



Beyond trees: Biogeographical regionalization of tropical Africa

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Abstract

Aim: To delineate bioregions in tropical Africa and determine whether different plant growth forms (trees, terrestrial herbs, lianas and shrubs) display the same pattern of regionalization, diversity and endemism as the whole flora.

Location: Tropical Africa (excl. Madagascar), from 20° N to 25° S.

Taxon: Vascular plants.

Methods: Analyses were based on occurrences of 24,719 vascular plant species distributed across tropical Africa extracted from the RAINBIO database. The majority of species (93%) were classified into four growth forms: terrestrial herbs, trees, shrubs and lianas. Biogeographical regions (bioregions) were delimited using a bipartite network clustering approach on the whole dataset and then separately for each growth form. Relationships among bioregions were investigated using non-metric multidimensional scaling ordination, flora nestedness and endemism patterns.

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Results: Analyses of the whole dataset identified 16 bioregions and 11 transition zones. These were congruent with most of the currently recognized phytogeographical classifications, and also highlighted previously under-recognized bioregions. Bioregion endemism rates were lower and species richness higher when compared to estimates from the White/*Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale* (AETFAT) classification. Analysed separately, plant growth forms showed contrasting geographical patterns. Bioregionalization was better resolved for closed forest types using trees and lianas and for open vegetation types using terrestrial herbs, while shrubs showed good discriminative power in all vegetation types.

Main conclusions: We show that distribution patterns based on solely trees are not sufficient to define floristic bioregions in tropical Africa. Analyses of spatial patterns using different growth forms are complementary, likely reflecting different evolutionary processes and ecological relationships. The contribution of growth forms to delimit geographical floristic patterns across tropical Africa is of critical importance for land use planning and management, and for selecting priority conservation areas.

KEYWORDS

African bioregions, diversity, endemism, growth forms, nestedness, network clustering, phytogeography, RAINBIO database

1 | INTRODUCTION

The existence of “geographically distinct assemblages of species and communities” (Vilhena & Antonelli, 2015), known as biogeographical regions, or bioregions, is a central concept in historical biogeography (Holt et al., 2013; Kreft & Jetz, 2010). Assemblage distinctiveness is typically characterized using taxonomic turnover (Kreft & Jetz, 2010) or endemic taxa (Linder, 2001a; White, 1983). The identification of bioregions, or biogeographical regionalization, is of prime importance for ecological and evolutionary studies, and also to establish global conservation agreements (Ladle & Whittaker, 2011).

Africa includes a wide array of contrasting ecosystems, from the species-poor Sahara Desert to the species-rich tropical rain forests and the endemic-rich fynbos vegetation in South Africa (Linder & Verboom, 2015). Biogeographical regionalization in Africa has challenged biogeographers over the past century (Friis, 1998; Linder et al., 2012). The first comprehensive maps based on plant distributions were produced by Lebrun (1936), Monod (1957), Keay (1959), Troupin (1966) and White (1979, 1983, 1993). The work of the latter, initiated and compiled along with members of the *Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale* (AETFAT), currently represents the most widely used chorological and vegetation classification for Africa. White (1983) defined three types of geographical areas based on plant species richness and degree of endemism (see White, 1993 for detailed explanations): (1) regional centres of endemism (RCE) are characterized by at least 1,000 endemic species and an endemism rate higher than 50%; (2) regional transition zones (RTZ) are characterized by less than 1,000 endemic species and an endemism rate lower than 50%; and (3) Regional

Mosaics (RM) are areas with an intermingling of vegetation types with distinct floras. Using this framework, White (1983, 1993) identified a total of 17 Afro-Malagasy phytochoria (nine RCE, five RTZ and three RM). However, although this remarkable and coherent chorological classification of Africa's vegetation was established using clearly defined concepts, it remains largely based on experts' (i.e. the AETFAT members) field observations and interpretation of empirical data, and hence has a limited reproducibility.

The development of computer-based categorization in parallel with the increasing availability of centralized species occurrence databases (Lavoie, 2013) has opened up the way for “numerical” biogeographical regionalization at global (Ficetola, Mazel, & Thuiller, 2017; Vilhena & Antonelli, 2015) and continental scales (Fayolle et al., 2014; Linder et al., 2005, 2012). Contrary to non-numerical inference, these numerical classifications are based on verifiable data using analytical methods leading to reproducible results (Linder et al., 2005; Vilhena & Antonelli, 2015). Denys (1980) was the first to undertake an analytical classification of Africa's vegetation using factorial analyses and distribution maps of 484 plant species. Linder et al. (2005, 2012) delimited bioregions using cluster analysis and the distribution data of 5,438 plant species. Both studies identified regions that were broadly congruent with those of White (1979). Focusing on tropical forests in Africa, Fayolle et al. (2014) identified six floristic clusters using correspondence analysis and tree inventories from 455 localities containing 1,175 tree species. These six clusters correlated well with broad climatic gradients, especially rainfall, and two of them were distinguished as “wet” and “moist” Guineo-Congolian forests. In all these studies, several bioregions in Africa remain only roughly and imprecisely delimited (e.g. Fayolle et al.,



2014; Linder et al., 2005), mainly because of a heterogeneous sampling effort (Magurran, 2017; Sosef et al., 2017), and because only a rather low proportion of the total flora—estimated to be c. 32,000 taxa for sub-Saharan tropical Africa (Klopper, Gautier, Chatelain, Smith, & Spichiger, 2007)—was used. In addition, several of the previous bioregionalizations were mainly based on tree distribution data (e.g. Denys, 1980; Fayolle et al., 2014) and thus ignore the potential contribution of other plant growth forms.

Evaluating the congruence between biogeographical regionalization and diversity patterns based on plant species of varying growth forms (e.g. trees, lianas, herbs and shrubs) is of interest for several reasons. First, plant growth forms are commonly recognized as rough proxies for functional-type subdivision (Lavorel, McIntyre, Landsberg, & Forbes, 1997) and can therefore reflect adaptation to specific ecological conditions (Galán de Mera, Hagen, & Vicente Orellana, 1999). They may respond differently to environmental conditions resulting in the variation of relative abundance, species richness and endemism along environmental gradients. Second, differences in life traits and cycles among growth forms may also affect biogeographical processes and distribution patterns (e.g. Engemann et al., 2016). For example, Thomson, Moles, Auld, and Kingsford (2011) found a “height effect” on seed dispersal distance, with taller species dispersing further than smaller species. Finally, since they are more easily collected, shrub or terrestrial herb species are expected to be better sampled than epiphytes, lianas or trees, potentially resulting in differing sampling bias among growth forms (Daru et al., 2017).

Evaluating congruence in diversity gradients and phylogeographical delimitations among growth forms will improve our understanding of the historical and environmental factors that have shaped global floristic patterns. The relative dominance of plant growth forms varies in space across tropical Africa (Sosef et al., 2017). However, few studies have compared plant distribution patterns within Africa across growth forms (but see Lovett, Rudd, Taplin, & Fridmodt-Moller, 2000) and none have been conducted at a continental scale.

Here, we revisit the bioregionalization of tropical Africa using the RAINBIO database (Dauby et al., 2016), one of the largest and most comprehensive tropical African floristic datasets. This dataset covers almost five times more species compared to previous attempts of bioregionalization (25,356 vs. 5,881 species for Linder et al., 2012). Specifically, we explore three main hypotheses regarding biogeographical regionalization in tropical Africa:

1. Biogeographical regionalization based on distribution data of the majority of plant species will not allow clear delimitation of bioregions in tropical Africa (White, 1965; p. 652).
2. Trees are good surrogates for delimitating bioregions in tropical Africa (Fayolle et al., 2014). We explore this hypothesis by inferring bioregions based on four growth forms, namely trees, terrestrial herbs, shrubs and lianas.
3. Previous diversity and endemism rate estimates based on the widely used chorological classification of White (1983) are biased due to limited sampling of the African flora (Linder et al., 2005).

