

Patterns of species richness and narrow endemism of terrestrial bird species in the Afrotropical Region

Helen M. de Klerk^{1,2,3*}, Tim M. Crowe¹, Jon Fjeldså², and Neil D. Burgess^{2,4}

¹Percy FitzPatrick Institute, University of Cape Town, Rondebosch, 7701, South Africa

²Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

³Present address: Western Cape Nature Conservation Board – Scientific Services Division, Private Bag X5014, Stellenbosch, 7599, South Africa

⁴WWF-US Conservation Science Programme, 1250 24th Street NW, Washington, DC 20037-1132, USA.

*All correspondence should be sent to the senior author's present address.

E-mail: hdeklerk@cncink.wcape.gov.za

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Abstract

Geographical patterns and peaks of species richness and narrow endemism (defined by range-restrictedness and range-size rarity) are described for terrestrial Afrotropical birds and subsets thereof based on residency, endemism, and taxonomy. Species richness for residents and Afrotropical endemics (species globally restricted to sub-Saharan Africa) peaks along the mountains and adjacent lowlands of eastern and southern Africa. Isolated mountains in central and western Africa and the lowlands of the north-eastern Congo Basin (Ituri) are highlighted to a lesser degree. Peaks of narrow endemism occur in these areas as well as in the Ethiopian Highlands (particularly for non-passerines), Somalia (particularly for passerines), and the Angolan Escarpment. Within residents, patterns of species richness vary greatly between Afrotropical endemics (which concentrate in forests on mountains and adjacent lowlands, and the southern *Brachystegia* woodlands) and non-endemic residents (which concentrate in Sudanian woodlands and the Ethiopian Highlands). Patterns of species richness of residents (species that breed in the Afrotropics) and non-breeding migrants (non-breeding visitors to the Afrotropics) also show notable differences. The latter concentrate in areas close to the Palaearctic, which forms their distributional range centres. Patterns of species richness and narrow endemism for Afrotropical endemics show broad-scale coincidence within mountains or mountain-lowland complexes, particularly the Cameroon-Bamenda Highland system, East African rift system and Eastern Arc mountains. However, fine-scale coincidence of peaks of species richness and narrow endemism within these complexes is low. Narrow endemism peaks occur in areas of topographical complexity, which may have conferred localized climatic stability over short-, medium-, and long-term climatic cycles (*sensu* Fjeldsa, 1994; Fjeldsa et al., 1997), allowing these areas to act as 'species pumps'. Species accumulate in areas of high productivity. Lack of fine-scale coincidence of narrow endemism and species richness peaks have implications for conservation prioritization exercises.

INTRODUCTION

Basic descriptions of geographical patterns of species richness and narrow endemism are useful to set the scene for biogeographical studies and conservation prioritization exercises. In biogeographical studies, patterns and peaks of species richness highlight areas that support relatively more species. Biogeographical analyses can then be aimed at attempting to discern whether the richness is the result of current environmental or historical factors. The extent to which peaks of species richness and narrow endemism coincide may help elucidate whether centres of narrow endemism result from factors favouring speciation or simply from mass effects (e.g. Prendergast et al., 1993; Gaston, 1994), where the number of narrowly endemic species is expected to correlate well with the total species richness. Or are peaks in species richness due to the presence of narrowly distributed specialists that facilitate niche packing? Coincidence of a number of narrow endemics (indicating the probable presence of neo-endemics and relicts) with peaks of species richness may indicate centres of speciation (type II refugia, Crowe & Crowe,

1982; species pumps, Fjeldsa et al., 1997), although see Tuomisto & Ruokolainen (1997) for problems of using current distributional patterns to investigate historical events. For prioritization exercises, it is helpful, as a first step, to examine general patterns and peaks of species richness (which is frequently used as a surrogate of diversity, e.g. Margules & Usher, 1981 and references therein) and narrow endemics (which are often seen as priorities requiring special protection) (e.g. ICBP, 1992; Drinkrow & Cherry, 1995; Gelderblom & Bronner, 1995). It is also useful to have an idea of the extent to which patterns and peaks of species richness and narrow endemism are congruent. In other words, do areas that cater for many species also cater for endemics, or will areas that have a concentration of narrow endemics concurrently also represent large numbers of wider spread species?

Few studies to date have examined the patterns of species richness and/or narrow endemism of all terrestrial birds (both non-passerines and passerines) for the whole of the Afrotropical region. Most have concentrated on a specific region (Kenya: Fanshawe & Bennun, 1991; Muriuki et al., 1997; southern Africa: Liversidge, 1962; Winterbottom, 1978; Clancey, 1986), habitat (forests: Diamond & Hamilton, 1980; Stuart et al., 1993; Burgess et al., 2000; Brachystegia woodland: Benson & Irwin, 1966), or group of birds (forest passerines: Diamond & Hamilton, 1980; waterbirds: Guillet & Crowe, 1985; restricted-range birds: ICBP, 1992; Stattersfield et al., 1998). The analysis of the terrestrial Afrotropical avifauna by Crowe & Crowe (1982; based on data from Hall & Moreau, 1970, and Snow, 1978) were rather coarser, because of the analytical limitations of available computer technology. Other studies addressed specific questions and did not aim to provide a general description of patterns (e.g. Pomeroy & Ssekabiira, 1990; Pomeroy, 1993). During the last 4 years, researchers at the Percy FitzPatrick Institute of the University of Cape Town (South Africa) and the Ornithology Department of the Zoological Museum, Copenhagen (Denmark) have been compiling up-to-date distributional maps for all bird species in the Afrotropical region at a 18 grid scale of resolution in order to reinvestigate patterns and peaks of terrestrial Afrotropical avifaunal species richness and narrow endemism. Burgess et al. (1997) present some cursory results on general patterns as part of a short communication introducing this programme.

The species to be included in such a study need careful consideration: should non-breeding migrants be excluded, for example (Liversidge, 1962)? Even among residents, general patterns observed may be affected by whether a species' distribution is restricted to the region under study, or whether it is centred outside of the study region, and only extending to some degree into the study region. Results and conclusions may well be affected by such issues. Consequently, in this study, patterns of species richness are examined independently for residents and non-breeding migrants, and for Afrotropical endemics (species that have a global distribution restricted to the Afrotropical region) and nonendemics.

Previous studies analysed endemic non-passerines and passerines separately (Crowe & Crowe, 1982; Pomeroy & Ssekabiira, 1990; Pomeroy, 1993). They did so because it has been supposed

that non-passerines and passerines show differences in general distributional patterns, resulting from possible differences in selection pressures acting on these species, with the diversity of passerines being due to a recent (Pleistocene) and currently active radiation (Moreau, 1966). Recent molecular studies, however, are throwing the latter paradigm into question (Roy et al., 1997). Although not a natural split (non-passerines do not represent a monophyletic group), this study analyses endemic nonpasserines and passerines separately to facilitate comparison with previous studies.

This paper aims to: (1) describe general patterns and peaks of terrestrial bird species richness in the Afrotropical region in terms of (a) 'residency' (residents and non-breeding migrants) and (b) 'endemism' (endemics and non-endemics); (2) describe general patterns and peaks of narrow endemism for terrestrial bird species endemic to the Afrotropics; (3) compare peaks of species richness and narrow endemism for terrestrial bird species endemic to the Afrotropics; (4) assess whether passerines and non-passerines exhibit generally different patterns of species richness and narrow endemism.

