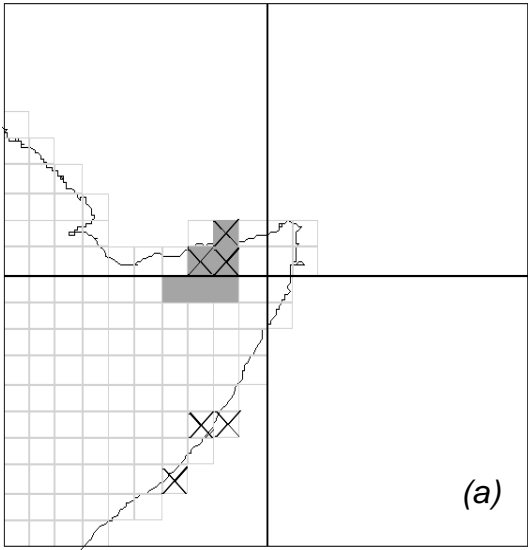


Fig. 2 (b)

Fig. 2 Dendrogram of relations between zones, defined for (a) terrestrial passerine and (b) non-passerine species endemic to the Afrotropics using the Bray–Curtis distance index and the UPGMC (unweighted pairwise group method using Centroid) clustering algorithm.



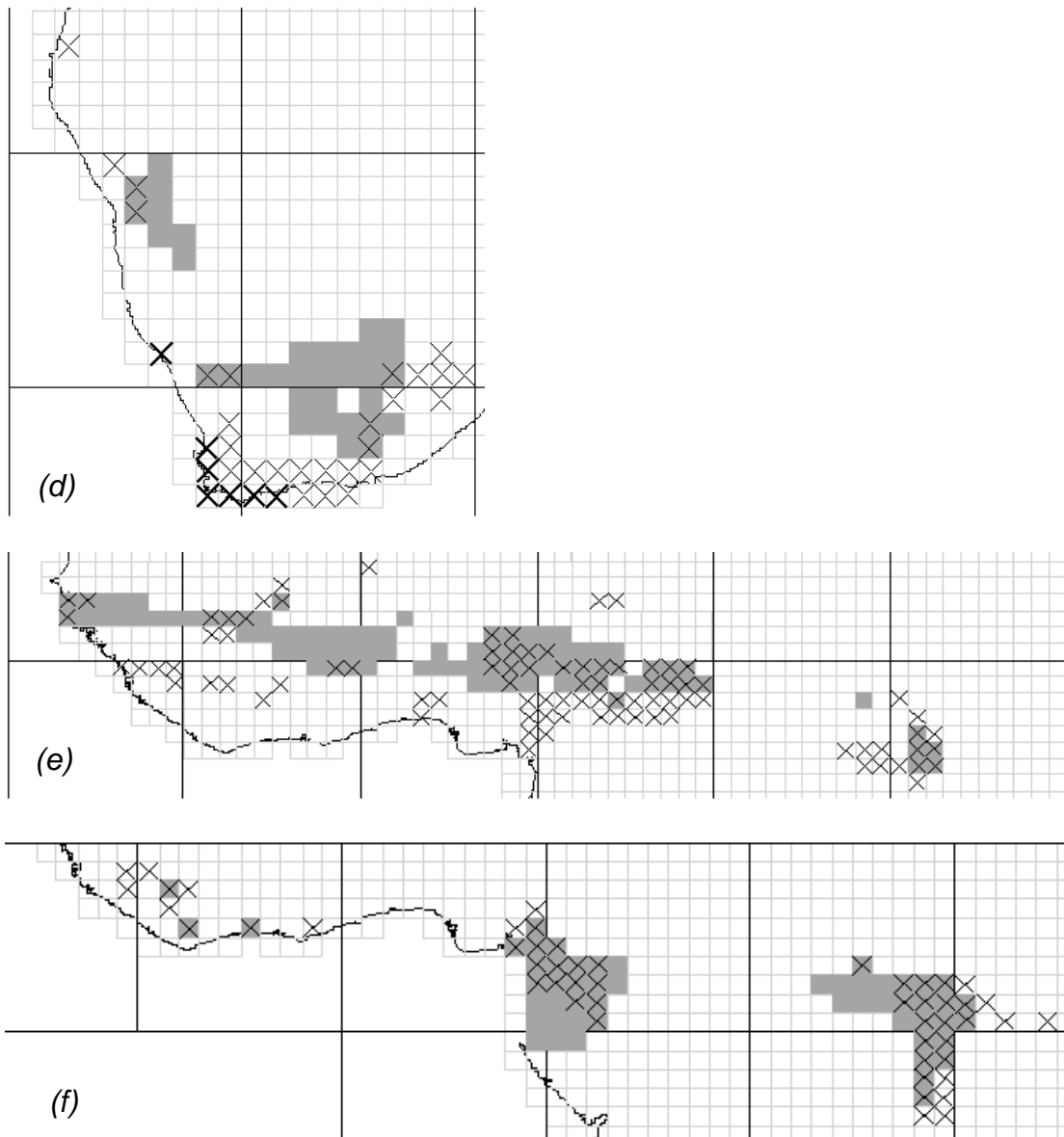


Fig. 3 Comparisons of peaks of species richness (solid grey) and narrow endemism (range-size rarity, e.g. Gaston, 1994) (hashed) for (a) the Northern Arid Subregion; (b) the Northeastern Subregion; (c) Southern Savanna Subregion; (d) the Southwestern Subregion; (e) Northern Savanna Subregion and (f) Guinea- Congolian Subregion.