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# The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa

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## ABSTRACT

**Aim** To test whether it is possible to establish a common biogeographical regionalization for plants and vertebrates in sub-Saharan Africa (the Afrotropical Region), using objective multivariate methods.

**Location** Sub-Saharan Africa (Afrotropical Region).

**Methods** We used 1° grid cell resolution databases for birds, mammals, amphibians and snakes (4142 vertebrate species) and *c.* 13% of the plants (5881 species) from the Afrotropical Region. These databases were analysed using cluster analysis techniques to define biogeographical regions. A  $\beta$ (sim) dissimilarity matrix was subjected to a hierarchical classification using the unweighted pair-group method with arithmetic averages (UPGMA). The five group-specific biogeographical regionalizations were compared against a regionalization developed from a combined database, and a regionalization that is maximally congruent with the five group-specific datasets was determined using a consensus classification. The regionalizations were interpreted against measures of spatial turnover in richness and composition for the five datasets as well as the combined dataset.

**Results** We demonstrate the existence of seven well-defined and consistent biogeographical regions in sub-Saharan Africa. These regionalizations are statistically defined and robust between groups, with minor taxon-specific biogeographical variation. The proposed biogeographical regions are: Congolian, Zambezi, Southern African, Sudanian, Somalian, Ethiopian and Saharan. East Africa, the West African coast, and the transitions between the Congolian, Sudanian and Zambezi regions are unassigned. The Cape area in South Africa, Afromontane areas and the coastal region of East Africa do not emerge as distinct regions but are characterized by high neighbourhood heterogeneity, rapid turnover of species and high levels of narrow endemism.

**Main conclusions** Species distribution data and modern cluster analysis techniques can be used to define biogeographical regions in Africa that reflect the patterns found in both vertebrates and plants. The consensus of the regionalizations between different taxonomic groups is high. These regions are broadly similar to those proposed using expert opinion approaches. Some previously proposed transitional zones are not recognized in this classification.

## Keywords

Amphibians, biochoria, biogeography, birds, cluster analysis, plants, mammals, regionalization, snakes.

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## INTRODUCTION

Africa is a continent of amazing natural diversity. The Mediterranean scrub of the southernmost tip of Africa has one of the richest endemic floras in the world (Goldblatt, 1978; Cowling *et al.*, 1992; Goldblatt & Manning, 2002; Linder, 2003). This contrasts with the world's largest desert, the Sahara, in northern Africa – the most extensive species-poor area outside the Arctic (Burgess *et al.*, 2004). The extensive savannas host the largest remaining mammalian megafauna on the planet (Fjelds  *et al.*, 2004). In the south, the Namib Desert is one of the most arid areas in the world, with a bizarrely adapted fauna (Seely, 2004). The equatorial rain forests are anomalously species-poor in global terms (Richards, 1973; Hamilton, 1976; Beentje *et al.*, 1994), but Afrotropical forests across the tropical belt are remarkably species-rich (Burgess *et al.*, 2007a; Cordeiro *et al.*, 2007), and the three widely separated glaciated mountains close to the equator (Rwenzori, Mount Kenya and Mount Kilimanjaro), and the extensive Ethiopian alpine plateau, harbour a very distinct biota (Friis *et al.*, 2010).

The grouping of these extremes into a coherent biogeographical system has challenged biogeographers over the past 100 years. The earliest classifications from over 100 years ago already recognized the separation of the savannas, desert and rain forest (Wallace, 1876; Engler, 1879–1882). During the 20th century, various other groupings of biologically distinct regions were proposed based on patterns in the distribution of the flora, fauna, biomes, geographical features or various combinations of these (e.g. Chapin, 1923, 1932; Dasmann, 1972, 1973; Udvardy, 1975; Diamond & Hamilton, 1980; Crowe & Crowe, 1982; White, 1983, 1993; Williams *et al.*, 1999; Cox, 2001; Olson *et al.*, 2001; de Klerk *et al.*, 2002a; Burgess *et al.*, 2004, 2006; Kreft & Jetz, 2010). Many of these systems were based on expert opinion (e.g. White, 1983; Burgess *et al.*, 2004) and are therefore non-replicable. Especially controversial aspects include the recognition and classification of habitat islands with high local endemism, such as the Afrotropical and Afroalpine biota (White, 1993), the transition zones between areas of endemism, the relationship between the northern and southern savannas (White, 1965) and the integration of the southern and tropical African regionalizations (Werger, 1978).

All existing biogeographical classifications are based either on vascular plants or on one or more vertebrate groups. There is an underlying assumption that such partial analyses can be used to predict the regionalizations for all other groups. For Africa we have analyses of biogeographical patterns for groups of plants (e.g. grasses, Clayton & Hepper, 1974; Clayton, 1976), for more or less random samples of plants (e.g. White, 1983; Linder, 2001; Linder *et al.*, 2005), for birds (Williams *et al.*, 1999; de Klerk *et al.*, 2002a), mammals (Turpie & Crowe, 1994) and amphibians and snakes (N.D.B., unpublished). One assumption of these schemes is that if all taxa in Africa are responding to the same environmental stimuli and were shaped by the same history, we might expect a coordinated

system of regions across groups. This would make it possible to bring all regionalizations together in a unified framework. The capacity to digitize and analyse large amounts of species distribution data now allows a quantitative and a more rigorous biogeographical analysis, not only of single groups (see Mackey *et al.*, 2008; Kreft & Jetz, 2010) but also across groups.

We use the large species datasets for sub-Saharan Africa, assembled by the University of Copenhagen for birds, mammals, amphibians and snakes (Burgess *et al.*, 1998a) and the University of Bonn for plants (Linder *et al.*, 2005), to seek a common biogeographical regionalization for the African biota. We use explicit multivariate methods to test whether these separate species distribution datasets confirm the broad biogeographical regions (rain forest, savanna, desert, etc.) that are generally presented for Africa. We compare the utility of combined (total evidence) and consensus (maximally congruent) approaches to infer a common, informative biogeographical regionalization. Finally, we focus on the problem zones, namely the Afrotropical/Afroalpine regions, the existence of two savanna regions and the relationship of the southern African biogeographical regions to those of tropical Africa, to explore the type of patterns that complicate African biogeographical regionalization.

## MATERIALS AND METHODS

### Study area

The study area comprises sub-Saharan Africa (Stuart *et al.*, 1990), also known as the Afrotropical Region (*sensu* Udvardy, 1975) or Ethiopian Region (*sensu* the Sclater–Wallace system; Wallace, 1876). This includes all of continental Africa south of 20° N. The use of this study region is in keeping with many studies on biogeography (e.g. Chapin, 1923, 1932), speciation (e.g. Hall & Moreau, 1970) and conservation (Udvardy, 1975; Olson *et al.*, 2001), for flora (Linder *et al.*, 2005) as well as fauna (Burgess *et al.*, 2002; de Klerk *et al.*, 2002a). Although the biota of North Africa and the Sahara is usually considered to be Palaearctic rather than Afrotropical (Dowsett & Forbes-Watson, 1993), there are also treatments that place the boundary along the northern margin of the Sahara (Cox, 2001) or along the Mediterranean coast (Kreft & Jetz, 2010). Drawing the border in the middle of the Sahara is practical in view of the low species density there. This maximizes African endemism, reducing the problems introduced by species with ranges centred outside the study area.

Biogeographical study of islands presents particular challenges, being affected by different forces from those acting on a continent (Whittaker *et al.*, 2008). We have therefore excluded all islands around Africa from this study [e.g. Unguja and Pemba (Zanzibar), Mafia and Madagascar in the Indian Ocean, and Bioko, S o Tom  and Pr ncipe in the Atlantic Ocean]. This parallels the approach taken in other studies (e.g. Pomeroy & Ssekabiira, 1990; Brooks *et al.*, 2001; de Klerk *et al.*, 2002a; Fjelds  & Burgess, 2008).