METHODS

Study area

The study area comprises continental Africa south of 20°N, termed sub-Saharan Africa (e.g. IUCN Species Survival Commission, 1990), or the Afrotropical region Chapin, 1932; Hall & Moreau, 1970; (sensu Udvardy, 1975; Snow, 1978; IUCN, 1986; IUCN/UNEP, 1987). The flora and fauna of the Sahara and North Africa are usually considered to belong to the Palaearctic rather than Afrotropical region (e.g. Dowsett & Forbes-Watson, 1993; Brown, Urban & Newman, 1982), and so are not considered in this study.

Yemen, on the southern tip of the Arabian peninsula, is variably included (e.g. IUCN, 1986; Maclean, 1990; Dowsett & Forbes-Watson, 1993) or excluded (e.g. Hall & Moreau, 1970; Udvardy, 1975; IUCN/UNEP, 1987) in the Afrotropical region. Hall & Moreau (1970) state that they consider this minor extension of range 'not important for analysis of speciation patterns within Africa', which reasoning is followed for the purposes of this study.

Speciation and biogeography studies, and consequent development of conservation strategies for islands represent a special case, being affected by different forces to those acting on a continent (e.g. Hall & Moreau, 1970), and therefore are not considered in this study (sensu Pomeroy & Ssekabiira, 1990).

Taxonomy

Taxonomy follows Sibley & Monroe (1990, 1993), which is based on the work of Sibley & Ahlquist (1990) (here jointly referred to as the 'Sibley compilations'). The Sibley compilations represent 1 of

only 2 complete, recent works covering all birds occurring in the Afrotropics. The second work is that of Dowsett & Forbes-Watson (1993), which is based on the taxonomy presented in Dowsett & Dowsett-Lemaire (1993) (here jointly referred to as the 'Dowsett compilations'). Specific taxonomic decisions in both the Sibley and the Dowsett compilations are contested (see Elgood, 1994; Stuart, 1995; and references cited below), as will be true for 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 it, overall, agrees with lessons from recent, more detailed molecular studies (J. Fjeldsa, pers. obs.). The Dowsett compilations, in contrast, are based on a traditional application of the biological species concept (Dowsett & Forbes-Watson, 1993), a deficiency pointed out by Brooke (1994), which tends to recognize fewer species (= 'lumping' sensu Hall & Moreau, 1970), which has implications for both biogeographical and conservation studies. Subsuming in 1 species multiple taxa, each with their own histories (Barrowclough, 1992), could camouflage informative patterns of speciation, and reduce the precision of conservation priority analysis (Fjeldsa, 2000).

Species included in the database

There are 1646 terrestrial bird species that breed on the mainland of the Afrotropical region or that regularly visit this region as non-breeding migrants (either from the Palaearctic region or Madagascar) (Sibley & Monroe, 1990, 1993; Dowsett & Forbes-Watson, 1993; Handbooks of the birds of the Western Palaearctic, I±IX; see Appendix for individual references). Waterbirds, defined as those species that are dependent on nonmarine aquatic habitats for feeding, breeding (sensu Guillet & Crowe, 1985) and/or roosting, were excluded from analysis, as they have been shown to have different distributional patterns to those of terrestrial species (Moreau, 1966; Guillet & Crowe, 1985). Pelagic species, defined as those that do not breed, roost or feed on the continental mainland, were specifically excluded, as were vagrant species that, according to Dowsett & Forbes-Watson (1993), have been only recorded incidentally in the region.

Definition of life-history and taxonomic categories

Terrestrial birds occurring in the Afrotropics fall into several life-history categories (Table 1).

Residency

Species can be resident (sedentary or exhibit localized movement over short distances), intra-African migrants, or non-breeding migrants. Intra-African migrants were not separated from sedentary species as insufficient data are currently available to enable rigorous definition and mapping of such species, as was the case for 15 nonbreeding migrants that have local populations that breed in the Afrotropics (e.g. *Egretta garzetta*, *Plegadis falcinellus*, and *Sterna albifrons*).

Endemism

Resident species can have their entire global range restricted to the Afrotropics (termed 'endemics' in this study). Alternatively, they may be centred in the Afrotropics but extend some distance beyond the bounds to include North Africa (e.g. Moreau, 1966; followed by Brown et al., 1982), southern Arabia (e.g. IUCN, 1986; Maclean, 1990; Dowsett & Forbes-Watson, 1993), Madagascar, or the islands of Comoro, Aldabara, Seychelles and Socotra (P. A. R. Hockey, pers. comm.). Lastly, they may be centred outside of the Afrotropics, but extend to some degree into the Afrotropics. The last two groups are classed as non-endemics. Combinations of these life-history traits form a number of classes (see Table 1).

Taxonomy

The endemic terrestrial database was split into nonpasserines (427 species) and passerines (1010 species).

Distributional data: ideal data vs. availability

Ideal data for both biogeographical and conservation studies should consist of presence and confirmed absence data in the form of point locality data, together with abundance and population trend data (e.g. Harrison, 1989) that have been derived from even sampling effort across the entire region under study. No such data source exists for birds for the Afrotropical region as a whole, even though atlases of point data (Hall & Moreau, 1970; Snow, 1978; here collectively referred to as the 'Atlases of Speciation'), range map data (Birds of Africa) and gridded data (e.g. Lewis & Pomeroy, 1989; Harrison et al., 1997) are available for parts of the region. These different data types all have inherent shortcomings. As a result of the constraints of large gaps in point data for the Afrotropics, particularly in some of the former French territories in West Africa, northern Mozambique and eastern Angola (Hall & Moreau, 1970; Crowe & Crowe, 1982), it was decided to use conservatively developed range maps based on point data presented in the Atlases of Speciation and numerous other published sources (see Appendix) using current knowledge of habitat requirements and specificity. Careful attention was paid to possible discontinuities in ranges resulting from local habitat changes (e.g. the dry Zambezi River valley that provides a real break in many species ranges that otherwise occur widely throughout the Zambezian miombo woodland;

see for example, Benson, Irwin & White, 1962) and naturally patchy distributions of certain species (e.g. *Heliolais erythroptera* and *Apalis alticola*). In the latter case, species were mapped as localities, as were species with very restricted ranges. As suggested by various authors (e.g. Gelderblom & Bronner, 1995; Williams et al., 1996a), range maps are viewed as potential distributions, which should not be taken as confirmed presence data.

Digitization

The Afrotropical region was divided into 1961 18 x 18 grid cells (approximately 110km²110km² measured near the equator; Fig. 1). This scale was chosen in keeping with the presumed level of accuracy in the most poorly sampled areas (as described above). The latitudinal variation in the area of these grid cells is relatively small (e.g. Williams et al., 1996a). However, it must be noted that the land area of many coastal grid cells will be somewhat smaller, and that of grid cells encompassing mountains somewhat larger, than average. WORLDMAP software (ver. 4.17.01, Williams, 1997) was used to digitize individual bird distributions into the 18 grid cell system. ARC/INFO (ver 6.1.1.) and ArcView (3.1)(Environmental Systems Research Institute, Redlands, California) were used to create the various species group subsets and perform various analyses. WORLDMAP software was also used to determine patterns and hotspots of species richness and range-size rarity.

