



# A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas

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**Abstract**

**Aim:** In tropical Africa, savannas cover huge areas, have high plant species richness and are considered as a major natural resource for most countries. There is, however, little information available on their floristics and biogeography at the continental scale, despite the importance of such information for our understanding of the drivers of species diversity at various scales and for effective conservation and management. Here, we collated and analysed floristic data from across the continent in order to propose a biogeographical regionalization for African savannas.

**Location:** We collated floristic information (specifically woody species lists) for 298 samples of savanna vegetation across Africa, extending from 18° N to 33° S and from 17° W to 48° E.

**Taxa:** We focused on native woody species.

**Methods:** We used ordination and clustering to identify the floristic discontinuities and gradual transitions across African savannas. Floristic relationships, specificity and turnover, within and between floristic clusters, were analysed using a (dis-)similarity-based approach.

**Results:** We identified eight floristic clusters across African savannas which in turn were grouped into two larger macro-units. Ordinations at species and genus levels showed a clear differentiation in woody species composition between the North/West macro-unit and the South/East macro-unit. This floristic discontinuity matches to the High (i.e. N&W) and Low (S&E) division of Africa previously proposed by White (1983) and which tracks climatic and topographical variation. In the N&W savannas, the floristic gradient determined by rainfall was partitioned into the Sudanian (drier) and Guinean (wetter) clusters. Within the highly heterogeneous S&E savannas and woodlands, six clusters were identified: Ugandan, Ethiopian, Mozambican, Zambezian, Namibian and South African.

**Main conclusions:** The proposed pan-African classification of savannas and woodlands might assist the development of coordinated management and conservation policies.

**KEYWORDS**

biogeographical regions, clustering, correspondence analysis, distance decay in similarity, floristic clusters, indicator species, rainfall and altitude/temperature gradients, savannas

**1 | INTRODUCTION**

Tropical savannas, where trees and C4 grasses coexist and tree canopies do not close, are usually found under drier conditions and under higher seasonality than tropical moist forests, which form a closed canopy, have a complex vertical structure and have few (if any) grasses (usually C3) in the understorey. Tropical forests and savannas are not rigidly determined by climate, and fire and herbivory may maintain the savanna state, particularly under mesic conditions, and prevent the transition to a forested state (Sankaran et al., 2005). Recent analyses of remotely sensed tree cover at global (Hirota, Holmgren, Nes, & Scheffer, 2011) and local scales (Favier et al., 2012) have shown that at intermediate rainfall (1,000–2,500 mm for Africa,

Staver, Archibald, & Levin, 2011), forests and savannas can both occur and may represent alternative stable states maintained through feedbacks between fire, herbivory and canopy cover (Favier et al., 2012; Hirota et al., 2011; Staver et al., 2011). Within this rainfall range, savannas are often wrongly viewed as degraded forests (Laestadius et al., 2011), while they actually are ancient ecosystems with a long evolutionary history (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Veldman et al., 2015) almost entirely distinct in species composition from forests (Swaine, Hall, & Lock, 1976).

In tropical Africa, savannas dominate the landscape, have high plant species richness, host diverse assemblages of large terrestrial herbivores, are of major socioeconomic importance, but currently threatened by various human impacts (Osborne et al., 2018). There

is, however, relatively little information available on the floristics and biogeography of the savanna biome at a continental scale, compared with tropical forests (e.g. Fayolle et al., 2014), although such information is of major importance for effective conservation and management. The definition of dry vegetation formations has been hotly debated (Dexter et al., 2015; Oliveras & Malhi, 2016) and it is not the purpose of this study to reopen the debate. For the African continent, we follow a contribution made in the Yangambi agreements, where vegetation formations were synthesized, labelled and defined in both French and English languages (Aubréville, 1957). The fundamental characteristic of savannas is their propensity to burn and to host large herbivores, specifically mammalian grazers and browsers (Charles-Dominique et al., 2016), and the associated importance of C4 grasses in the understorey (Aubréville, 1957; Dexter et al., 2015; Ratnam et al., 2011).