The Afrotropical Region was divided into 1954  $1^\circ \times 1^\circ$  grid cells (*c.* 110 km  $\times$  110 km measured near the equator), which is a compromise between accuracy and detail (Kreft & Jetz, 2010). We have omitted those coastal grid cells that have less than 25% land cover within them, leaving 1877 grids. Note that the grid cells at the southern extreme are *c.* 15% smaller than those at the equator.

## Data

Databases for sub-Saharan vertebrates were compiled at the Zoological Museum and the Center for Macroecology, Evolution and Climate at the University of Copenhagen, and the plant database was assembled at Bonn, with contributions from York and Copenhagen universities, Conservation International and WWF-US. The development of the databases has involved a review of all available scientific literature, consultations with more than 25 experts and visits to 12 museums in eight countries, as well as new fieldwork in the East African Region (e.g. Burgess *et al.*, 1998a, 2007b; Brooks *et al.*, 2001; de Klerk *et al.*, 2002a,b; Fjelds  & Tushabe, 2005; Linder *et al.*, 2005; Fjelds  *et al.*, 2010; databases available at <http://130.225.211.158/subsaharanafrika/subsaharan.htm>, accessed 13 January 2011, Zoological Museum, University of Copenhagen).

The mammal database (Table 1; Galster *et al.*, 2007, updated to 2010) follows the taxonomy of Wilson & Reeder (2005) with the addition of newly described species. Maps are based on data from more than 1000 published papers and books, and from visits during 2004–05 to the Smithsonian Institution (Washington, DC) and the Field Museum of Natural History (Chicago, IL). The bird database is based on more than 500 published papers, atlas studies (for 15 African countries) and specimen data held at the Zoological Museum in Copenhagen (Hansen *et al.*, 2007a, updated to 2010). The amphibian database uses data from more than 400 publications (Hansen *et al.*, 2007b, updated to 2010), cross-checked for both taxonomy and distributions against the Global Amphibian Assessment (<http://www.iucnredlist.org/initiatives/amphibians>). The reptile database is based on more than 15 years' work by the late Jens B. Rasmussen, including visits to more than 20 museums and referring to over 300 published papers (Rasmussen *et al.*, 2007, updated to 2010).

The plant dataset includes 5881 species, which constitute around 13% of the 44,850 species in sub-Saharan Africa (Klopper *et al.*, 2007) derived from herbarium records and published distribution maps; sources are documented in Linder *et al.* (2005).

For plants and most of the amphibians and reptiles, no extrapolated ranges were produced, thus the dataset is somewhat biased towards well-collected areas. For birds and mammals, range maps have been conservatively extrapolated from point data for all except the rarest species, and have been refined over more than 10 years by checking original papers and national distribution atlases, and using information on the availability of suitable habitat. The degree of interpolation depends on expert judgment, and for species which are little-known and generally considered rare, ranges are not extrapolated between confirmed records. Negative records were also taken into account – for instance, when a species is not recorded in a well-studied site with seemingly appropriate habitat, or where the area contains a related (competing) species.

## Delimiting biogeographical regions

All datasets were created within the  $1^\circ$  grid structure of the Africa3 map within WORLDMAP software v4.2 (<http://www.nhm.ac.uk/science/projects/worldmap/index.html>), and were exported as presence–absence data matrices for further analysis. We generated six matrices: five separate taxon matrices for mammals, birds, amphibians, reptiles and plants, and a combined matrix containing all species. All cells with fewer than five species were manually removed from each data matrix. This is because cells with very few species can bias results by giving strong and misleading signals.

We define a biogeographical region as a set of grid cells that are more similar in species composition to each other than to any other grid cells. We use two approaches to delimit these regions. One approach clusters cells together based on the similarity of their species composition using an agglomerative algorithm. It is designed to find the core of each region. The second approach seeks to identify and map the transitions between the regions.

The similarities among the cells were calculated using the  $\beta$ (sim) metric. This, like the Jaccard or Sørensen metrics, does

**Table 1** Statistics for the taxon databases from sub-Saharan Africa used in this study.

Clade	Number of species included	Total number of grid records	Average number of $1^\circ$ grid cells per species, in total 1877 grid cells in the study area	Standard deviation of number of grid cells per species
Mammals	1103	608,856	552	319
Birds	1790	431,636	241	308
Amphibians	769	36,562	47.5	39.6
Reptiles	480	49,879	106	181
Vascular plants	5881	169,480	28.8	52.7

not take shared absence (zero values) into account (e.g. Jardine, 1972; Sneath & Sokal, 1973; Everitt, 1993; Murguía & Villasenor, 2003; Finnie *et al.*, 2007). For biogeographical regionalization, presence-only measures are important because areas which lack many species and share none (e.g. Sahara and the Namib) should not be found to be similar purely due to shared absences. The Jaccard and Sørensen are both sensitive to radical differences in the species richness of the cells (Born *et al.*, 2007; Kreft & Jetz, 2010). We therefore used  $\beta(\text{sim})$ , which is not sensitive to major differences in species richness, as the similarity is calculated using the richness of the more species-poor grid cell.

The cells were clustered by applying the hierarchical unweighted pair-group method with arithmetic averages (UP-GMA) classification algorithm to the  $\beta(\text{sim})$  dissimilarity matrix. This method results in the smallest distortion of the values over a wide range of applications (Sneath & Sokal, 1973), and has recently been confirmed by Kreft & Jetz (2010) to provide the best performance in biochoric analysis. As a greedy clustering approach it includes outliers in their nearest groups, rather than emphasizing them. The non-hierarchical or partitioning algorithm, *k*-means, has been used recently for clustering grid cells into biogeographical zones (Heikinheimo *et al.*, 2007; Rueda *et al.*, 2010), but the a priori specification of the number of groups to be found by the algorithm and the inability to determine the inter-group relationships limits its usefulness. We tested the distortion in translating the multidimensional similarity matrix into a phenogram with a co-phenetic analysis. For each analysis, the implicit similarity among the grid cells for the phenogram was extracted. This inferred similarity was correlated against the  $\beta(\text{sim})$  dissimilarity matrix with a Mantel test. We used a subjective estimate of fit quality, with  $0.8 < r < 0.9$  a good fit,  $0.7 < r < 0.8$  a poor fit, and  $r < 0.7$  a very poor fit (Rohlf & Fisher, 1968). All multivariate analyses were conducted in R (R Development Core Team, 2011), using the packages *VEGAN* (Oksanen *et al.*, 2011), *MASS* (Venables & Ripley, 2002) and *CLUSTER* (Maechler *et al.*, 2011).

Translating the cluster diagrams into sets of regions (or number of clusters) requires explicit rules (Kreft & Jetz, 2010) because many different sets of regions could be delimited. We used three basic ranking rules. First, the regions could not be nested within each other. Second, a phenon line was employed to provide a rigorous definition of the groups. Finally, six to eight regions were defined. We wished to determine whether the currently used biogeographical regionalizations for Africa were supported by our data, and also whether regionalizations based on different groups were congruent. Because there are a very large number of different ways in which the regions could be delimited that would be incongruent, we sought the most congruent regions that still followed the three ranking rules. Consequently, if a previously recognized region was not retrieved, it was usually because it was either not retrieved as a coherent group or was nested within another region. Thus we did not use any intrinsic cut-off rules, such as those based on the number of endemic species recognized, or a pre-defined level of similarity.