Analyses

Measuring species richness and narrow endemism

In this study, species richness is calculated simply as a count of the number of species present in a grid cell. It is calculated for all 6 of the species groups described in Table I. Narrow endemism can be defined as a continuous or discontinuous variable. Discontinuous measures include the rare-quartile, which gives greatest weight to the most restricted species (Gaston, 1994), and richness of species with a specified range-size, such as BirdLife International's 'restricted-range birds' that have a historical range-size of less than 50 000km² (ICBP, 1992). Discontinuous definitions can be arbitrary and assemblages usually comprise species exhibiting a variety of range-sizes, which seldom separate into discrete groupings (Gaston, 1994). Consequently, continuous measures of narrow endemism are often used, such as weighted richness by inverse rangesize, termed range-size rarity (e.g. Csuti et al., 1997), which although dominated by rare species, considers all species (e.g. Williams et al., 1996a). This ensures that some components of diversity are not 'missed' because they narrowly fail to meet some set cut-off (e.g. Crowe, 1993; Crowe & Brooke, 1993). This study used 2 measures of narrow endemism. Four 18 grid cells (48 400 km²) roughly equate to the BirdLife International's 50 000km² definition, such that species with a range-size of 4 or few grid cells were defined as range-restricted species, and used as a discontinuous measure of narrow endemism, termed range-restrictedness, for the purposes of this study. There are 83 species

terrestrial Afrotropical endemics which meet this criterion (15 non-passerines and 74 passerines). Range-size rarity (*sensu* Csuti et al., 1997) was used as a continuous measure of narrow endemism.

Narrow endemism values were not calculated for migrants or species not endemic to the Afrotropics, since range-size calculations within the Afrotropics for such species would only constitute a portion of their total ranges. This could result in a widespread species that has a distribution that only marginally reaches into the Afrotropics being artificially identified as rangerestricted (a narrow endemic).

Peaks of species richness and narrow endemism

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., 1996b). However, there was concern that an arbitrary cut-off may bias results of comparisons of hotspot sets. Consequently, a sensitivity analysis was conducted by defining hotspots at 5% intervals from 5% to 50% for species richness and narrow endemism. Only 5% hotspots are mapped in the figures.

Range-restricted species occupy 120 (6%) grid cells (termed range-restrictedness hotspots). Consequently, 6% hotspots were also calculated for species richness for comparison with the range-restricted hotspots. The sensitivity analysis for this comparison defined range-restricted species as the 25% most rangerestricted species. As results did not change as the range-size criterion was varied, these results are not presented.

Comparison of patterns and peaks

The Spearman rank correlation was used to test for significant similarities or differences (measures of congruence) in distributional patterns of species richness between database subsets (e.g. Zar, 1984). These correlations were calculated using STATISTICA software (release 5.1 A, for Windows, Statsoft, Tulsa, U.S.A.). Autocorrelation between grid cells within individual data bases exist, as all species barring single-cell endemics contribute to the species richness score of > 1 grid cell within a data base. As a result, grid cells do not represent truly independent data points. The effect of this autocorrelation on the results can be tested for by developing a frequency distribution of correlation values from randomly sampled subsets of grid cells within a particular data base (R. Navarro, pers. comm.). Frequency distributions were based on 1000 iterations. If the correlation value obtained for analysis of the full data set lies within the frequency distribution of the correlation values of the analysis of random samples, then it can be assumed that the effect of autocorrelation is not invalidating the results. Coefficients and two-tailed probabilities derived from

randomization tests are displayed alongside results for coefficients for the full databases. Analysis of congruence of patterns between non-passerines and passerines are additionally confounded by the fact that both groups have low species richness values over large areas that have arid climates. This coincidence of low species richness values in a large percentage of grid cells could result in correlation analyses showing significant and large coincidence of patterns regardless of whether there is good coincidence in areas of medium and high species richness. Consequently correlation analyses between non-passerines and passerines were also run on data subsets from which species-poor grid cells had been deleted. Species-poor grid cells were defined consecutively as the 5, 10, 15, 20, and 25% of grid cells with the lowest species richness scores. Correlation values changed by < 0.03 , such that coincidence of grid cells with low species richness values was not seen to have an effect on the correlation results, and so only results based on the full datasets are presented here.

There are autocorrelation problems between data sets used to calculate species richness and narrow endemism scores for grid cells so that the Spearman rank correlation could not be used to gauge the extent to which patterns of species richness and narrow endemics are related (interdependent). Autocorrelation in this instance results as the same species may contribute to both the species richness score and the narrow endemism score of a particular grid cell. These data sets also suffer from within data set autocorrelation described in the preceding section. Consequently, relations between species richness and narrow endemism (both measures) are gauged by calculating the Phi (or Cramer) coefficient (Zar, 1984) for hotspot matches. The Phi coefficient is also used to test the magnitude of coincidence, or 'correlation', of hotspots between species groups. The significance of the relationship can be assessed by considering the significance of the contingency table (namely X^2 with Yates correction for continuity or Fisher exact test, depending on frequency size) (Zar, 1984). Phi results for species group comparisons are displayed for each percentage hotspot definition to evaluate whether the percentage cut-off used to define hotspots influenced results

RESULTS

Patterns and peaks of species richness

Patterns of species richness for terrestrial birds in the Afrotropical region peak in the vicinity of the Ruwenzori mountains and adjacent Semliki lowlands, which grid cell contains 469 of the 1646 Afrotropical endemics (32.66%) (e.g. Fig. 2a, b). The Ruwenzori-Semliki grid cell falls within an area that generally shows a high species richness level stretching from the upper reaches of the Uelle River in the north of the Democratic Republic of Congo (DRC, formerly Zaire), along the Albertine Rift-Mitumba Chain and west of Lake Victoria through Uganda, the Kenyan highlands, and the Eastern Arc Mountains of Tanzania (as defined by Lovett, 1988), to the Nyika Plateau in

northern Malawi. Other areas of high species richness include isolated mountains in West Africa, namely Loma (between southern Guinea and north-eastern Sierra Leone), Nimba (between south-eastern Guinea and western Ivory Coast), and Macenta (south-eastern Guinea), as well as the Cameroon-Bameda Highland block and adjacent lowlands. Areas in central and southern Africa highlighted by species richness are the Angolan Escarpment, the *Brachystegia* woodlands of Zambia and Zimbabwe with particular peaks in southern DRC and north-eastern Angola, namely the Katanga and Mwinelunga (as defined by Fjeldsa et al., 1997), Mitumba Mountains/Lake Upemba area, the northern Muchinga Mountains (eastern Zambia), Mt. Mulanje (south-eastern Malawi), and the Chimanimani mountains (between eastern Zimbabwe and western Mozambique).

Residents vs. non-breeding migrants

Patterns and peaks of species richness of terrestrial residents and non-breeding migrants show negligible coincidence (Table 2, 3, Fig. 3a±d). What little coincidence is evident between the patterns is found along the Rift Valley system and the mountains just south thereof, and along the West African forest-savanna transition (compare Fig. 3a, b with Fig. 3c, d). High species richness tallies of residents not seen in nonbreeding migrants are found in highland/lowland complexes within the Guineo-Congolian forests, the eastern coastal vegetation mosaics of Zanzibar±Inhambane and Tongaland±Pondoland (Phytochoria nomenclature follows White, 1983), and the Highveld grassland and Drakensberg (South Africa). Non-breeding migrants concentrate in the Sudanian woodland belt that stretches across Africa below the Sahel, with particular concentrations in the western foothills of the Ethiopian Highlands and the Ethiopian Rift Valley, and from there south into the arid regions of Kenya, and to the north and east (Haud) of the Ethiopian Highlands. A minor concentration of non-breeding migrants in southern Africa is due to a few species that concentrate in the east of central and southern Africa (e.g. *Cuculus poliocephalus*, *Falco amurensis*, *Aquila pomaria*, *Locustella fluviatilis*, and *Hippolais olivetorum*) and the Kalahari (e.g. *Falco vespertinus*, *Lanius collurio*, and *L. minor*), and a migrant from Madagascar, *Cuculus rochii*.