We explore this by comparing species richness and endemism patterns based on previous studies (Linder et al., 2005; White, 1983, 1993) to those obtained with RAINBIO (Dauby et al., 2016) using White's phytogeographical system.

2 | MATERIALS AND METHODS

2.1 | Species occurrences and growth forms: the RAINBIO database

Vascular plant species distribution data were extracted from RAINBIO, a database of 593,861 unique georeferenced occurrences collected between the years 1782 and 2015, and representing 25,356 species in tropical Africa (Dauby et al., 2016; Sosef et al., 2017). RAINBIO covers tropical Africa sensu Klopper et al. (2007) broadly defined as sub-Saharan Africa excluding southern Africa and Madagascar, from 20° N to 25° S. In contrast to previous phytogeographical analyses (e.g. Fayolle et al., 2014; Linder, 2014; Linder et al., 2012), RAINBIO contains significant data for the main islands of the Gulf of Guinea.

Approximately 91% of all species, represented by 99% of the specimens, recorded in RAINBIO have been scored for one of nine different growth forms (Dauby et al., 2016). We considered the four most species-rich growth forms, representing c. 93% of the complete dataset: (1) terrestrial herbs (206,151 records, 10,481 species), (2) trees (145,325 records, 3,658 species, including “woody” monocots such as stemmed palm species and large *Dracaena*'s), (3) shrubs (134,795 records, 5,206 species) and (4) lianas (65,122 records, 1,757 species).

2.2 | Bioregions delimitation and sampling units

To delimit bioregions, we applied a recently developed network-based approach (Vilhena & Antonelli, 2015). This approach, based on a two-step procedure using taxon presence data, has been shown to be more efficient for bioregionalization of continental-scale data than widely used distance-based clustering methods (Bloomfield, Knerr, & Encinas-Viso, 2017). First, a bipartite network representing the relationship between all species and localities is constructed to identify the “nodes”, i.e. taxa linked with sampling units in which they are present. Second, the network structure is simplified using the map equation algorithm (Rosvall, Axelsson, & Bergstrom, 2009; Rosvall & Bergstrom, 2008). This algorithm uses an efficient random walk process along the network to highlight groups of nodes among which the “information” flows quickly, thereby identifying well-connected areas that represent sampling localities or units that tend to share species (Rosvall & Bergstrom, 2008). We used an interactive web application “INFOMAP BIOREGION” (Edler, Guedes, Zizka, Rosvall, & Antonelli, 2017) to perform this identification process. This application relies on an adaptive spatial resolution where sampling units vary in size according to the record density (Vilhena & Antonelli, 2015), which is convenient for dealing with geographical heterogeneity of botanical collections across Africa. We parameterized “INFOMAP BIOREGION” so that each sampling unit (a

cell of given latitude and longitude extent) ranged from 0.25° (minimum cell size) to 2° (maximum cell size), and contained at least 100 records (minimum cell capacity) and divided up to 0.25° when containing more than 1,000 records (maximum cell capacity). Consequently, this analysis was done on 587,597 specimens and 24,720 species. The optimal solution was selected from ten trials of the clustering algorithm, and the number of cluster cost was set at the default value (1.0).

All clusters identified by the network-based approach should not necessarily be interpreted as distinct bioregions, since this method also allows to identify “transition zones” between bioregions (Bloomfield et al., 2017; Vilhena & Antonelli, 2015). Here, we defined bioregions as clusters satisfying all of the following criteria: (1) at least 1,000 records; (2) an endemism rate of over 5% and (3) including more than 10% of characteristic species. We define “endemism rate” as the proportion of species restricted to a delimited region, whereas a “characteristic species” is a species with at least 50% of the records occurring in a delimited region. The proportion of characteristic species is expected to be less biased by taxonomic error and sampling or border effects than endemism rate. Both criteria led to identical selection of regions (see Table S1.1). “Transition zones” were defined as clusters with more than 1,000 records, but with a strict endemism rate lower than 5% or fewer than 10% of characteristic species. Finally, bioregions located outside or at the southern edge of the RAINBIO study area were excluded (Figure S2.1).

2.3 | Floristic relationships among bioregions

We characterized relationships among bioregions by computing their floristic dissimilarity, shared endemism and nestedness. Floristic dissimilarity was calculated for each pair of bioregions using the Bray–Curtis index (Bray & Curtis, 1957), which varies from 0 (same species composition and relative frequencies) to 1 (no shared species). Bioregion plant assemblages were then represented by an ordination in two-dimensional space using non-metric multidimensional scaling (NMDS; Kruskal, 1964) applied on the matrix of Bray–Curtis dissimilarity. This metric results in lower “stress value” (i.e. higher correlation between dissimilarity index and Euclidean distance in the ordination space) than other commonly used dissimilarity measures (Legendre & Legendre, 1998).

To highlight another facet of biogeographical affinities between the bioregions, we computed the number of shared species that are endemic to each pair, triplet, quadruplet (or more) of the bioregions, subsequently defined as “shared endemic species”. Groups of bioregions with at least 30 shared, endemic species were represented on the NMDS ordination space by overlying lines linking pairs of bioregions, or surrounding triplets (or more) of bioregions; the thickness of lines being proportional to the numbers of shared endemics.

Finally, we investigated the floristic nestedness pattern among bioregions. For each pair of bioregions A and B, we calculated the percentage of species of bioregion A occurring within bioregion B, and vice versa, providing an asymmetric matrix (Table S1.2). Nestedness values (above the 90th percentile) were represented in a circular plot using the “circlize” R package (Gu, Gu, Eils, Schlesner, & Brors, 2014).

2.4 | Biogeographical differences between plant growth forms

We calculated species richness and the number of endemic species for each growth form for each inferred bioregion. We then assessed the congruence of species richness and endemism patterns across bioregions for each pair of growth forms using Spearman’s rank correlation coefficient. We checked whether growth forms show congruent beta-diversity patterns across bioregions by computing the correlation between floristic dissimilarity matrices of each bioregion obtained using species belonging to each growth form. In addition, we assessed whether species distribution ranges across bioregions varied between growth forms.

Finally, we compared the biogeographical delimitations obtained by applying the bipartite network clustering analysis on each growth form separately. To balance the effect of lower sampling size compared to the initial analysis using the complete dataset, we changed the following parameters in “INFOMAP BIOREGION” (Edler et al., 2017): maximum grid cell size = 4°, minimum cell capacity = 50 records and maximum cell capacity = 500 records.

2.5 | Comparison of RAINBIO endemism and species richness estimates with previous biogeographical studies

For each phytochorion identified by White (1983, 1993), we compared the White (op. cit.) and Linder et al. (2005) estimates of species richness and the numbers of strict endemics with those obtained using the RAINBIO database. A shapefile of the phytochoria defined by White (1983) was used (Figure S2.2) and values for each phytochorion were extracted from RAINBIO. Six phytochoria that are not sufficiently covered by the RAINBIO dataset (Cape RCE, Karoo-Namib RCE, Kalahari/Highveld RTZ, Tongaland-Pondoland RM, Sahel RTZ, Sahara RTZ) were not included.