We used two methods in our search for a unified biogeographical regionalization for Africa. Both methods are somewhat problematic and make certain assumptions. However, these assumptions are very different; consequently, any regions located by both methods should be robust. The first method is analogous to a total evidence approach: all five datasets were combined in *WORLDMAP*, and this combined matrix was analysed by the same methods as the individual taxon matrices. There are several factors which may result in the combined analysis being dominated by one clade. First, the total number of species in a group could result in that group having an undue influence. This would strongly favour the plants, which include more species than all vertebrates combined. Second, a group recorded from a large number of grid cells could have more influence than one known from fewer grid cells. This would give the mammals an advantage. However, mammals also have the widest distribution ranges (on average in 552 of the 1877 cells included in the study) which might reduce their grouping signal. Finally, it is possible that the strength of the biogeographical signal is most important. We do not know the relative impacts of these factors; consequently, we follow the conservative route of not weighting the datasets. Using all datasets increases the chance that all grid cells are placed in a biogeographical region, allowing us to establish a complete biogeographical map.

The second method seeks the consensus regionalization of the five taxon datasets. The regionalizations from the five individual taxon analyses were used as input. Cells were assigned to a region if that cell was identified as belonging to that region in at least three, four or all of the five separate taxon analyses. This method leaves cells that are assigned differently in a specified number of the individual taxon analyses as 'unplaced'. The advantage of this method is that each taxon is treated equally, irrespective of how many species it contains, how many grid cells it has been recorded in, or how strong the biogeographical signal is. Thus the plants, which have eight times more species than the amphibians, cannot override the amphibians, and each taxon effectively contains a 'veto' on the placement of each cell.

To assess how similar the maps produced by the individual taxa are to the combined matrix map, we use standard confusion matrix methods from remote sensing and species distribution modelling, including the kappa statistic (*sensu* Monserud & Leemans, 1992; Heikinheimo *et al.*, 2007).

### Evaluating regional transitions

Transitional regions are areas with high levels of species turnover, and which are situated between major biogeographical regions. Some authors (Wilson & Shmida, 1984; Williams, 1996) specify that turnover must only measure species replacement with no overlap, while others argue that patterns of species richness form part of community turnover. Indices have been developed to measure both aspects of turnover – absolute replacement and species richness trends – separately (Williams, 1996; Williams *et al.*, 1999). Species replacement is

measured as neighbourhood segregation, which quantifies complete spatial replacement with no overlap, and is based on Rapoport's segregation index (see Williams *et al.*, 1999, for details). This is calculated by counting all possible species replacement pairs in a neighbourhood of nine cells, and standardizing this against the total richness within the nine-cell region (Williams, 1996). Species richness gradients are measured as neighbourhood heterogeneity, calculated as the sum of squares of deviations from the mean richness within a nine-cell neighbourhood (Williams *et al.*, 1999). WORLDMAP was used to calculate these measures for all datasets.

## RESULTS

### General

A comparison of the zonation maps produced by cluster analysis of the five individual taxon groups, the combined matrix and the consensus analyses reveals both extensive congruence and areas of differences (Figs 1–3), on the basis of which we can recognize seven regions: Saharan, Sudanian, Congolian, Ethiopian, Somalian, Zambezan and Southern African. However, the five analyses result in strikingly different patterns of relationships among these regions (Fig. 1). The cophenetic correlation between the similarity matrices and cluster results was generally poor (Table 2), especially for plants, where there is a very poor fit ( $r < 0.7$ ). This is probably a result of the large numbers of grid cells (or operational taxonomic units). Neighbourhood segregation (Fig. 4) and differentiation (Fig. 5) are similar among the datasets.

### Taxon datasets

The biogeographical map for the mammals (Fig. 1a) recognizes a combined Congolian and Guinean Region, with a disjunction at the 'Dahomey Gap' in Benin. There are also large Saharan and Sudanian regions, with the latter including the Ethiopian uplands. A large Somalian Region, which includes most of Kenya and the eastern half of Ethiopia, is defined in north-east Africa. Further south, there is a huge Zambezan Region that constitutes a wide band across south-central Africa, from Angola to Mozambique, including the whole of Tanzania, and extending to the northern borders of Namibia, Botswana and South Africa. The whole of southern Africa (including Namibia, Botswana, South Africa, Swaziland and Lesotho) is included in one region, which we refer to as the Southern African Region. At a finer biogeographical resolution, the Guinean zone is separated from the Congolian zone, and the Southern Africa Region is divided into a Kalahari–Namibian zone and a South African zone.

The biogeographical map for birds (Fig. 1b) is largely similar, albeit with minor shifts in the positions of the boundaries between the regions, and the recognition of the Ethiopian uplands as a separate region. This does not include the Bale Mountains, which are to the east of the eastern Rift. The border between the Zambezan and Congolian regions is

further north than for mammals, with Uganda included in the Zambezan Region and the Zimbabwe uplands and south-western Angola included in the Southern African Region.

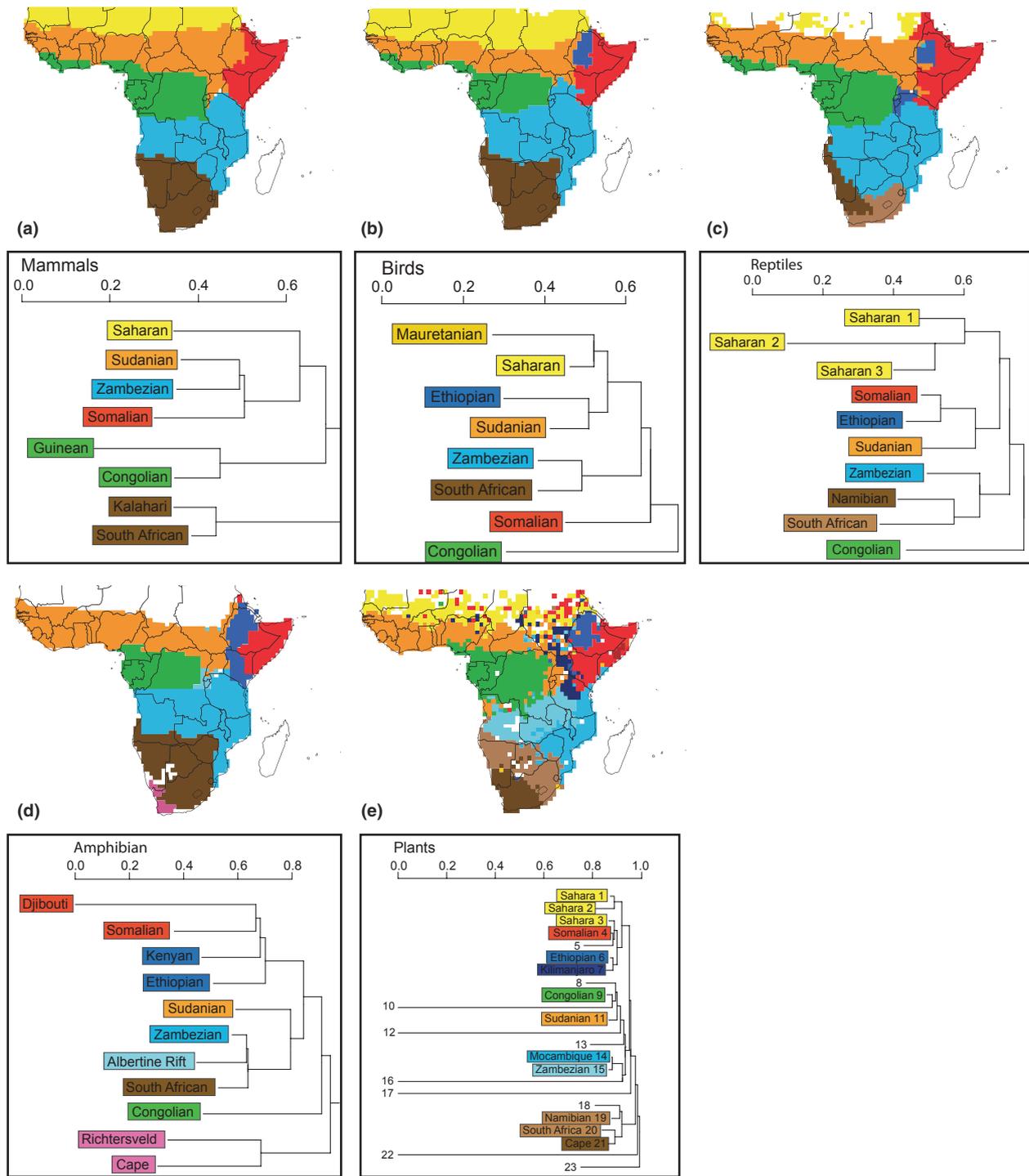
The regionalization for reptiles (Fig. 1c) differs in three ways from that of mammals. The Ethiopian Region, recognized for birds at a slightly lower level, is also recognized for reptiles, and the Albertine Rift (the western rift) uplands of south-western Uganda, Rwanda and Burundi are also included in this region. Curiously, this extended Ethiopian Region is combined at a lower level of similarity with the Somalian Region. The Zambezan Region is enormous, and includes both the Kalahari and the northern Namibian regions. Southern Africa is split into a Namaqua–Namib region in the west, and a south-eastern region.