Endemics vs. non-endemics resident

Patterns and peaks of species richness of endemics and non-endemic residents show low to non-significant coincidence (Table 2, 3, Fig. 4a-d). Non-endemic residents concentrate in the Sudanian woodlands and from the northern parts of the Ethiopian Highlands into the Somali coastal hills (Warsengalia), whereas endemics predominate in the Guineo-Congolian forests, the southern savanna's and Highveld grasslands of southern Africa (compare Fig. 4a, b with Fig. 4c, d). Patterns coincide along parts of the Rift Valley system.

Passerines vs. non-passerines

Overall patterns of species richness of endemic terrestrial passerines and non-passerines are correlated (Table 2, Figs 5a, 6a), although only just over half of the peaks (hotspots) of species richness of non-passerines and passerines coincide (Table 3, Figs 5b, 6b). Table 3 shows that the percentage used to define hotspots does not affect Phi results. There is a preponderance of non-passerines in the Ethiopian Highlands, Sudanian woodlands, and the eastern coastal vegetation mosaics of Zanzibar-Inhambane and Tongaland-Pondoland. Endemic terrestrial passerines are slightly more numerous than non-passerines at the ends of the Arid Corridor (e.g. van Zinderen Bakker, 1969) in the Somali-Masai bushland from Tanzania to Somalia and in the Kalahari and Karoo of South Africa and Botswana, as well as along the Angolan Escarpment and in the southeast of the DRC (Lake Pemba-Mitumba Mountain area and Mwinelunga centre).

Patterns and peaks of narrow endemism

As with species richness, peaks of narrow endemism (only calculated for species groups endemic to the Afrotropical region) occur along the Albertine Rift and in the Kenyan, northern Tanzanian, and Eastern Arc mountains, the Cameroon-Bamenda highland system, and the Angolan Escarpment (e.g. Figs. 4f, 5d, 6d, 7a-c). The Fynbos and Highveld of South Africa score more highly according to narrow endemism than they do according to total species richness (compare Fig. 4e, f with Fig. 4c, d). Although some West African mountains are highlighted by species richness peaks (described in the section 'patterns and peaks of species richness'), narrow endemism peaks accentuate these mountains more strongly, and identify additional mountains in this region (roughly in the region of the Bomi Hills and Mt. Nieta in Liberia). Non-passerines endemic to the Afrotropics have a greater concentration of narrow endemics in the Ethiopian Highlands than do passerines (cf. Figs 5c, d, 6c, d, 7b, c). Passerines, in turn, highlight the Angolan Escarpment, Katanga-Mwinelunga-Marungu centres, the Chimanimani range, the Warsengalia hills (northern Somalia) and isolated localities along the Somali coast (Fig. 5c, d) more strongly than do non-passerines.

Although patterns of range-size rarity for passerines are well correlated with those for non-passerines (Table 2), peaks of range-size rarity show only 50% coincidence (Table 3), and peaks of range-restrictedness are non-significant (Table 4).

Relations between peaks of species richness and narrow endemism

General patterns of species richness and range-size rarity appear to show quite high coincidence (e.g. compare Fig. 4c, d with Fig. 4e, f; Table 2). Important differences, however, do occur (Table 4), and coincidence of hotspots of species richness and narrow endemism are low (range-size rarity, Table 3) to nonexistent (range-restrictedness hotspots, Table 4). Hotspots of narrow endemism (both measures) not identified by hotspots of species richness are in the Ethiopian Highlands (particularly for non-passerines), the Warsengalia hills (northern Somalia), and isolated localities along the Somali coast (particularly for passerines) and Angolan Escarpment. Additional species richness peaks not highlighted by measures of narrow endemism include the lowlands of the north-eastern Congo basin (Ituri), the Mwinelunga centre and Chimanimani mountains.

DISCUSSION

Relations between peaks of species richness and narrow endemism

Coincidence of peaks of species richness and narrow endemism is low (whether narrow endemism is defined as range-size rarity or range-restrictedness). Although the exact locality of peaks of species richness and narrow endemism differ, most occur within mountains or mountain-lowland complexes that are highlighted for both measures, particularly the Cameroon-Bamenda Highland system, east African rift system and Eastern Arc mountains. There are a few range-restrictedness

hotspots that are not associated with these complexes, and these are in west Africa (in the region of the Dahomey Gap and the Niger River), the Angolan Escarpment and adjacent coastal plain, and the Ethiopian Highlands (including an extension east to the Ahmar Mountains and the Golis Range±Ahl Mado in northern Somalia). The few species richness hotspots that are disjunct from these complexes are concentrated in three areas, namely, around the Congo River mouth, the Chimanimani mountains (eastern Zimbabwe), and between the shore of Lake Malawi±Nyasa and Mt. Mulanje (Mozambique).

It is possible that certain areas within these complexes have acted as species pumps (sensu Fjeldsa et al., 1997), and that the species have consequently redistributed throughout these complexes, peaking in areas that currently are able to sustain high numbers of species. This idea is similar to that of Fjeldsa & Lovett (1997), and is supported by preliminary analysis of the environmental characteristics of these hotspots (de Klerk et al., pers. obs.), which show that species richness hotspots have significantly higher total annual and mean monthly productivity values (as measured by the NGDC Montly Generalized Global Vegetation Index from NOAA-9: Kinenman, Ohrenshcall, et al., 1992) than range-restrictedness hotspots. Range-restrictedness hotspots, in turn, have significantly higher topographical complexity (coefficient of variation of altitude) than do species richness hotspots. Fjeldsa and co-workers (Fjeldsa , 1994; Fjeldsa et al., 1997) suggest that topographical complexity is likely to confer localized climatic stability over short, medium, and long term climatic cycles. They also suggest that species become redistributed from the 'species pumps' into the lowlands, which are assumed to be more productive. However, species richness hotspots do not occur, on average, at lower altitudes than range-restrictedness hotspots (de Klerk et al., pers. obs.).

The lack of fine-scale coincidence between peaks of species richness and narrow endemism emphasize the importance of not basing conservation priorities on total species richness alone (e.g. ICBP, 1992; Pomeroy, 1993; Fjeldsa, 1994), as such a strategy is not effective for minimizing global extinction and for preserving speciation potential (Fjeldsa, 2000).

Non-passerines vs. passerines

This study found high correlation of overall species richness patterns between passerines and non-passerines, as did Crowe & Crowe (1982), and Pomeroy (1993). However, peaks of species richness show only roughly 50% correlation. Range-size rarity, which is influenced by species richness (Williams et al., 1996a), also shows strong overall correlation between passerines and non-passerines, although comparisons of peaks are still lower than comparisons of peaks of species richness, showing 30 to 50% coincidence. Range-restrictedness hotspots show very low coincidence of peaks for passerines and non-passerines. However, these latter comparisons are complicated by the fact that there are less than half as many non-passerine species as there are

passerine species, and the fact that on average, nonpasserines have larger range-sizes than passerines (300.76 ± 16.45 grid cells vs. 180.26 ± 7.35 grid cells; see also Pomeroy & Ssekabiira, 1990).