Apart from the bipartite network analysis, all analyses were conducted in R 3.3.2 (R Core Team, 2016). Maps were prepared with ArcMAP 10.4.1 (ESRI, 2016) and projected using the cylindrical equal-area Behrmann projection.

3 | RESULTS

3.1 | Bioregion identification

A final list of 16 bioregions and 11 transition zones was identified for tropical Africa (Figure 1, Tables 1 and S1.1, Appendix S3 in Supporting Information); three of the bioregions will be referred to below as “sub-bioregions” as they resulted from a second nested bipartite network analysis. One of the clusters obtained from the first bipartite network analysis corresponded to the Guineo-Congolian forests and was highly oversampled compared to the others (49% of the total number of records, for only 19.6% of the surface area). Hence, we applied a second bipartite network analysis within this cluster to investigate phytogeographical delimitations within

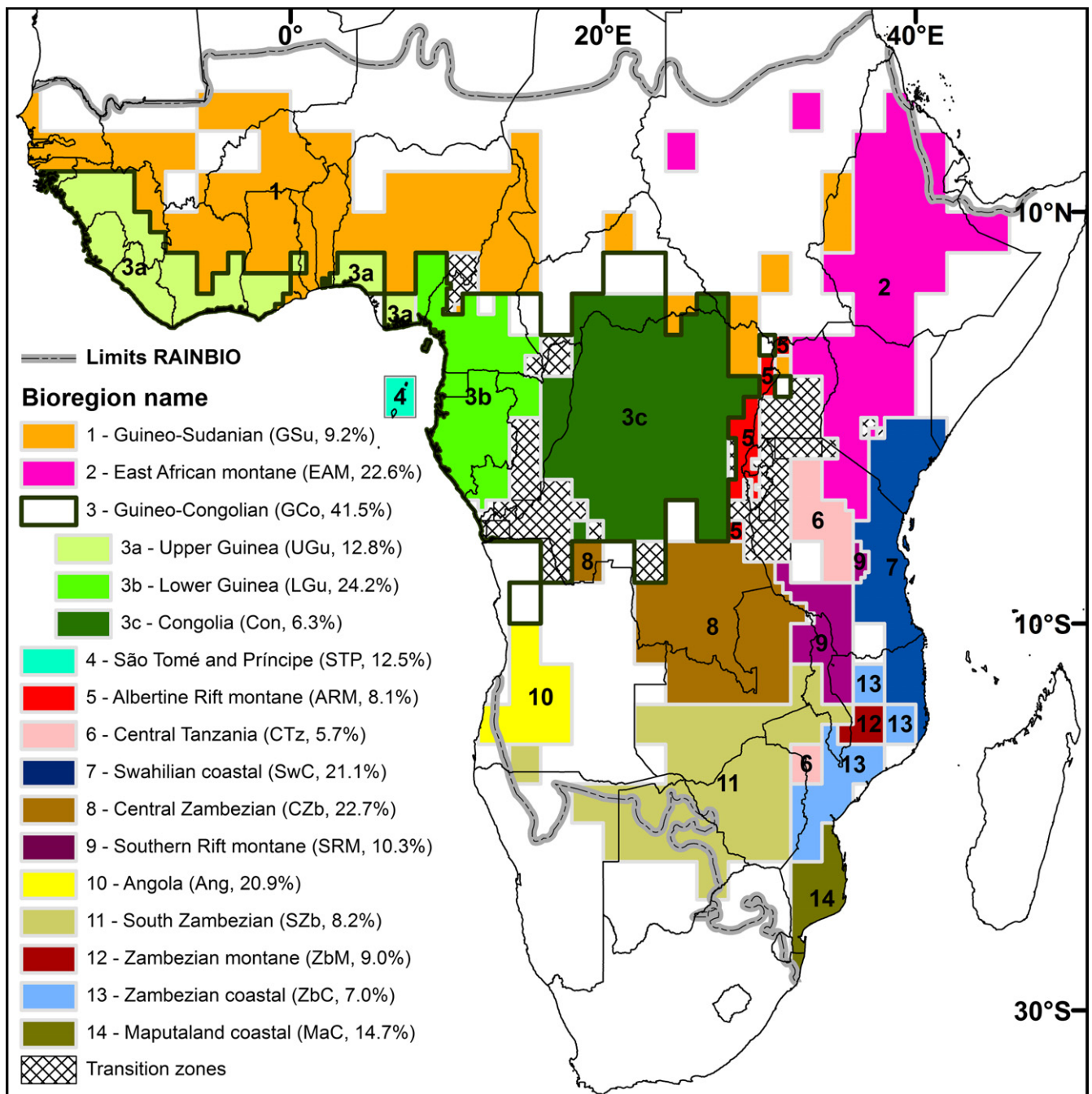


FIGURE 1 The main floristic bioregions and transition zones of tropical Africa based on bipartite network clustering analysis of 24,719 plant species. Only regions with at least 1,000 records are represented. Hatching indicates transition zones, with strict endemism rates lower than 5%. Abbreviations (three-letter codes) used in following tables and figures as well as strict endemism rates for each bioregion are indicated in brackets

Guineo-Congolian forests. This two-step analysis resulted in a total of 60 (sub-)clusters (Figure S2.1, Table S1.1), which were filtered out and classified (see Materials and methods) to obtain the final map (Figure 1, Appendix S3).

West and Central Africa were subdivided into four large (sub-) bioregions of mostly lowland areas: the Guineo-Sudanian bioregion in the North and the Guineo-Congolian bioregion, which was further subdivided into Upper Guinea, Lower Guinea and Congolia

(Figure S2.3). Two of the islands of the Gulf of Guinea, São Tomé and Príncipe, also formed a distinct bioregion. The third largest island of the Gulf of Guinea, Bioko, was identified as a transition zone (Table S1.1, Figure S2.1). Eastern and southern Africa—not including South Africa and Namibia as they are not covered by the RAINBIO dataset—were subdivided into 11 bioregions, four of which are associated with montane areas (East African montane, Albertine Rift montane, Southern Rift montane and Zambebian montane), four

TABLE 1 Summary statistics for the 14 tropical African bioregions and 3 sub-bioregions, based on the RAINBIO database (Figure 1). For each statistic, the three highest values are highlighted in grey in the table (not considering the Guineo-Congolian region which is divided in three sub-bioregions)

Bioregion names	Surface (km ²)	No. records	Collection density (records/100 km ²)	No. families (% endemic)	No. genera (% endemic)	No. species (% endemic)
1. Guineo-Sudanian	2,360,475	58,662	2.49	198 (0)	1,329 (0.8)	4,631 (9.2)
2. East African montane	1,459,472	40,999	2.81	203 (1.5)	1,388 (8.1)	5,349 (22.6)
3. Guineo-Congolian	2,889,129	290,920	10.07	222 (3.6)	1,806 (13.5)	10,060 (41.5)
3a. Upper Guinea	688,969	70,112	10.18	194 (1.5)	1,313 (1.8)	4,324 (12.8)
3b. Lower Guinea	676,088	148,432	21.95	209 (1.4)	1,498 (5.1)	6,928 (24.2)
3c. Congolia	1,524,072	38,807	2.55	180 (0)	1,205 (0.6)	3,875 (6.3)
4. São Tomé and Príncipe	1,040	3,026	290.96	121 (0)	430 (0.2)	758 (12.5)
5. Albertine Rift montane	137,558	19,276	14.01	185 (0)	1,059 (0.6)	3,211 (8.1)
6. Central Tanzania	240,215	6,840	2.85	143 (0)	682 (0)	1,975 (5.7)
7. Swahilian coastal	535,924	47,977	8.95	222 (0.5)	1,483 (4.3)	5,534 (21.1)
8. Central Zambebian	881,580	26,697	3.03	190 (0)	1,147 (1.1)	4,583 (22.7)
9. Southern Rift montane	261,163	22,269	8.53	193 (0)	1,251 (2)	4,730 (10.3)
10. Angola	283,184	1,597	0.56	115 (0)	395 (0.5)	770 (20.9)
11. South Zambebian	1,241,128	8,536	0.69	167 (0)	902 (0.8)	2,490 (8.2)
12. Zambebian montane	59,472	3,810	6.41	151 (0)	604 (0.2)	1,216 (9.0)
13. Zambebian coastal	327,983	8,193	2.5	174 (0)	962 (0.6)	2,286 (7.7)
14. Maputaland coastal	165,506	5,376	3.25	147 (0)	720 (2.5)	1,508 (14.7)