Amphibian regionalization (Fig. 1d) is similar to that for the birds. However, the Guinean coast is not included in the Congolian, but rather in the Sudanian Region. As in the birds, Zimbabwe is included in the Southern African Region, rather than the Zambezan Region. Most unusual, though, the Richtersveld and the south-western Cape are segregated at a deep level in the phenogram from the Southern African Region. These two areas are grouped with each other and could be recognized as a coherent winter-rainfall region. The Somalian and Ethiopian regions are closely allied.

The regionalization for plants (Fig. 1e) is not as coherent as for other taxa. The Southern African and Zambezan regions are similar to those recognized for mammals. To the north, the Congolian, Sudanian, Saharan and Somalian regions are evident, but they interdigitate. There are also suggestions of an upland zone including western Ethiopia and parts of the eastern Rift in East Africa. However, the picture is obscured by poor group formation in the cluster diagram, indicating that the grouping is weakly supported. This also results in many small groupings scattered among the major groups (indicated in Fig. 1e by the many different colours). This is in stark contrast to the clearly defined groupings observed in the animal datasets.

### Combined analyses

Analysis of the combined evidence dataset consisting of all data for all five taxa shows a remarkably clean pattern (Fig. 2). Seven major regions (Saharan, Sudanian, Ethiopian, Somalian, Congolian, Zambezan and Southern African) are retrieved. The Saharan Region divides into three subregions: Sahara north of  $c. 18^\circ \text{N}$ , Sahel south of this and a Nubian Desert subregion. The Congolian Region is also subdivided. The boundary between the Guinea and Congo subregions is along the Sanaga River in Cameroon. A broad southern transition region (the Shaba subregion) reaches in an arc from the Angolan Atlantic coast to the southern Ugandan uplands. The Somalian Region in north-east Africa is fragmented: the Horn of Africa can be separated from the Somalia subregion in the narrower sense, and the Ethiopian uplands can be separated from the coast at Djibouti. The Southern Africa Region is also readily fragmented into five subregions: south-western Angola,

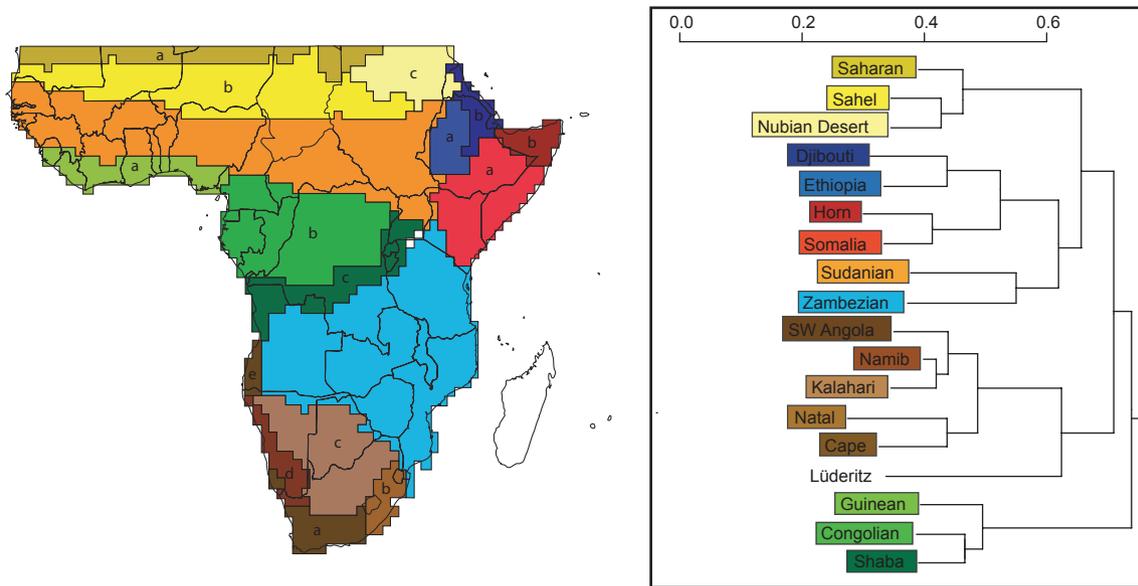


**Figure 1** Biogeographical cores: cluster maps and simplified phenograms for five taxon databases: (a) mammals, (b) birds, (c) reptiles, (d) amphibians, and (e) plants: yellow, Saharan Region; orange, Sudanian Region; green, Congolian Region; dark blue, Ethiopian Region; red, Somali Region; pale blue, Zambezan Region; dark brown, Southern African Region; purple, Cape; pink, Richtersveld; pale blue, Albertine Rift. The maps are based on a 1° grid.

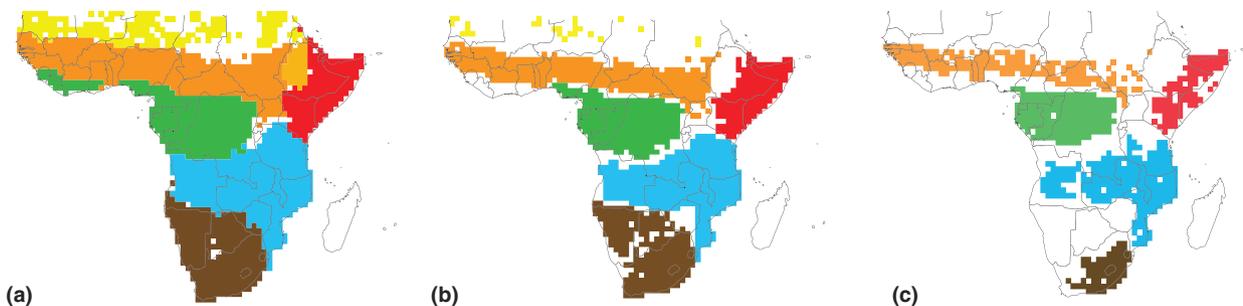
the Namib coast, a large central Kalahari subregion, a Pondoland–Natal subregion and a large southern Cape subregion. The only regions that are not readily subdivided are the Zambezan and Sudanian. The Zambezan Region includes the whole triangle from Angola to Kenya and south to South

Africa. The Sudanian Region is similar to that retrieved in all other studies.