Although the exact localities of hotspots of species richness and narrow endemism for non-passerines do not coincide well with those for passerines, most of the hotspots occur close to each other, and mainly within the general complexes of Cameroon-Bamenda Highland system, East African rift system and Eastern Arc mountains. There is a preponderance of non-passerine species richness hotspots in the Ethiopian Highlands and Chimanimani mountains whereas passerine species richness hotspots are slightly more numerous along the Angolan Escarpment and in the southeast of the DRC (Lake Pemba-Mitumba Mountain area and Mwinelunga centre). However, when hotspots of range-size rarity are considered, the four aforementioned areas are identified by both non-passerines and passerines, although exact match localities within these areas are not always found. These observations do not show differences in distribution patterns that can support Moreau's (1966) assertion that current patterns of passerines and non-passerines reflect differences in selection pressures acting on these two 'groups'. Such differences can only be elucidated through detailed phylogenetic studies (e.g. Roy et al., 1997).

Residents vs. non-breeding migrants

Distributions of non-breeding migrants are centred in the Palaearctic. It is therefore not surprising that patterns of species richness of non-breeding migrants peak in the north of the Afrotropics, closest to their 'source', as predicted by island biogeography (MacArthur & Wilson, 1967) and areography (Rapoport, 1982) theory. This also explains why patterns of species richness of non-breeding migrants differ significantly from species resident in the Afrotropics, that have distributions centred inside of the Afrotropics.

Endemics vs. non-endemics resident

Patterns of species richness of Afrotropical endemics differ from those of species that are not endemic to the Afrotropics (non-endemics). There are few species that are classified as non-endemic, namely 97. Of these about half (50) are species that are chiefly distributed in the Palaearctic, only extending to some extent into the Afrotropics, and consequently their patterns of species richness will be determined by island biogeography as with non-breeding migrants. The remaining 47 species that are defined as non-endemics are chiefly associated with the arid systems that run across the north of the Afrotropics and east to the Arabian peninsula and/or north around the west coast of Africa to the Morocco, Algeria, Tunisia, and Liberia. These species add to the peak of species richness observed for non-endemic species in the northern savanna/sahel area, and further increase the difference of species richness patterns of non-endemics from those of Afrotropical endemics. Coincidence of high numbers of residents and migrants, and endemics

and non-endemic residents in the Rift Valley is due to the regions' high topographical and habitat diversity, and the role it plays as a major migration flyway (Fanshawe & Bennun, 1991).

Comparisons with other studies

The results of this study generally corroborate those of Crowe & Crowe (1982), which due to the coarser geographical scale of analysis did not identify certain species richness peaks identified here, namely the Ethiopian highlands, the mountains from the Eastern Arc to the Chimanimani's, the Congo-Zambezi watershed (Lake Upemba-Mitumba mountains, Marunga and Mwinelunga centres) and mountains in West Africa. Pomeroy (1993) and the Endemic Bird Area (EBA; ICBP, 1992; Stattersfield et al., 1998) study highlight all of these peaks. Four EBA's identified by the ICBP are not identified by this study, namely the Cape Region, the south-east African grasslands, the south-east African coast and south Zambia. The Cape Region, south-east African coast and south Zambia EBA's all have a configuration which covers more than four 18 cells, which is why they are not identified by this study. The majority of both species richness and narrow endemism peaks are also identified by studies based purely on forest birds (Diamond & Hamilton, 1980; Burgess et al., 2000). Surprisingly, some peaks identified by our study which must contain a number of forest species are not identified by Burgess et al. (2000), namely the Marunga and Mwinelunga centres, areas from north of Lake Victoria to central southern Kenya, and from north of Lake Malawi (Nyasa) south to the Chimanimani mountains. The fact that these areas are not identified as hotspots based on forest birds indicates that they have lower numbers of forest birds relative to other forest areas, a point borne out by Diamond & Hamilton (1980).

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TABLE I.

Residency, endemism, and taxonomic categories used to derive analysis groupings. BB = species that breed in the Afrotropical region, BP = Palaearctic migrants to the Afrotropical region that have local breeding populations within the Afrotropical region, PM = Palaearctic migrants to the Afrotropical region, and MM = migrants from Madagascar to the Afrotropical region. ES = species globally restricted to the Afrotropical region, ER = species that have a distribution centred in Afrotropical region but extending out of the Afrotropics, and NE = species that have a distribution centred outside the Afrotropics but extending into the Afrotropical region. NP = non-passerines, and P = passerines.

Residency	Endemism				Taxonomy	
Breeding residents (BB)	ES	NP	①	497	③	1437 (all endemics)
		P	②	1010		
	ER			47	④	97 (all non-endemic residents)
	NE			50		
Migrants	BP			15	⑤	112 (all migrants)
	PM			96		
	MM			1		

⑥ 1534 (all residents)

TABLE II.

Correlations between species richness patterns of species groups, and range-size rarity between passerines and non-passerines, using the Spearman rank correlation. Results from randomised subsample tests (as described in the Methods) are presented in italics and bracketed.

Comparison	Spearman rank rho (R_s for <i>randomised subsample</i>)	t (df)	Significance (2 tailed)
Species richness: Passerines vs. non-passerines	0.909 (<i>0.922</i>)	96.690 (1959)	$P \ll 0.01$ ($P = 0.001$)
Species richness: Endemics vs. non-endemic residents	0.157 (<i>0.221</i>)	7.015 (1959)	$P \ll 0.01$ ($P = 0.001$)
Species richness: Residents vs. migrants	0.266 (<i>0.131</i>)	12.212 (1959)	$P \ll 0.01$ ($P = 0.001$)
Range-size rarity: Passerines vs. non-passerines	0.813 (<i>0.822</i>)	89.629 (1959)	$P \ll 0.01$ ($P = 0.001$)

TABLE III.

Phi comparisons of hotspots between species groups and biodiversity measures. Significant values are in bold.

<i>Comparison</i>	<i>Percentage cut-off used to define hotpots</i>									
	5%	10	15	20	25	30	35	40	45	50
		%	%	%	%	%	%	%	%	%
<u>Species richness:</u>										
Passerines vs. non-passerines	.46	.45	.45	.49	.54	.55	.54	.51	.51	.53
	4	6	4	4	4	7	6	4	3	6
Endemics vs. non-endemic residents	.00	.02	.00	.01	.00	.00	.00	.00	.00	.00
	0	2	2	1	1	1	1	3	5	8
Residents vs. migrants	.00	.01	.01	.03	.03	.02	.01	.01	.01	.01
	1	4	2	5	4	9	5	2	1	
<u>Range-size rarity</u>										
Passerines vs. non-passerines	.33	.33	.37	.40	.42	.41	.47	.49	.54	.54
	8	1	5	6	9	7	8	4	3	1
<u>Species richness vs. Range-size rarity</u>										
Endemics	.44	.31	.31	.29	.31	.33	.39	.37	.38	.37
	4	8	8	1	0	7	6	8	9	6
Passerines	.37	.24	.19	.19	.26	.29	.34	.34	.34	.35
	2	4	0	8	9	6	4	9	7	4
Non-passerines	.33	.32	.33	.30	.33	.35	.37	.37	.36	.38
	6	4	6	3	5	4	8	6	1	6

TABLE IV.

Phi comparisons of hotspots between species groups and biodiversity measures. Significant values are in bold.