corresponded to mid-elevation plateau areas (Central Tanzania, Central Zambebian, South Zambebian, Angola) and three to lowland coastal areas (Swahilian coastal, Zambebian coastal and Maputaland coastal) (Figure S2.3). Transition zones occurred mainly (1) between Lower Guinea and Congolia, (2) around the Cameroon Volcanic Line and (3) East of the Albertine Rift bioregion (Figure 1).

3.2 | Bioregion diversity and endemism

The number of families, genera and species were highly correlated among bioregions (Figure S2.4). Lower Guinea (#3b, Figure 1), Swahilian coastal (#7) and East African montane (#2) bioregions had the highest numbers of recorded families (203–222), genera (1,388–1,498) and species (5,349–6,928) (Table 1, Table S1.1), and also displayed among the highest rates of species endemism (21%–24%), together with the Central Zambebian (#8) (23%) and Angolan (21%) bioregions (Figure 1).

3.3 | Floristic relationships among bioregions

The first axis of the NMDS analysis separated bioregions from West and Central Africa and those from eastern and southern Africa (Figure 2). This subdivision above the bioregion level was more visible when overlaying numbers of shared endemic species between and among (sub-)bioregions. Many shared endemic species (2,483 species) were found between Lower Guinea (#3b), Upper Guinea (#3a), Congolia (#3c) and Guineo-Sudanian (#1), and most particularly between the pairs Lower Guinea and Congolia (624 species), Lower Guinea and Upper Guinea (435 species), Upper Guinea and Guineo-

Sudanian (386 species), and the triplet Lower Guinea, Upper Guinea and Guineo-Sudanian (357 species). São Tomé and Príncipe (#4) only shared endemic species (54 species) with Lower Guinea (#3b). In eastern Africa, high levels of shared endemic species (982 species) were found between the East African montane (#2), Swahilian coastal (#7) and Southern Rift montane (#9) bioregions. The Angola (#10) and Zambebian montane (#12) bioregions were each connected to single bioregions, Central Zambebian (#8) and Zambebian coastal (#13) respectively. Only the East African montane (#2), Albertine Rift montane (#5) and Central Zambebian (#8) bioregions shared at least 30 endemic species with western-central bioregions (Figure 2).

Floristic nestedness patterns among bioregions (Figure 3) identified two geographically coherent groups of bioregions linked to each other, once again separating West and Central Africa from eastern and southern Africa.

3.4 | Comparison of plant growth forms

Terrestrial herbs were the dominant growth form in all bioregions, often accounting for >50% of the species. Of the four analysed growth forms, lianas were least frequent, except in the Guineo-Congolian (sub-)bioregions (#3a, 3b, 3c) where their species richness was similar to that for shrubs (Figure 4). Shrubs displayed the highest rates of strict species endemism in most bioregions, exceeded only by terrestrial herbs in five bioregions dominated by open vegetation (Table 2). Trees and lianas displayed below-average rates of endemism, except in the Guineo-Congolian (sub-)bioregions (Table 2).

Species richness and endemism patterns among bioregions were mostly similar for the different growth forms (Figure S2.5): correlation

between them was higher between lianas and trees, and shrubs and trees, and lowest between herbs and lianas, and herbs and trees. Mantel correlation tests on floristic similarity matrices between bioregions and growth form followed the same general trend (Table S1.3).

The network clustering analyses conducted separately on each growth form produced classifications with contrasting geographical resolution in West and Central Africa versus eastern and southern Africa (Figure 5): while the tree and liana datasets resulted in the identification of a single, large bioregion in eastern and southern Africa, several clusters were obtained for this area using the herb and shrub datasets. In contrast, the herb dataset was the only one showing no subdivision within the Guineo-Congolian region. Overall, the delimitation obtained for the shrub dataset was most similar to that obtained with the complete RAINBIO dataset (Figure 1).

The biogeographical ranges of the different growth forms are shown in Figure S2.6. About 50% of the species were endemic to one bioregion and about 12% of the species were represented in >5 different bioregions. Shrubs tended to have more restricted distributions (8% of the species present in >5 bioregions and 53% of the species endemic to one bioregion), while terrestrial herbs tended to be more widespread (12.5% of the species present in >5 bioregions and 47% of the species endemic to one bioregion).

3.5 | Endemism and species richness within White's phytogeographical system

We compared the RAINBIO sampling with previous studies using White's phytogeographical system (Figure S2.2, Table 3). Our results show that White (1983, 1993) underestimated species richness and

overestimated endemism rates for most phytochoria. In contrast, Linder's dataset (Linder et al., 2005), while representing only c. 20% of the species of the RAINBIO dataset, provides similar phytochoria endemism rankings to those inferred from the RAINBIO data. For both datasets, the highest percentage of endemic species was observed for the Guineo-Congolian and the Zambezi RCE while the lowest values were found for Guineo-Congolia/Sudania RTZ and the Lake Victoria RM (Table 3).

4 | DISCUSSION

4.1 | Biogeographical regionalization of tropical Africa

Our network-based analysis using the RAINBIO database retrieved a total of 16 (sub-) bioregions (Figure 1) for tropical Africa. The delimitation of these bioregions is highly congruent with previous African bioregionalization attempts (Clarke, 1998; Denys, 1980; Fayolle et al., 2014; Linder et al., 2005, 2012; White, 1983), although for the first time we present a bioregionalization that is more geographically detailed than previous attempts. These results also refute White's claim that no clear picture would emerge when all species of a region are taken into account to delimitate biogeographical regions (Linder et al., 2005; White, 1965).

Above the scale of the bioregion, endemism and nestedness patterns highlight a distinction between West and Central Africa on the one hand, and eastern and southern Africa on the other (Figures 2 and 3). While the eastern and southern parts of Africa are characterized by a mosaic of 10 different bioregions, West and Central Africa