The confusion analyses show that all the individual taxon datasets fit the combined analysis very well (Table 3), for mammals and birds the kappa of 0.86 and 0.85, respectively,



**Figure 2** Biogeographical regionalization and phenogram based on the combined matrix: yellow, Saharan Region (subregions: a, Sahara; b, Sahel; c, Nubian Desert); pale brown, Sudanian Region; green, Congolian Region (subregions: a, Guinea; b, Congo; c, Shaba); dark blue, Ethiopian Region (subregions: a, Djibouti; b, Ethiopia); red, Somalian Region (subregions: a, Somalia; b, Horn); pale blue, Zambeزيan Region; dark brown, Southern African Region (subregions: a, Cape; b, Natal; c, Kalahari; d, Namib; e, south-west Angola). The map is based on a 1° grid.



**Figure 3** Biogeographical regionalization based on the three levels of consensus: (a) three of five datasets; (b) four of the five datasets; (c) all datasets. Yellow, Saharan Region; pale brown, Sudanian Region; green, Congolian Region; dark blue, Ethiopian Region; red, Somalian Region; pale blue, Zambeزيan Region; dark brown, Southern African Region. The maps are based on a 1° grid.

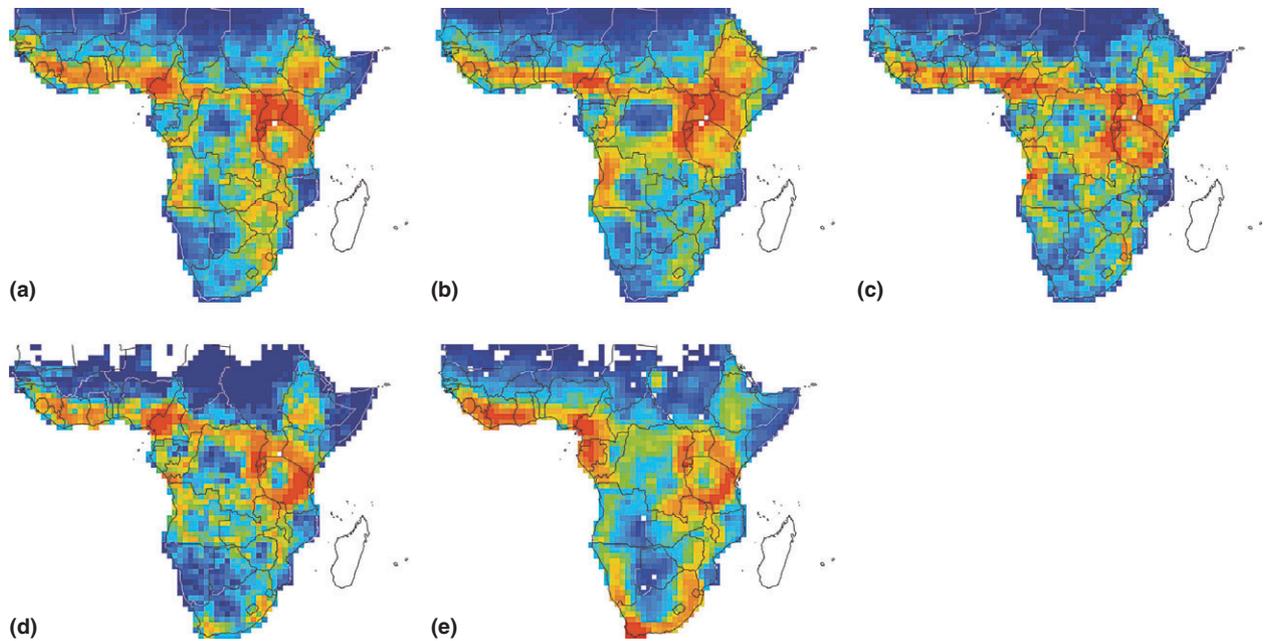
**Table 2** Co-phenetic correlation value for each taxon dataset from sub-Saharan Africa. In the vascular plants the phenogram is only a poor reflection of the distribution data.

Clade	Co-phenetic correlation
Mammals	0.7946
Birds	0.7740
Amphibians	0.8158
Reptiles	0.7584
Vascular plants	0.6758
Combined	0.7656

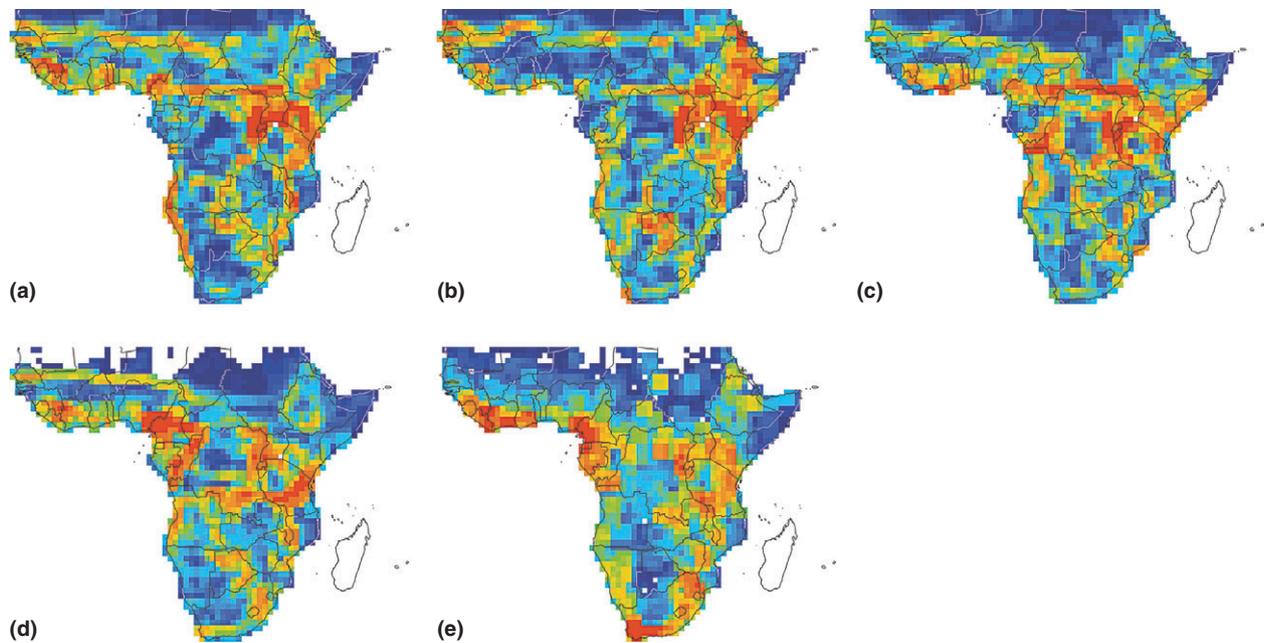
can be interpreted as a nearly perfect fit (Monserud & Leemans, 1992). The relatively low match of the amphibians with the total evidence map ( $\kappa = 0.60$ ) is probably due

to their absence in the Sahara, creating a large zone of mismatch.

The consensus map, requiring consensus of regionalization of each grid cell in at least three of the five separate taxon datasets (Fig. 3a), results in 12.9% of the cells not being placed. Most of the unplaced cells are from the Sahara, where many cells are ‘empty’ due to the presence of fewer than five taxa from any taxon dataset. Again, seven regions (Saharan, Sudanian, Congolian, Ethiopian, Somalian, Zambeزيan and Southern African) are recognized, which are very similar to those recovered by the combined evidence analysis. One difference is that in the consensus map, the Shaba subregion of the southern Democratic Republic of the Congo is included in the Zambeزيan Region, and not the Congolian Region. Furthermore, the consensus recognizes the ‘Dahomey Gap’



**Figure 4** Neighbourhood segregation (Williams, 1996) for the five taxon datasets from sub-Saharan Africa, showing the rate of species turnover: (a) mammals, (b) birds, (c) snakes, (d) amphibians and (e) plants. The colour ramp grades from pale blue for low values, to red for high values of segregation. The maps are based on a 1° grid.