<i>Comparison</i>	<i>Percentage cut-off used to define hotspots</i>
	6%
<u>Species richness vs. Range-restricted hotspots</u>	
Endemics	.072
Passerines	.073
Non-passerines	.010
<u>Range-restricted hotspot</u>	
Passerines vs. non-passerines	.054

APPENDIX I. References used to compile distributional information for 1646 terrestrial bird species occurring on the Afrotropical mainland.

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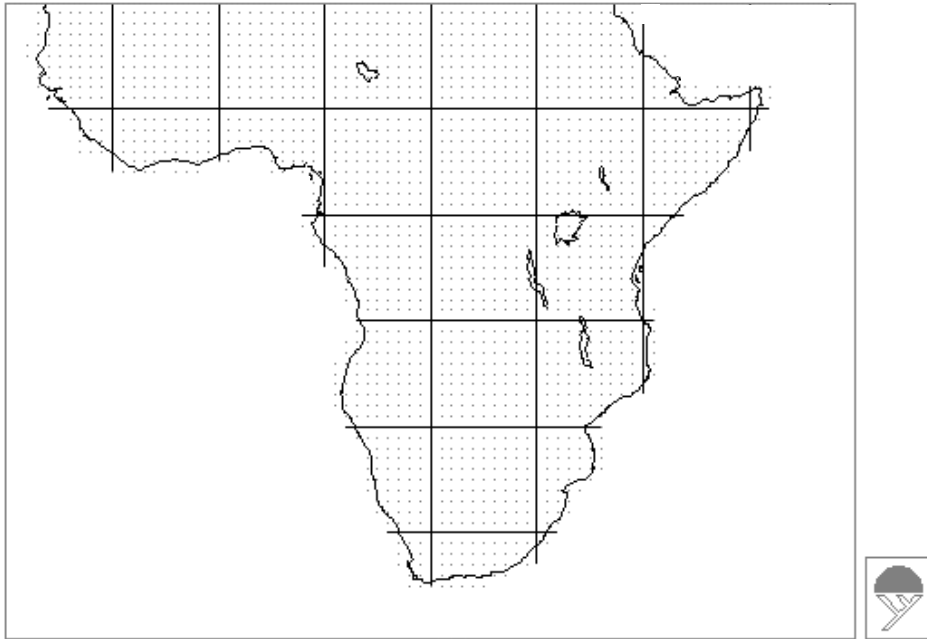
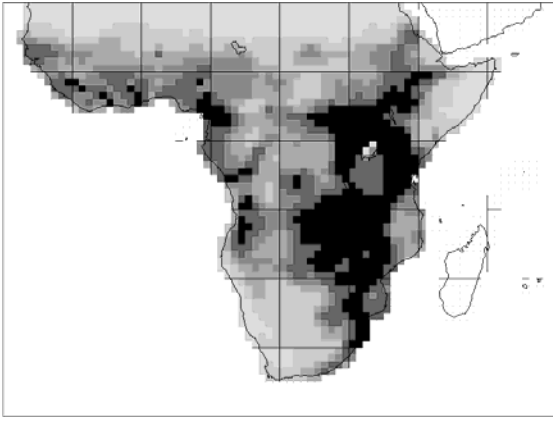
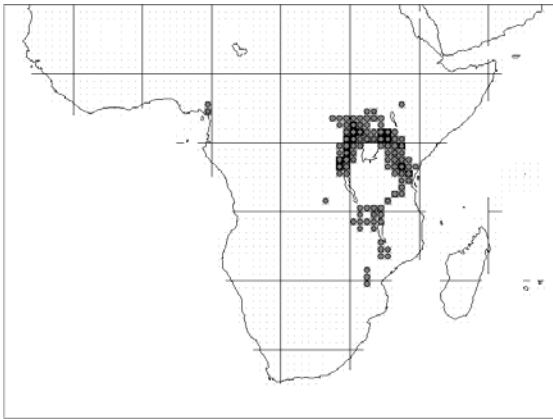


Fig. 1. The 1x 1 grid system used to digitise occurrence data for terrestrial bird species in the Afrotropical region.



(a)



(b)

Fig. 2. Patterns (a) and hotspots (b) of species richness for all terrestrial bird species occurring in the Afrotropics. Darkest shades represent highest scores graduating to lowest scores represented by lightest shades.

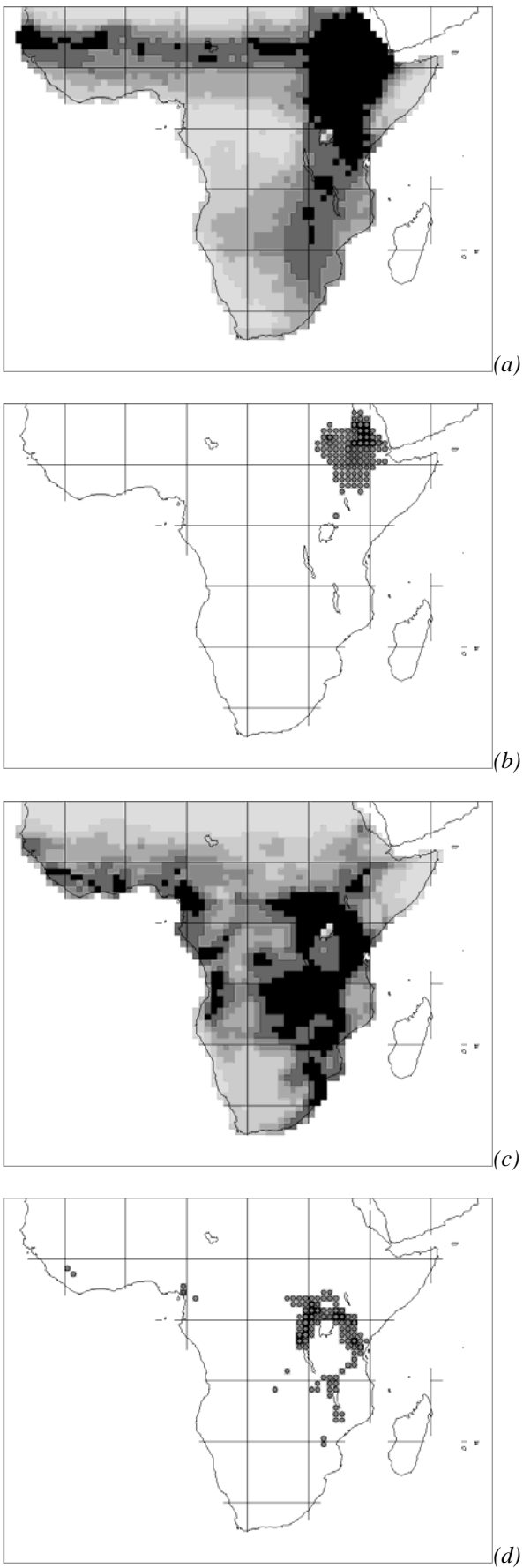
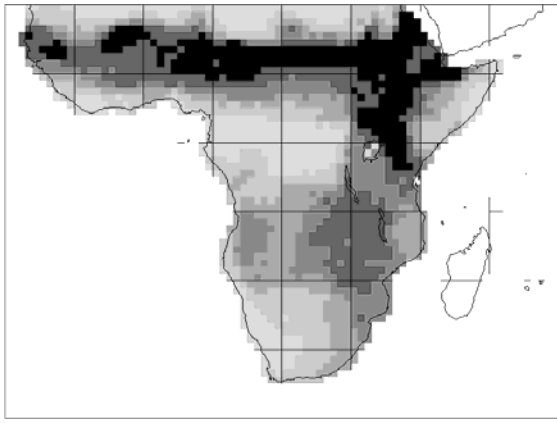
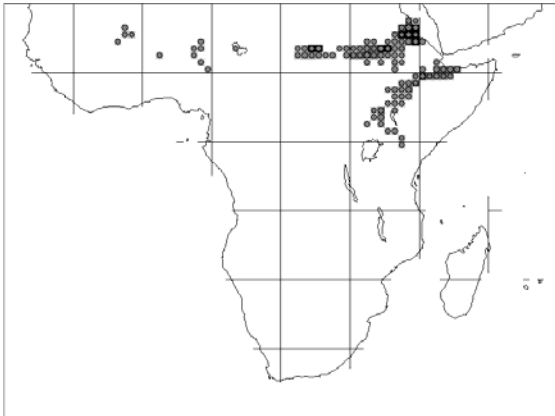