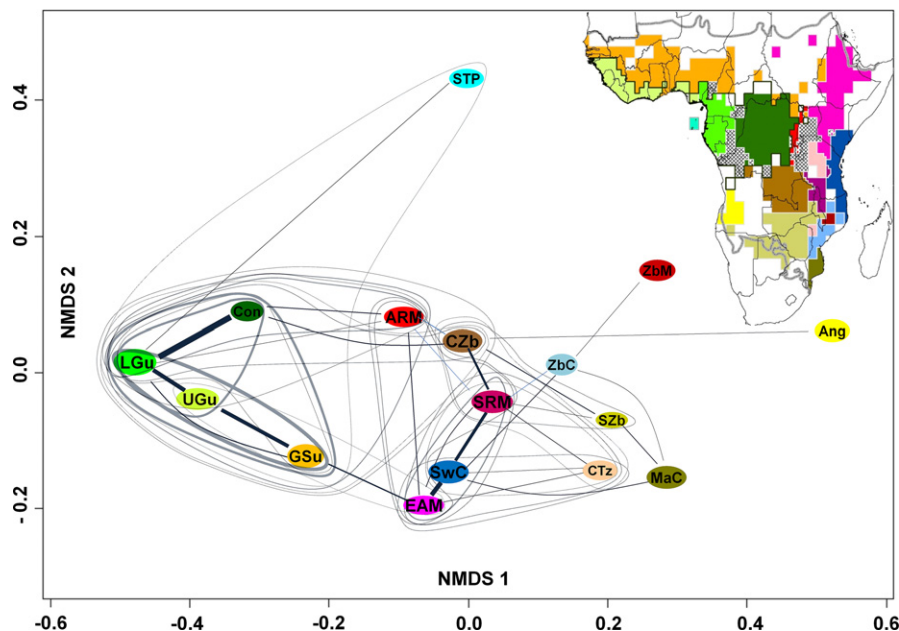


FIGURE 2 Non-metric multidimensional scaling (NMDS, stress value = 0.08) ordination of the floristic assemblages of the 16 tropical African bioregions based on the Bray–Curtis distance. Each bioregion is represented by a three-letter code detailed in Figure 1, the font size of which is proportional to the logarithm of the number of endemic species. Colour codes for bioregions are the same as in Figure 1 (see the inset). Line segments connecting pairs of bioregions and closed lines surrounding three bioregions or more indicate bioregions sharing at least 30 endemic species (from 30 to 630 spp., proportional to line thickness)

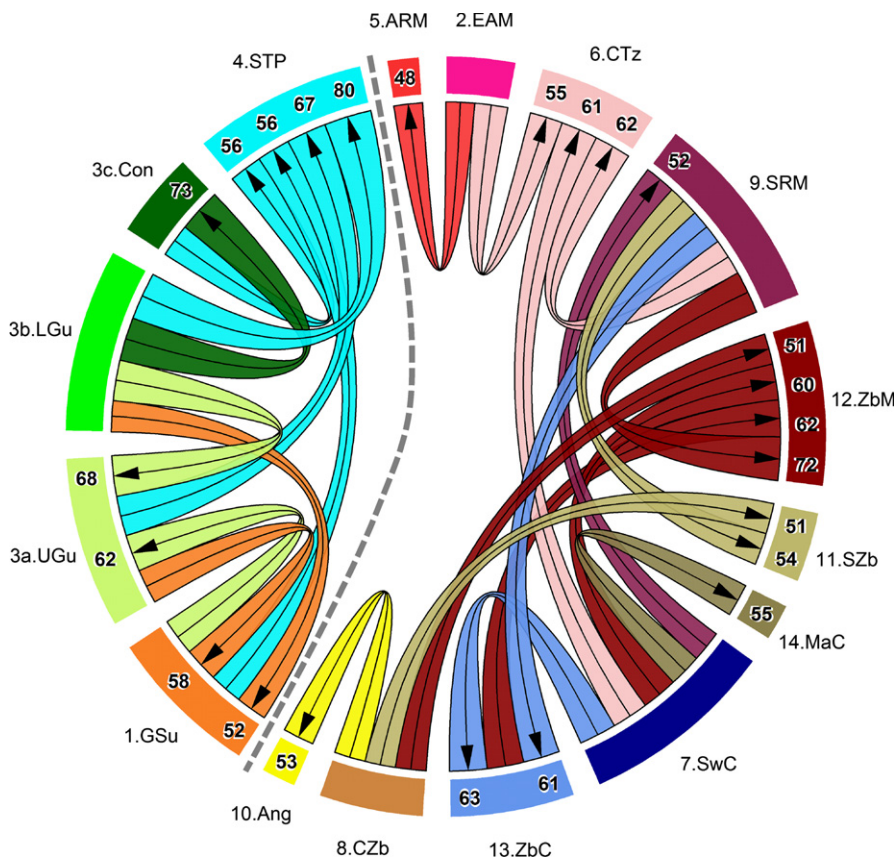


FIGURE 3 Nestedness patterns of plant species among the 16 floristic bioregions of tropical Africa. Values express the percentage of species of the “destination” bioregion (arrow head) nested within (i.e. occurring in) the “origin” bioregion (start of arrow). Only values above the 90th percentile are shown. Dashed line highlights the separation between the West and Central African regions from the eastern and southern African ones. See Table S1.2 for the underlying matrix and Figure 1 for abbreviations of bioregion names

contain only five bioregions (four large and one small, Figure 1). The phylogeographical complexity of East Africa has already been highlighted by Linder et al. (2005, 2012) who suggested that this area presents a “very complex biogeographical mixture” generated by distinctive responses of biologically different taxa to complex topographical and environmental gradients.

Our analyses highlighted several areas not previously recognized as bioregions. The São Tomé and Príncipe bioregion (#4) covered the islands of the Gulf of Guinea and represented the smallest bioregion in our study area coupled with the highest collection density of tropical Africa (Table 1; Sosef et al., 2017). This bioregion is also characterized by its high rate of endemism, as already shown by several studies (Droissart, 2009; Jones, 1994; Sosef et al., 2017). São Tomé and Príncipe (#4) has not been assessed in most previous classifications (Table S1.4), but has been identified as a distinct entity by Stévant (2003) and Droissart (2009), based on distribution patterns of Orchidaceae. Indeed, Stévant (2003) considered the oceanic islands of the Gulf of Guinea as a distinct biogeographical entity within the Guineo-Congolian (#3). This statement is based on the observation of a high level of endemism of the whole flora, including the presence of endemic genera. In any case, this bioregion appeared to be linked to the Lower Guinea (#3c) sub-bioregion, and to a lesser extent to the whole Guineo-Congolian (#3) and Guineo-Sudanian (#1) bioregions (Figure 2). This relationship was also illustrated by the fact that this bioregion had a significant subset of its flora (80%) nested within the Lower Guinea sub-bioregion (Figure 3), and by the

fact that São Tomé ended up in Moist Central African cluster in the study by Fayolle et al. (2014).

The new Central Zambezan (#8) and South Zambezan (#11) bioregions are located in southern (mostly south-eastern) DRC/northern Zambia, and southern Zambia/most of Zimbabwe respectively. The Central Zambezan (#8) harboured one of the highest endemism rates of the study area (Table 1, 22.7%). These two bioregions are included in both White’s large phytochorion Zambezan RCE (Figure S2.2; White, 1983) and the Zambezan central region delimited by Linder et al. (2005). White qualified the Zambezan RCE as being the “richest and most diversified flora, and certainly shows the widest range of vegetation types” (White, 1983; pp. 89). Thus, it is not surprising that this phytochorion was divided into several bioregions with the inclusion of additional data. The Zambezan phytochorion was also divided into three narrower phytochoria in the analyses of Linder et al. (2005). However, there was no further subdivision of the Zambezan RCE when analysing a larger plant and animal dataset (Linder et al., 2012). The Central Zambezan bioregion (#8) encompass, among others, the Upper Katanga area in southern DRC and northern Zambia, which is known for its endemic-rich plant communities associated with metalliferous substrates (Meerts & Hasson, 2016).