**Figure 5** Neighbourhood heterogeneity (Williams, 1996) for the five taxon datasets from sub-Saharan Africa, showing the change in species richness: (a) mammals, (b) birds, (c) snakes, (d) amphibians and (e) plants. The colour ramp grades from pale blue for low values, to red for high values of heterogeneity. The maps are based on a 1° grid.

between the Guinea and Congo subregions. The consensus of four taxa leaves 36.6% of the cells unplaced (Fig. 3b), and still recognizes six regions (the Ethiopian is now no longer visible), and reveals transition zones between the regions. Most importantly, the West African coast is unplaced, as are the

Ethiopian and East African uplands. Many of the unplaced cells are due to low numbers of amphibian and reptile species in the Sahara, rather than due to conflict. The consensus of all five datasets leaves 61.2% of the cells unplaced (Fig. 3c). Impressively, the cores of five biogeographical regions are still

**Table 3** Kappa ( $\kappa$ ) values of the confusion matrices for different taxon groups compared against the total evidence matrix. Values of 0.6 and greater show strong agreement between the relevant taxon matrix and the total evidence matrix, and of 0.8 and greater are 'near complete agreement' (Monserud & Leemans, 1992).

	Total evidence (kappa)
Mammals	0.86
Birds	0.85
Amphibians	0.60
Reptiles	0.77
Plants	0.72

retrieved. The Saharan Region is not retrieved, due to the complete absence of amphibians from that region.

### Species turnover rates

The neighbourhood segregation patterns, which measure species replacement rate, are largely similar for the five taxa (Fig. 4). In all taxa, East Africa is an area of very high turnover, and this belt extends westwards along the northern margins of the Congo Basin, and through West Africa to Senegal. The central Congo Basin shows very low rates of turnover, and the south-central African Plateau shows medium levels. The western escarpment of Angola again shows higher replacement values for all taxa. The plants differ from the other taxa in showing very high replacement rates along the southern African coastal regions, and especially in the heart of the Cape Floristic Region at the south-western tip of Africa. Here, values of 6.0–11.5% were recorded. For comparison, the next highest cells are in West Africa, with Abidjan at 7.9% and Mount Cameroon at 7.8%. This pattern was also retrieved for the combined dataset, where the top five cells were from the Cape (0.69–0.9%), after which cells from West Africa (Mount Cameroon, Man Plateau in Côte d'Ivoire) were intermixed with the remaining Cape cells.

Birds, mammals and reptiles show a similar pattern of neighbourhood heterogeneity (Fig. 5), which measures gradients in species richness, with a high rate of change along the northern transition between the rain forest and savanna, in East Africa and the Albertine Rift. All three taxa also show secondary areas of change along the border between the Sudanian savanna and Sahel, and along the west coast from the Congo River to the Cape. Mammals, birds and amphibians show high rates of change towards the northern edge of the Southern African region. Plants show four large areas of major change: West Africa, the Cameroon–Gabon area, the East African uplands from the Albertine Rift to the Southern Highlands of Tanzania, and finally the eastern and south-western part of southern Africa, in particular the Cape region. In amphibians, a third set of patterns are shown, with West African and Cameroonian centres. The Albertine Rift area is also retrieved, but centred over the Rwenzori Mountains. The southern border of the Congolian rain forests, all the way from

the East African coast over the Tanzanian Southern Highlands to Angola, is also a zone of rapid change in species richness in amphibians.

## DISCUSSION

### Congruence among datasets

We found a large degree of congruence in the African species-level biogeographical patterns of plants, mammals, birds, amphibians and reptiles. This congruence is evident from a visual comparison of the clade-based maps, from the consensus classification (which is almost perfect if a congruence of three of five taxa is used, and where the core biogeographical regions are retrieved by all five taxa), as well as from the confusion matrix analysis. Globally, patterns of richness and endemism are positively and significantly correlated among mammals, amphibians, birds and reptiles (Lamoreux *et al.*, 2006). However, congruence in the biogeographical regions has not been reported previously. Udvardy (1975) found that, at a global scale, there was agreement amongst zones developed by zoologists, except for areas of a transitional nature, but that the botanical zones were more different. At a continental scale, Rueda *et al.* (2010) observed substantial incongruence in the regionalization of trees, butterflies, reptiles, amphibians, birds and mammals in Europe. Consequently, it is unclear whether the congruence demonstrated in Africa is unusual, or whether this a global pattern, at least in tropical regions.

The reasons for congruence or incongruence would be very interesting to understand. The nature of the underlying data might affect the results, but a biological explanation seems more likely. Congruence could be the consequence of the vertebrate distributions being influenced by the vegetation and flora (predicted by Rueda *et al.*, 2010), by common responses to the same climatic parameters or by a common underlying history. Interpreting the common response as being driven by the vegetation is consistent with the idea that the vegetation functions as a giant ecosystem engineer that creates the habitat for animals (Linder *et al.*, in press), e.g. hot pyrophytic savanna (Bond *et al.*, 2005; Beerling & Osborne, 2006) or shady cool forests (Pinto *et al.*, 2010) can be found under the same climate. This is consistent with the very different structure in the dendrograms between the plants and the vertebrates. The poor structure in the plant dendrogram may reflect the individual response of each species to local environmental variations, while the highly resolved vertebrate dendrograms, with long branches separating the biogeographical regions (Fig. 1), could be the response to the spatially broader integrated vegetation structure, which is itself a spatially more coherent expression of the floristic patterns. The incongruent patterns in East Africa could be the result of the much smaller-scale variation between vegetation types in the region (Lind & Morrison, 1974). The importance of a common climatic response is shown by the absence of amphibians from much of the Sahara (Fig. 1d), and the different patterns of the reptiles in southern Africa. Such

biological differences might also account for the different placements of the boundaries between savanna and forest, both to the north and the south of the Congolian Region. The recognition of a separate Ethiopian Region by birds, reptiles and amphibians, but not by mammals, might also be the result of different climatic responses. Historical explanations have been invoked in the differentiation of the forest regions in Africa (Lovett & Friis, 1996; Fjeldså & Lovett, 1997; Couvreur *et al.*, 2008). These could result in the floristic fragmentation of these regions and so reduce the capacity to retrieve them as biogeographical regions. This could possibly account for the inconsistency in the retrieval of a separate Guinean Region. A detailed exploration of the explanations for congruent biogeographical regions in Africa could be very interesting, but is beyond the scope of this paper.

The combined evidence and consensus methods for obtaining a biogeographical regionalization of Africa are highly complementary. The combined evidence approach places every grid cell, and results in a well-resolved classification in which all seven main regions can be recognized, and subregions delimited in most of them. The consensus approach is clearly more conservative and less well resolved, but it separates the well-supported core biogeographical regions from the areas not supported by most groups of organisms. This offers support for the recognition of the seven (or six) core regions in Africa. Conducting both analyses offers both a detailed result and gives an indication of the support of the placement of each grid cell in this detailed result.