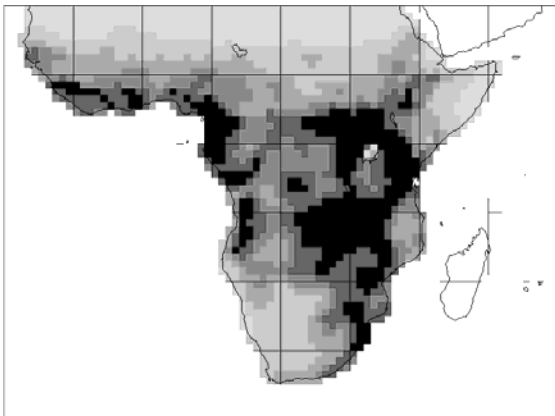
Fig. 3. Patterns and hotspots of species richness for terrestrial migrants to the Afrotropics (a) and (b), terrestrial residents in the Afrotropics (c) and (d). Darkest shades represent highest scores graduating to lowest scores represented by lightest shades.



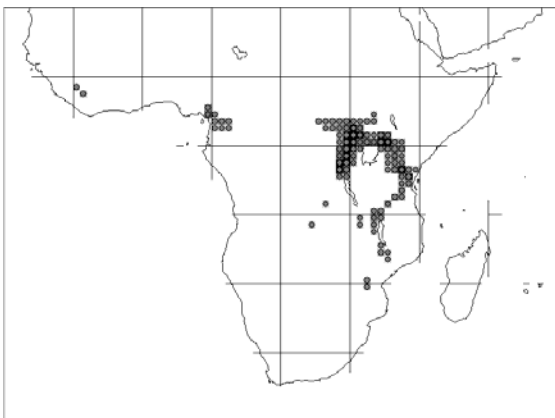
(a)



(b)



(c)



(d)

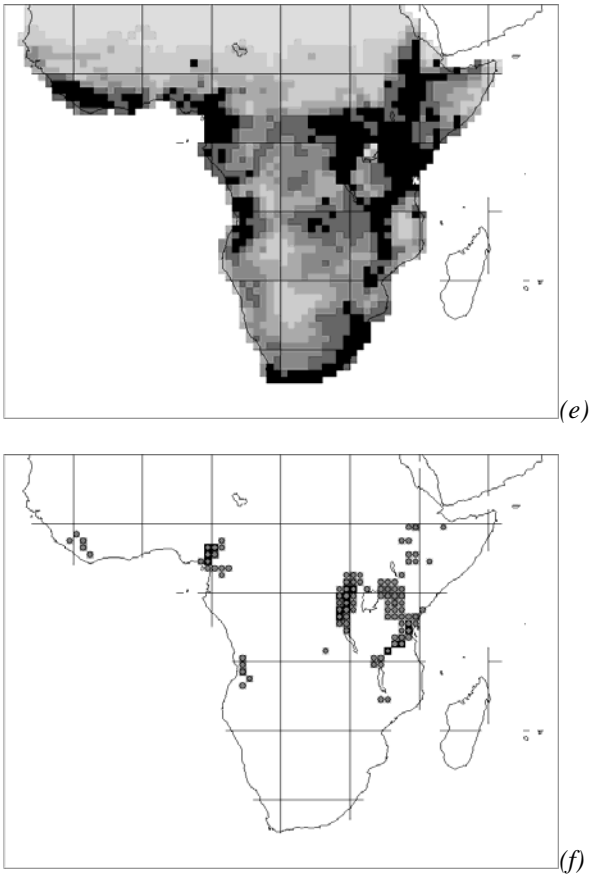


Fig. 4. Patterns and hotspots of species richness for non-endemic residents (a) and (b), terrestrial Afrotropical endemics (c) and (d). Patterns and hotspots of range-size rarity of terrestrial Afrotropical endemics (e) and (f). Darkest shades represent highest scores graduating to lowest scores represented by lightest shades.

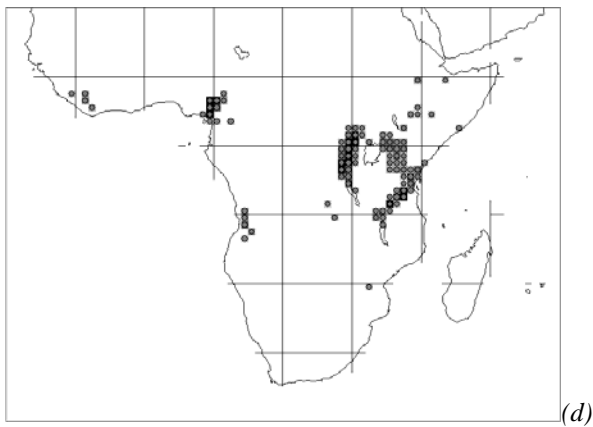
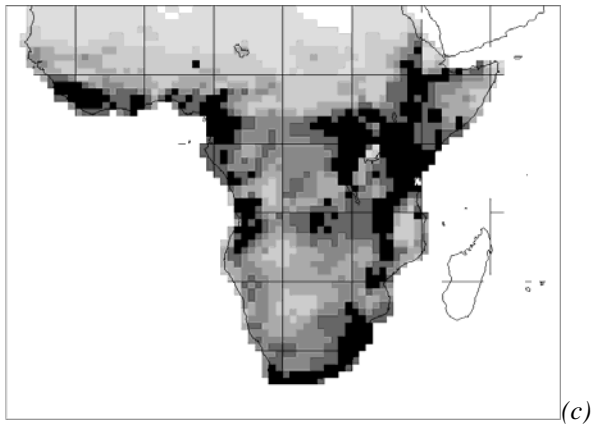
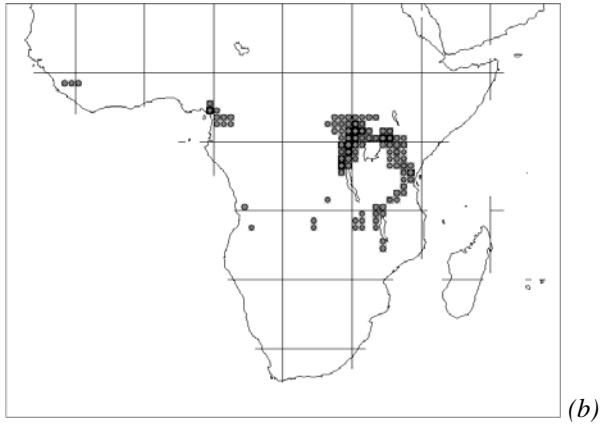
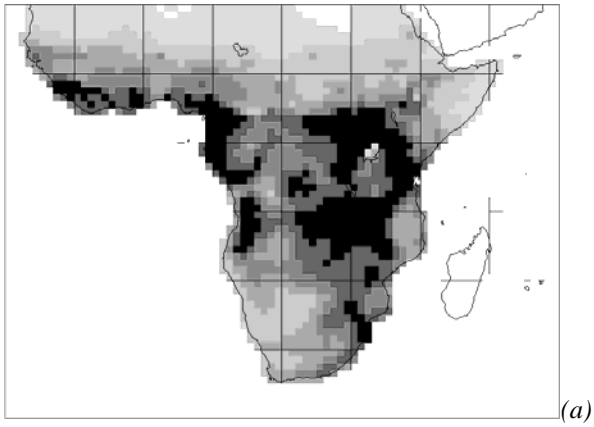


Fig. 5. Patterns and hotspots of species richness (a) and (b), and range-size rarity (c) and (d) for endemic passerines. Darkest shades represent highest scores graduating to lowest scores represented by lightest shades.