The Zambezan montane (#12) bioregion, surrounded by the Zambezan coastal bioregion (#13), covers a small, mainly mountainous, area around Mount Mulanje in Malawi, and Cucutea, Inago and Namuli mountains in northern-central Mozambique (Figure 1;

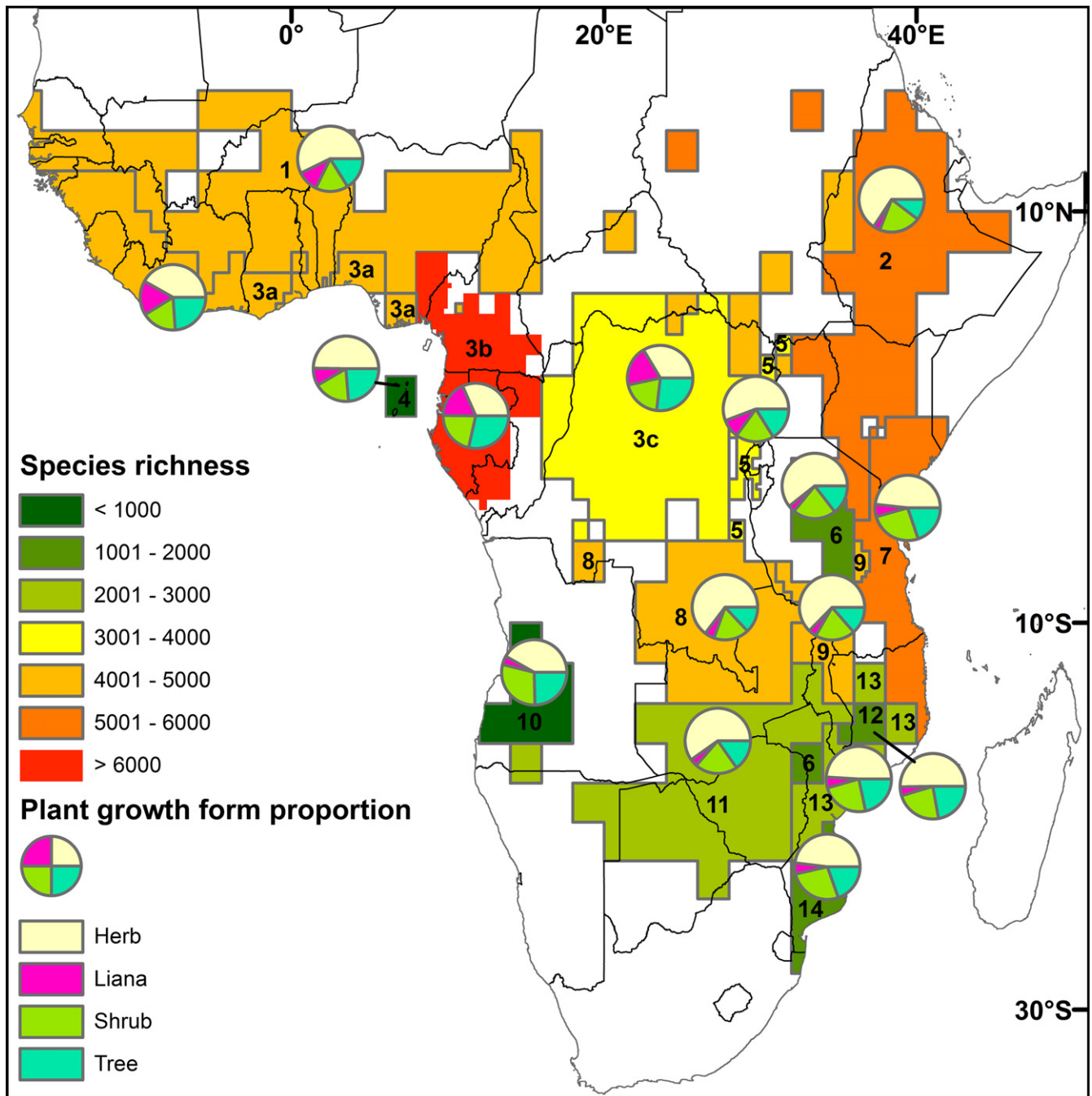


FIGURE 4 Plant species diversity patterns for the 16 bioregions of tropical Africa. Pie charts indicate for each region the proportion of herb, tree, shrub and liana species. The colour indicates the range of species richness per bioregion

Figure S2.3). These small mountains are defined as granitic inselbergs surrounded by rain forests (Bayliss et al., 2014). They were already described in the vegetation maps of Flora Zambesiaca (Wild & Barbosa, 1968) as Moist Evergreen forests surrounded by savanna-dominated areas. These areas have recently been highlighted as containing a rich biodiversity with numerous endemic species (Bayliss et al., 2014; Timberlake et al., 2007, 2009). In addition, the Zambezian montane bioregion (#12) appeared to be floristically different from other bioregions with few shared endemics

(Figure 2). Our results also confirm the floristic distinctness of this region from neighbouring mountain ranges stretching over Tanzania, Kenya and Ethiopia (Bayliss et al., 2014; Burgess et al., 2007) even if a significant proportion of its flora is shared with other bioregions especially the Southern Rift montane (#9) (72%, see Figure 3). The fact that, with the availability of more data, we can now separate this bioregion from the other bioregions, strongly underlines its floristic uniqueness and stresses the importance of conservation efforts in the region (Bayliss et al., 2014). The Zambezian montane

TABLE 2 Species endemism rate (%) in tropical African bioregions for each plant growth form. The highest value for each bioregion (sub-bioregion) is highlighted in grey

Bioregion names	Herb	Liana	Shrub	Tree
1. Guineo-Sudanian	14	3	12	4
2. East African montane	30	10	34	16
3. Guineo-Congolian	23	53	50	52
3a. Upper Guinea	10	14	18	16
3b. Lower Guinea	20	30	46	40
3c. Congolia	5	11	14	12
4. São Tomé and Príncipe	7	14	23	13
5. Albertine Rift montane	10	9	15	8
6. Central Tanzania	9	3	6	3
7. Swahilian coastal	19	21	27	26
8. Central Zambezan	31	8	25	10
9. Southern Rift montane	14	4	10	5
10. Angola	26	3	29	9
11. South Zambezan	11	1	16	4
12. Zambezan montane	13	2	12	2
13. Zambezan coastal	9	3	12	5
14. Maputaland coastal	19	8	27	11

(#12) bioregion, however, does not include Mt. Chipero and Mt. Mabu localized south of this area (Bayliss et al., 2014). This may be explained by the lack of data from these less well-explored regions in the RAINBIO dataset. For instance, most botanical data from recent expeditions to these mountains (Bayliss et al., 2014; Timberlake et al., 2007, 2009) were not included in the RAINBIO database. The Zambezan-Angolan region identified by Linder et al. (2005) partly matches our Angola bioregion (#10, Figure 1). However, this area remains largely under-collected (Linder et al., 2005 and see below for a caveat on collection density; Sosef et al., 2017).

Our results separate the Zanzibar-Inhambane RM of White (1983) into two main bioregions: Swahilian coastal (#7) and Zambezan coastal (#13). This is consistent with the study of Clarke (1998) who divided the Zanzibar-Inhambane region into the Swahilian RCE (north) and Swahilian/Maputaland (south) RTZ, while White (1983, 1993) considered them together as a mosaic, because he perceived this region as floristically depauperate, containing only several hundred endemic species and just four endemic genera. Our study supports the division and suggests that these two bioregions should be considered as regional centres of endemism with >5% endemic and >10% characteristic species (Table S1.1). Both regions include the East African coastal forests characterized by high levels of plant species diversity and endemism (Burgess & Clarke, 2000; Burgess, Clarke, & Rodgers, 1998; Couvreur, Gereau, Wieringa, & Richardson, 2006). These regions were not identified by Linder et al. (2005, 2012), being part of the “Zambezan central” region and the “Mozambique” region respectively (Table S1.4).