## Regions

### General

The Congolian, Sudanian, Zambezan, Somalian, Ethiopian, Southern African and Saharan regions are identified by most clades, and are also evident in the combined evidence and consensus analyses (except the Ethiopian Region). These common regions are very similar to the phytochoria proposed by White (1983), and the biomes map developed by the WWF for their ecoregions project (Burgess *et al.*, 2004, 2006). However, there are also a number of differences between our combined evidence regionalization and the chorological classification of White (1983). First, White identified two regional mosaics (RMs) which were not recognized in our regionalization scheme, namely the Lake Victoria RM and the Zanzibar–Inhambane RM. It is not surprising that we did not detect the RMs, because these mostly lack endemics and so are not delimited as distinct areas. Instead, their cells are grouped within those regions with which they share most biota, which are generally geographically adjacent. Regional mosaics might have been expected to conform to some of our zones of high turnover. However, this does not seem to be the case as, for example, the Zanzibar–Inhambane regional mosaic of White is not recognized in any of our regionalization or turnover maps. Second, our classification does not conform to that proposed by White in southern Africa, the reasons for

which are discussed below. Finally, White recognized two altitudinally driven and fragmented Afromontane and Afroalpine phytochoria. We found no support for the recognition of these regions, although such patterns could possibly emerge by analysing distributions of lineages (at an appropriate taxonomic level) instead of species.

### Congolian

The Congolian Region, as defined by the combined evidence analysis, is a close match to the Guineo–Congolian region delimited by White (1979, 1983) and Kreft & Jetz (2010). However, this belies a complex underlying set of patterns, revealed by the separate taxon datasets, and consequently evident on the consensus analysis.

African tropical rain forests are traditionally separated into three regions. Along the East African coast several small relicts are found, these are usually distinct from the main, Central and West African, forest block (White, 1979). The Kakamega Forest in western Kenya constitutes a Congolian outlier (Wagner *et al.*, 2008). Neither of these is retrieved in our analyses. Presumably the forest effect is diluted by the surrounding vegetation, due to our larger grid cell sizes. The Congolian and Guinean forests also form two regions; these are retrieved only by the combined evidence dataset, with the boundary placed at the Sanaga River in Cameroon to the east of Mount Cameroon. There is some support for this boundary from vascular plants (Lawson, 1996), primates (e.g. Anthony *et al.*, 2007) and the mammals analysed by Kreft & Jetz (2010). Analyses of mammals, reptiles and birds recognize the extension of the Congolian Region along the West African coast. Analyses of these taxa also reveal the ‘Dahomey Gap’ in Benin. This biogeographical interval has also been identified by analyses of plants (Brenan, 1978; White, 1983), amphibians and mammals (Jenkins, 1992) and birds (de Klerk *et al.*, 2002a). It is evident in the vegetation maps as a region where the Sudanian savanna reaches the ocean (White, 1983), thus splitting the Guinean forest into two blocks. Recent phylogeographical research has started to unravel some of the complex patterns within this region, revealing refugia and centres of endemism (Sosef, 1996; Anthony *et al.*, 2007; Couvreur *et al.*, 2008; Marks, 2010). Recent studies using DNA to discriminate geographical areas have shown that many of the species of rain forest birds that are currently regarded as ‘shared’ between the Guinea and Congo areas should be recognized as different species separated since the late Miocene (Fjeldså & Bowie, 2008).

The northern Congolian forest zone boundary is strongly defined in all groups of animals, and slightly less well defined in plants, as a zone with a high turnover in species composition (Fig. 4). This contrasts particularly with an almost complete absence of spatial turnover in species composition from the central part of the Congo Basin, which contains a widespread fauna (Williams *et al.*, 2003). West Africa (the Guinean coast and its hinterland) reflects the transition between the less seasonal (coastal) rain forest and

the more seasonal (inland) Sudanian savannas. This region is mostly topographically subdued, with a relatively even north-to-south rainfall gradient; consequently, the idiosyncratic nature of species climatic tolerance limits results in the absence of congruent biogeographical boundaries. The southern Congolian boundary is generally weakly defined, with few species replacements or species drop-outs, except at the Angola scarp (Figs 4 & 5). This region is characterized by a broad transitory zone with interdigitation of north-south-trending savanna ridges and forested valleys, leading towards the well-drained uplands in the southern parts of the Congo. Further south, in Zambia, *Brachystegia* savanna is the norm, with evergreen forest restricted to wetlands. At the 1° scale this results in a gradual transition and no clear biome boundary. Not surprisingly, there is no congruent classification for this region; in the consensus analysis it is an unplaced area, but in the combined evidence analyses it is separated as the Shaba subregion. White (1983) recognized this complex situation by labelling the region as transitional.

#### *The savanna regions and East Africa*

Our data corroborate the early detailed analysis by White (1965) showing that the northern and southern savannas are different, and show that this difference is recognized by all biotic groups investigated here. Indeed, only the mammal dataset groups the two savanna regions as sister regions (Fig. 1a), supporting the results obtained by Kreft & Jetz (2010).

The extent of the Sudanian Region in the north closely fits that proposed by White (1965, 1983), but there is incongruence among the taxon datasets as to the placement of the eastern border, with the mammal analysis including the uplands of Ethiopia in the Sudanian Region.

The Zambezan Region in the south, defined by the combined analysis, extends further east and north than White's delimitation, with the inclusion of the Zanzibar-Inhambane RM, the Lake Victoria RM, the Ethiopian uplands (Afromontane region in White), and much of the Somalia-Masai area. Neither the separate analyses nor the more detailed combined evidence analysis retrieved East Africa as a region.

Almost all of East Africa falls into a transition zone between the Somalian Region on the arid northern edge, the Zambezan Region on the seasonally dry western and southern edge and the Congolian Region on the wet aseasonal western edge. There is also a chain of mountains running down the middle of the East African area, and a zone of forest/savanna on the coastal margins – with the mountains and the lowlands containing mixed biogeographical signals from the Congolian and Zambezan regions, as well as large numbers of local endemics (Emberton *et al.*, 1997; Burgess *et al.*, 1998b, 2007b). All of these biotas intermix, depending on local topography and rainfall patterns. The high rates of turnover and strong gradients of richness are evident in all groups in our data (Fig. 4a–e). Usually, biogeographical regions consist of a

central area of low species replacement surrounded by a border of high species replacement (as seen in the Congolian, Sudanian and Southern African regions). We suggest that East Africa presents a very complex biogeographical mixture. The different biologies of the taxa generate idiosyncratic responses to complex climatic and topographical patterns, resulting in incongruent biogeographical signals. Assigning the area to any region (for example the Zambezan Region) will obscure much of this complexity. This is exemplified by the area along the Albertine Rift in Central Africa: in the combined evidence analysis, it is assigned to the Congolian Region, in the reptile analysis to the Ethiopian Region, in the mammal analysis it is partitioned between the Congolian and the Sudanian regions, in the bird analysis it is assigned to the Zambezan Region and in the amphibian analysis it is a separate region. Not surprisingly, in the consensus analysis (Fig. 3) it is unplaced. Maybe the best solution is to recognize the whole of East Africa (from the Kivu province of Congo, Uganda, Kenya and north-central Tanzania) as a large RM. This is equivalent to a much enlarged Lake Victoria RM.

#### *North-east Africa*

A relatively large Somalian Region is recognized for all groups, and is somewhat smaller than the Somalia-Masai region of White. The region has low species numbers in all groups and turnover rates are also low. The levels of endemism in the region are high for plants (Thulin, 1993) and reptiles (Burgess *et al.*, 2004). Thulin (1994) argued for this region to have been a refugium for arid-adapted plants, from which they have colonized Socotra, Arabia, East Africa and even southern Africa. The low turnover rates contrast with the high local turnover in the mountainous regions to the west and southwest.

#### *Ethiopian*

Four out of five datasets recognize an Ethiopian Region, which could be part of the Afromontane Region of White (1983), as it is centred on the Ethiopian uplands. The Ethiopian Region extends southwards to the Albertine Rift for reptiles, the Kenyan uplands for amphibians and to the Eastern Arc for plants. However, neither combined nor consensus maps show any southward extension of the Ethiopian Region.