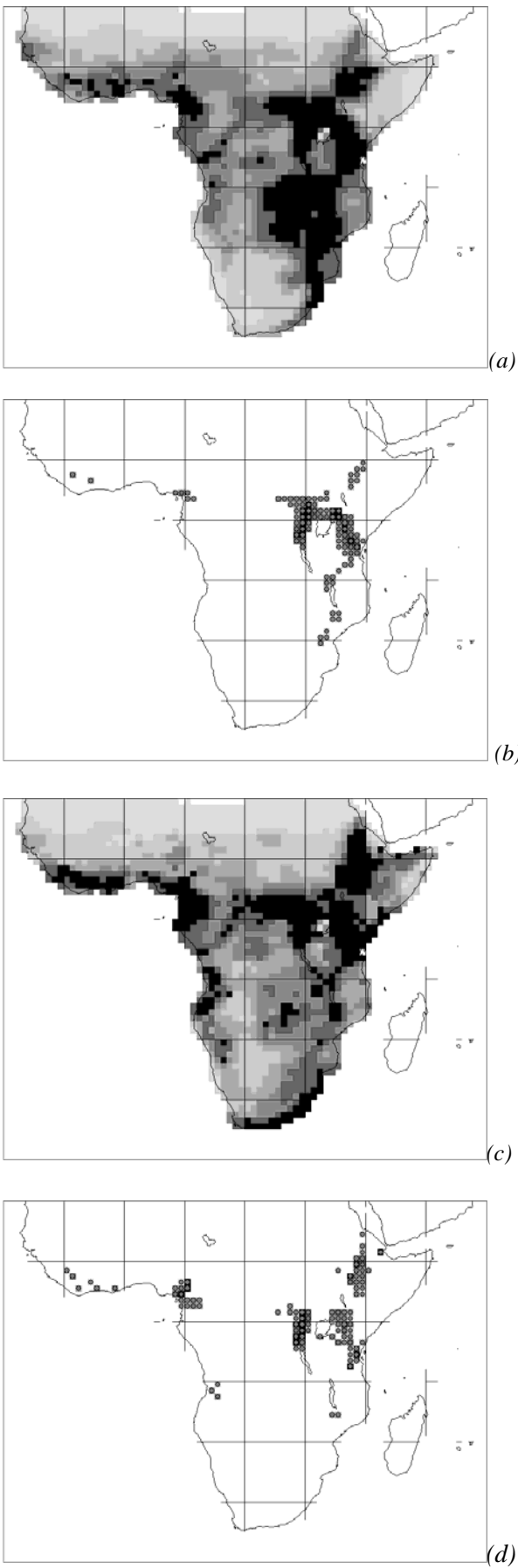
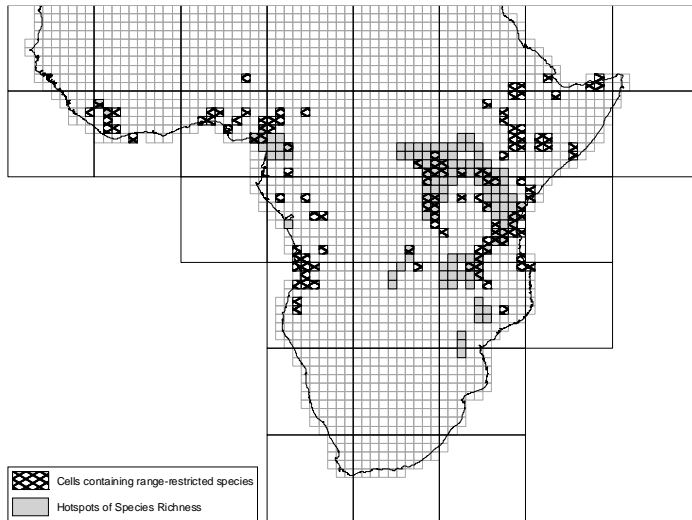
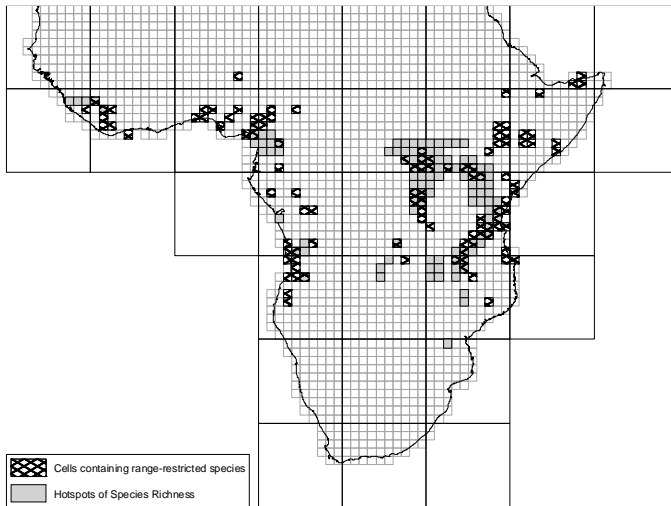


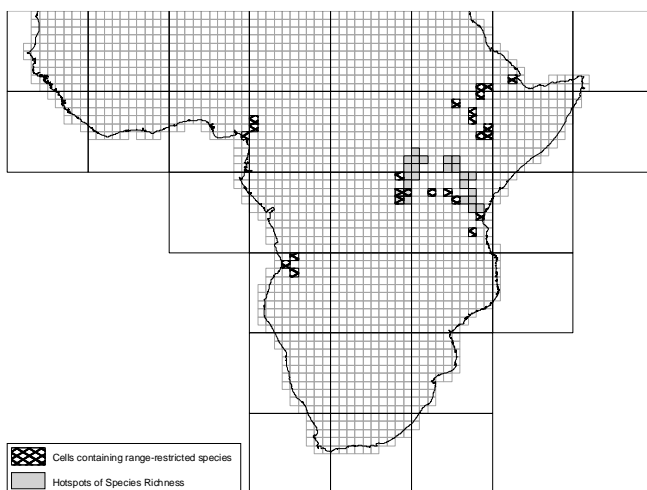
Fig. 6. Patterns and hotspots of species richness (a) and (b), and range-size rarity (c) and (d) for endemic non-passerines. Darkest shades represent highest scores graduating to lowest scores represented by lightest shades.



(a)



(b)



(c)

Fig. 7. Hotspots of range-restrictedness (hashed) and species richness (light, solid shading) for all terrestrial Afrotropical endemics (a), endemic passerines (b), and endemic non-passerines (c).