4.2 | Delimitations within the Guineo-Congolian bioregion

Interestingly, our analysis placed the floristic boundary between the Upper Guinea and Lower Guinea bioregions at the Cross River area in eastern Nigeria (Figure 1) and not in the Dahomey Gap as previously inferred by White (1979) and Fayolle et al. (2014). White (1979) suggested that the Dahomey Gap “provides a better separation” between Upper and Lower Guinea mainly based on the distribution of Ebenaceae tree species. Our results are more in line with those of Clayton and Hepper (1974) (based on the distribution of West African grasses), Léonard (1965) (based on the distribution of species of the Euphorbiaceae family) and Linder et al. (2005, 2012) where Upper Guinea extends up to eastern Nigeria. Together, these results suggest that the Cameroon Volcanic Line should be considered as a stronger phyto-geographical boundary than the Dahomey Gap in Benin and Togo. Interestingly, this topographic barrier is also visible at the intraspecific genetic level for species with a west to central African distribution (e.g. *Erythrophleum ivorense* A. Chev. Duminil et al., 2013).

4.3 | Transition zones or regional mosaic?

Our study revealed 11 areas that were qualified as transition zones. These zones displayed low endemism rates (Figure 1) suggesting overlap and/or mixture between biogeographical regions. This result is supported by the fact that most of these areas are characterized by strong floristic turnover rates (see Sosef et al., 2017). Some of these zones correspond to those of White (1983), for example the Lake Victoria RM (Figure S2.2) with our large area from southern Uganda to western Tanzania and eastern Democratic Republic of the Congo, including some parts of Rwanda-Burundi. It also partially matches Linder et al. (2005) Congolian transition region, which he also qualified as a RM. Hence, the qualification of RM is perhaps more appropriate than Transition zone for some of these cases. These examples highlight the fact that the method we used does not distinguish between mosaic and transition zones unless the sampling is dense enough to delimit the area into a sufficiently fine-scale grid.

Surprisingly, the Cameroon Volcanic Line, located over a large mountainous area stretching NE–SW from the Gulf of Guinea to c. 600 km inland, was also identified as a transition zone. This region presents one of the best collected and most species-rich areas of tropical Africa (Cable & Cheek, 1998; Cheek, Harvey, & Onana, 2010; Cheek, Onana, & Pollard, 2000; Cheek, Pollard, Darbyshire, Onana, & Wild, 2004; Harvey, Pollard, Darbyshire, Onana, & Cheek, 2004; Harvey, Tchiengué, & Cheek, 2010; Linder, 2001b; Sosef et al., 2017) and has been described as an important part of the Afromontane and tropical Afroalpine regions (Gehrke & Linder, 2014; White, 1978, 1981). However, although our network-based analyses can distinguish it from other regions, its endemism rate is only 3.4% (Table S1.1, Figure S2.1). This rate is likely to be underestimated because of the rough delimitation enforced by squared grid

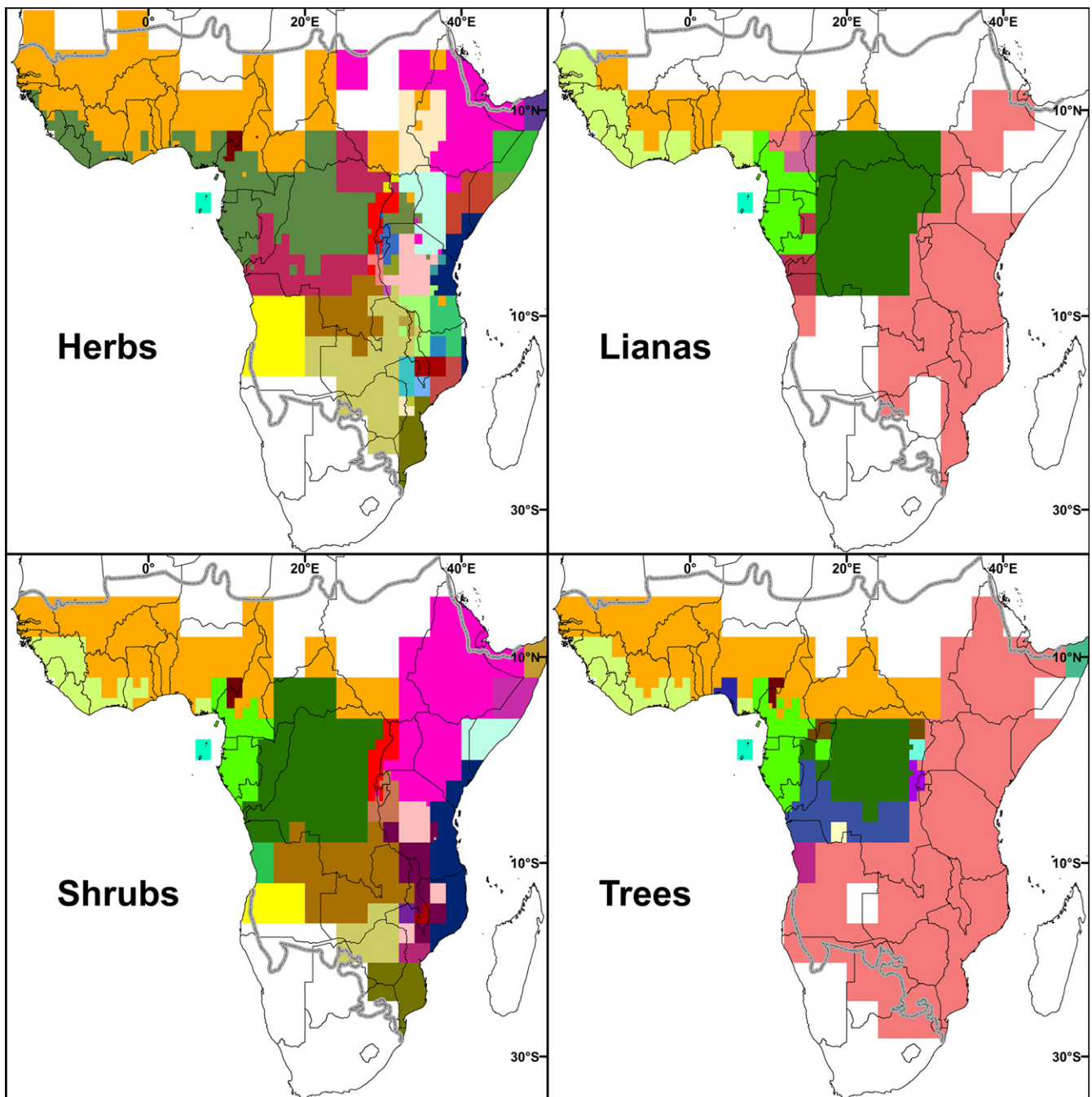


FIGURE 5 Bioregionalization of tropical Africa based on datasets restricted to each plant growth form

cells. Such an imprecise delimitation leads to the inclusion of many lowland species and excludes some records of actual endemics leading to decreasing endemism rates (see Figure S2.7), an issue already highlighted by White (1981) and Linder et al. (2005, 2012).