#### *Sahara*

The boundary between the Saharan and Sudanian regions seems to be almost entirely due to species drop-outs (compare Fig. 5c, which shows a change in diversity, and Fig. 4c, which shows no change in species composition). Furthermore, there are relatively few species that occur widely in the Sahara. The Saharan Region is the only one that extends far beyond the African continent, as the Sahara-Sindian Region, which reaches to the arid western part of the Indian subcontinent

(Wickens, 1976; Brenan, 1978; Kreft & Jetz, 2010), and is generally species-poor. Part of the poor geographical definition of the region could be due to mixed affinities: Leonard (2000) showed for Jebel Uweinat on the Libyan–Egyptian–Sudanian border that the lower elevation flora is Sudanian, and the upper elevation flora Saharo–Sindian, and that the level of endemism to the Saharo–Sindian Region is low. Furthermore, the amphibians are, for obvious reasons, absent from much of the region.

#### *Southern African*

Contrary to all previous treatments (e.g. Werger, 1978; White, 1983), but consistent with Kreft & Jetz (2010), we recognize a single Southern African Region. White recognized five regions: the Cape, Karoo–Namib and Afromontane regional centre, one transitional zone (Kalahari–Highveld) and one RM (Tongaland–Pondoland). These segregations are recognized by the combined evidence analysis (as five areas), but not by any of the taxon-based analyses.

The absence of a Cape Region from any of the cluster diagrams is surprising, especially for the plants, as this region is recognized as a separate plant kingdom at the same level of difference as the rest of the Palaeotropics (Good, 1974; Takhtajan, 1986; but see Cox, 2001), and its distinction has long been recognized (Marloth, 1908; Goldblatt, 1978), although there are arguments that it should be combined with the neighbouring Succulent Karoo Region (Born *et al.*, 2007). There are several factors that might have led to our analyses not recognizing the Cape, or Greater Cape, regions. First, the high level of plant species turnover within the Cape Region (Fig. 4e; Born *et al.*, 2007) means that, although the same genera are found throughout the region, there are proportionally very few common species across this region. Therefore, an analysis based on shared species will not retrieve a Cape Region. Second, the interdigitation of arid, north-western elements in the drier inter-montane valleys with mesic south-eastern elements found along the coastal flanks of the mountains dilutes the fynbos elements. This interdigitation is particularly strong along the south-eastern coastline, where Afromontane, coastal thicket, fynbos and karoo elements co-occur in a very small area (Cowling, 1983). The non-fynbos species often have a widespread distribution (especially the forest elements), and so provide strong evidence to link these grids to the rest of the South African grids. Finally, the level of endemism among vertebrates is not exceptional in the Cape Region, and no Cape Region was detected by for mammals by Kreft & Jetz (2010) or birds by de Klerk *et al.* (2002a).

The grouping together of the other southern African zones is not surprising, except possibly the arid Namib biota. This is, however, very species-poor and its lack of recognition could be a result of this lack of evidence. Compared with the regions recognized in tropical Africa, the recognition of a single Southern African Region (albeit with subregions) seems a reasonable solution.

#### *Afromontane Region and centres of endemism*

The Afromontane is not retrieved as a separate region by any of the datasets, thus confirming the results of Linder *et al.* (2005), but contrary to White (1978, 1983) and Wickens (1976). The African montane flora and at least some of the fauna is clearly differentiated from the surrounding lowland biota, although there is often no abrupt transition in the floristic composition (Hamilton & Perrott, 1981; Lovett, 1998). The evolutionary processes also appear to be different, with diversification happening at different times (e.g. Roy, 1997). Further evidence of this in our data is the high species turnover (as measured by neighbourhood segregation in Fig. 4a–e) in the region of the Albertine Rift, the Eastern Arc Mountains, the Southern Rift and the Ethiopian Highlands. Furthermore, the dominant trees are common from Ethiopia to Cameroon and Cape Town (Chapman & White, 1970; White, 1978, 1983).

There are two explanations for the failure of objective analytical methods to retrieve the Afromontane Region. The most likely explanation is that a high intermontane turnover at species level obscures the biotic commonality among the mountains, similar to the explanation for the failure to retrieve a Cape flora region. Consequently, each montane region is included in its surrounding region, except the large Ethiopian Region.

The second possible explanation is that the grid sizes are too large, and consequently also include the biota of the surrounding lowland habitat matrix. The coarse scale of the analysis grid means that smaller-scale features, such as mountains, might be lost within the broader groups, and the mixture of lowland and montane elements in the montane grids then dilutes the effect of the narrow endemics (see also de Klerk *et al.*, 2002b; Linder *et al.*, 2005). Using a finer grid scale will result in numerous spurious absences, which makes the classification of grid cells into broad zones problematic. One way to address the grid scale challenge might be to use natural features as the units, rather than a rigid grid system. This was done very successfully in the Cape flora by Moline & Linder (2006), using previously defined broad habitat units (Cowling & Heijnis, 2001), and in Australia (Mackey *et al.*, 2008). Such natural units would have to be pre-defined, however, and the success of the approach would thus depend on the availability of easily defined area delimitations.

The recognition of an Ethiopian Region is consistent with both explanations. This region represents the northern extreme of the Afromontane Region. This area is also the largest spatially coherent area, and includes several complete grid cells. This removes the dilution effect. The inability to link the southern Afromontane grid cells to this core is consistent with a species-level replacement removing much of the biogeographical signal.

The Afroalpine Region is also not recognized. This archipelago-like region is found only above 3500 m in Ethiopia, Kenya, Uganda, Congo, Rwanda and Tanzania, and shares no species with the lower slopes (Hedberg, 1955, 1957, 1986;

White, 1983; Gehrke & Linder, 2009). However, it always occupies only a small part of a grid cell, and could be regarded as an extreme zonal environment, rather than a biogeographical region, rather like saline wetlands or coastal mangroves.

## CONCLUSIONS

Biogeographical regionalization, reflecting both plant and animal distribution data, is possible at the continental scale. We find core areas with a high level of congruence among the clades, and transition zones, or regional mosaics, which contain a mixture of different geographical elements. The best approach might be to recognize, as White (1983, 1993) did, a small number of very broad regions, and to separate the transitional areas, which are mixtures of neighbouring regions. In the main regions, the biota will then be largely endemic to that region at the species level. The transition zones might have an endemic element, but linking elements predominate.

These geographical regions contain substantial internal structure. Most regions contain several vegetation types, both zonal and azonal. An extreme example is the Southern African Region, which includes the hyper-arid Namib, the winter-rainfall semi-desert Succulent Karoo, the summer rainfall semi-arid Nama Karoo, the heathlands of the fynbos, savanna, steppe and montane grassland, evergreen montane forest, evergreen lowland forest and thicket (Mucina & Rutherford, 2006). A second form of internal structure is the presence of centres of endemism, islands of high species richness and endemism embedded within the region (e.g. Mount Cameroon in the Guinea–Congolian Region, the Eastern Arc Mountains within the Zambezi Region, and the fynbos in the Southern African Region; see Linder, 2001). A third form of structure concerns the biotic elements, usually (but not always) defined by supra-specific clades, and which often cross biogeographical boundaries. These biotic elements might often contain a historical signal. The Afromontane–Cape flora (Linder, 1990; Griswold, 1991; Galley *et al.*, 2007) constitutes a biotic element at generic level, linking African areas with a temperate climate. This is analogous to the arid track (Verdcourt, 1969; de Winter, 1971; Thiv *et al.*, 2011) which links the arid areas of the south-west (e.g. Kalahari), the north-east (Ogaden) and sometimes the north-west (Mauritania).

The rich biological diversity of Africa can be described using these concepts of biotic elements, biogeographical regions, vegetation types and centres of endemism. Here we have explored the structure of the biogeographical regions, and in a future paper we will explore the biotic elements.

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## BIOSKETCH

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