4.4 | Incongruence in diversity and phytogeographical patterns among growth forms

Most classifications proposed for Africa have been mainly based on tree species distribution (Fayolle et al., 2014; Léonard, 1965; White, 1979) despite the importance of considering other plant growth

forms to understand diversity patterns (e.g. Engemann et al., 2016). Additionally, most ecological studies in tropical forests only focus on tree components (Decocq, Beina, Jamoneau, Gourlet-Fleury, & Closeset-Kopp, 2014), omitting other growth forms (e.g. Anderson-Teixeira et al., 2015; Liang et al., 2016). Our results suggest that tree species cannot be used as a proxy of the whole flora for delimitating phytogeographical boundaries in tropical Africa. We show that other growth forms provide complementary information. Indeed, bioregionalization was better resolved in closed forest vegetation types when using trees and lianas, in open vegetation types using terrestrial herbs, while shrubs showed good discrimination power in all

TABLE 3 Plant species richness and endemism of the tropical African phytochoria as delimited by White (1983), comparing his estimates (White, 1993) and Linder's dataset (Linder et al., 2005) with that obtained from RAINBIO. The two last columns give the proportion of species (SR) or endemic species (ES) sampled with RAINBIO relative to the estimates given by White (1983). Only phytochoria sufficiently covered by the RAINBIO database are indicated. SR = species richness; ES = number of endemic species; ER = endemism rate; RCE = regional centre of endemism; RTZ = regional transition zone; RM = regional mosaic

Phytochorion	White's estimates			Linder's plant dataset			RAINBIO dataset			Proportion sampled (%)	
	SR	ES	ER (%)	SR	End	ER (%)	SR	ES	ER (%)	SR	ES
Guineo-Congolian RCE	8,000	6,400	80	1,375	399	29	9,597	3,027	31	120	48
Zambezian RCE	8,500	4,590	54	1,725	377	22	9,008	2,368	26	106	52
Sudanian RCE	~3,750	~1,238	~33	684	6	1	4,341	240	5	116	20
Somali-Masai RCE	>2,500	>1,250	>50	931	103	11	5,998	1,197	20	240	96
Afromontane RCE	4,000	3,000	75	1,564	78	5	8,287	769	9	208	26
Guinea-Congolia/Zambezia RTZ	2,000	~50	~2.5	571	28	5	2,694	149	5	135	298
Guinea-Congolia/Sudania RTZ	≤2,000	?	?	711	5	1	5,420	181	3	271	N/A
Lake Victoria RM	3,000	? Very few	?	504	3	1	3,925	135	3	131	N/A
Zanzibar-Inhambane RM	3,000	? Several hundred	?	576	48	8	5,709	1,052	18	191	N/A

vegetation types (Figure 5). This contrasts with the good congruence observed among biogeographical patterns when analysing plants, mammals, birds, amphibians and reptiles (Linder et al., 2012).

High congruence across both bioregion delimitation and diversity patterns, between lianas and trees, is in agreement with what has been observed at a finer spatial scale in Bolivian rain forests (Macía, Ruokolainen, Tuomisto, Quisbert, & Cala, 2007), and suggests that floristic patterns for these two growth forms result from common ecological and historical processes.

The floristic patterns inferred from shrubs closely resemble those inferred when considering the complete dataset (Figures 1 and 5). In addition, shrub species tend to be more range-restricted than other growth forms (Table 2; Figure S2.6). Thus, shrub floristic patterns could be considered as a good proxy for delimitating bioregions and inferring floristic diversity at least at the scale of tropical Africa, with the exception of the Sahel and Sahara given the low prevalence of shrubs in those regions (Sosef et al., 2017).

4.5 | Updating species richness and endemism for bioregions

Based on White's (1983) African vegetation delineation, we revaluated species and endemism values for each phytochorion. For all phytochoria, we found higher species richness values (Table 3) than estimated by White (1983, 1993) or Linder et al. (2005). Our numbers are quite close to those reported by Clarke (1998), who estimated the Swahilian RCE to have 4,000 species (1,200 endemic), while the Swahilian/Maputaland RTZ would be inhabited by 3,300 species (100 endemic) (Table 1, Table S1.1). Based on the RAINBIO dataset, the most species-rich regions are the Guineo-Congolian RCE, the Zambezian RCE and the Afromontane RCE, each harbouring more than 8,000 species (Table 3). Less species-rich regions are Guinea-Congolia/Zambezia RTZ (2,694 species) and Lake Victoria RM (3,925 species). In addition, the RAINBIO dataset suggests lower

endemism rates than suggested by White (1983, 1993). For example, endemism rates are five times lower than White's estimates for the Sudanian RCE (5% vs. 33%) and Afromontane RCE (9% vs. 75%).

Although White (1993; p. 236) argued that the figures he used to define phytochoria in his chorological classification of Africa (see Table 2) are "not arbitrary" and based "on the patterns that exist on the ground and have been chosen to reflect that reality", his mapping was based on a limited dataset (only a small part of the species was used, and of our dataset nearly 50% of the records were collected since 1980, see Sosef et al., 2017) and not on a computer-based categorization. Comparing White's estimates with those obtained using the RAINBIO database, we show that the endemism threshold he used to define the main categories for Africa may have overestimated the number of endemic species in some bioregions. Higher species richness was already shown by Linder et al. (2005), who also found endemism rates to be less than 30% for all of White's phytochoria (except for the Cape RCE). The authors indicate that the low levels of endemism they found were possibly linked to sampling artefacts, as their sampling was biased towards more widespread species. Alternatively, Linder et al. (2005) also suggested that White underestimated species richness and thus overestimated endemism due to limited information on species' distributions and underestimation of their respective distribution ranges. Taking into account a larger updated database covering most plant species from tropical Africa confirms Linder et al.'s (2005) second hypothesis: compared to White (1993), species richness is much higher while endemism is overestimated. Linder et al. (2005) on the other hand slightly underestimated endemism rates.

5 | CONCLUSIONS

Three key conclusions can be drawn from our results: (1) Centralized databases and adequate classification algorithms, are essential tools



for objective biogeographical regionalization. (2) The limited attention to non-tree growth forms in previous biogeographical regionalizations for Africa have neglected their distinct contributions to phytogeographical patterns, leading to a biased perspective. (3) Previous phytogeographical analyses have tended to underestimate plant species richness and overestimate endemism of the main bioregions of tropical Africa. Our approach of redefining phytogeographical regions in tropical Africa using the RAINBIO database provides a timely framework for a wide range of scientists and conservationists. Our results align well with previous works; however, we improved boundary accuracies between bioregions, and detected new or poorly described bioregions. We achieved a finer characterization of the main African plant bioregions in terms of species richness and endemism, which will inform both future policy and management initiatives, and the selection of priority conservation areas. Spatial patterns for main plant growth forms may underline different evolutionary processes, dispersal capacities or ecological tolerances, and their respective contributions to global floristic patterns should be taken into account. Finally, the limited coverage of RAINBIO on tropical Africa only stresses the need to continue combining and sharing existing datasets, while at the same time collecting more data to fill the gaps that still remain in our knowledge of the African flora.

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DATA ACCESSIBILITY

The GIS layer used to generate Figure 1 for this study is available as a shapefile from: <https://doi.org/10.5281/zenodo.1155216> and https://github.com/gdauby/africa_bioregions

BIOSKETCHES

Vincent Droissart is a tropical botanist interested in assessing plant diversity patterns at local and regional scales in Africa. A large part of his research is also focused on taxonomy and conservation of African orchids.

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The RAINBIO consortium (<http://rainbio.cesab.org>) aims to synthesize plant distribution data across tropical Africa in order to undertake studies in conservation, biodiversity and evolution of the African flora.

Author contributions: V.D., G.D., O.J.H. and T.L.P.C. conceived the ideas; G.D., V.D., O.J.H., D.J.H., B.A.M., B.S., M.S.M., T.S., A.B.O., J.C.S. and J.J.W. provided data; V.D., G.D. and O.J.H. analysed the data; V.D., G.D. and T.L.P.C. led the writing with assistance from all other co-authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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