In Africa, the vegetation formations located north of the Guineo-Congolian Region have been distinguished from those in the south (Droissart et al., 2018; Linder et al., 2005, 2012; White, 1983). The identification of the major phytochoria of Africa was first proposed based on the distribution of *Diospyros* species (Ebenaceae, White, 1979). The phytochoria, delineated with White's expertise and a huge literature review, were later supported by data and statistical analyses (Denys, 1980; Droissart et al., 2018; Linder et al., 2005, 2012), although in the biogeographical regionalization of the whole sub-Saharan Africa of Linder et al. (2012), plant patterns were less distinct than those of other taxa. At the global scale, Olson et al. (2001) delineated terrestrial biomes and subdivided them into finer-scale ecoregions. The savanna biome in Africa (i.e. tropical and subtropical grasslands, savannas and shrublands in Olson's terminology) is represented by several ecoregions, including the Sahelian Acacia Savanna, the West Sudanian Savanna and the East Sudanian Savanna. It is also represented by several woodland types, including the Central Zambezan Miombo Woodland, the Zambezan and Mopane Woodland, the Angolan Miombo Woodland, and the Kalahari Acacia-Baikiaea Woodland. Other classifications proposed for savannas at a more local scale could be mentioned. For instance, a division of fine-leaved (Mimosoideae) versus broad-leaved savannas (Detarioideae) has been proposed, and was associated with soil fertility and/or rainfall (see, for instance, Scholes et al., 2002 in the Kalahari). The dominance of different lineages, and specifically the Mimosoideae (*Senegalia* and *Vachellia* being the dominant genera), Combretaceae (*Combretum* and *Terminalia*) and Detarioideae (*Brachystegia* and *Julbaernardia*, essentially), in different floristic regions of African savannas mentioned by White (1983), have recently been revisited (Osborne et al., 2018) with functional traits but their distribution of dominant lineages relied on White's map.

Existing biogeographical regionalization of African vegetation (e.g. Droissart et al., 2018; Linder et al., 2012) was, however, mostly based on herbarium samples or distribution data and might suffer from the false presence artefact (Jetz, Sekercioglu, & Watson, 2008). Although there are many advantages of using herbarium data in diversity studies (Baldwin et al., 2017) when merged on a grid scale they can lead to "virtual" assemblages. To avoid this artefact, we used a new

collation of data consisting of the so far largest collection of localized lists of tree and shrub species in African savannas in order to identify large-scale variation in woody species composition (i.e. beta diversity) at a continental scale and propose a biogeographical regionalization. The latter could be used to coordinate conservation and management efforts at a continental scale. To achieve this, we followed a somewhat classical approach, combining ordination and clustering methods (Mackey, Berry, & Brown, 2008) first developed for the analysis of beta diversity in forest tree species (Fayolle et al., 2014). Floristic relationships, specificity and turnover within and between floristic clusters were analysed using a (dis-)similarity-based approach (DRYFLOR 2016). We additionally examined the relationship between the environment (climate and altitude at the continental scale) and the floristic clusters to highlight possible deterministic influences, although the relationships with soils and fire regime, which might also be important determinants, were not addressed here.

## 2 | MATERIALS AND METHODS

### 2.1 | Description of the floristic data

We compiled data on the woody plant species composition for 298 samples across African savannas. In this study, we regard savannas as a biome with a C4 grass layer and a heterogeneous tree cover. Our samples thus included the terms "woodland (e.g. Miombo woodland)", "savanna woodland", "tree savanna" and "shrub savanna" agreed in Yangambi (Aubréville, 1957) in what may be thought of as the savanna biome *sensu lato*. We specifically excluded "grass savanna", true grasslands that lack trees over large areas and that are now considered as a separate biome (Parr et al., 2014). We note that in his vegetation map of Africa, White (1983) avoided "savanna" but instead used the term "wooded grassland". We excluded some examples of what has been called "dry tropical forest", i.e. those without a grassy understorey, with evergreen trees and lacking characteristic savanna trees (e.g. Hawthorne, 1993; Swaine, Lieberman, & Hall, 1990). We included woody species, specifically trees and shrubs, including palms and cycads, but excluded woody geophytes, lianas and suffrutices. Grass and forb species were excluded because many available datasets recorded only woody plants. The samples were located by longitude and latitude and extended from 18° N to 33° S and from 17° W to 48° E. The species lists were collated from published books and papers, monitoring programmes of protected areas, the authors' personal data and a few websites, and assumed that the original species identifications were sound. Species taxonomy was standardized with the African Plant Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php>) in September 2017, with the exception of African *Acacia* species that were assigned to the *Senegalia* and *Vachellia* genera according to Kyalangailwa, Boatwright, Daru, Maurin, and Bank (2013). Non-native species, including those of very ancient and uncertain origin such as *Tamarindus indica*, were excluded from floristic analyses. Occurrence data were available for a total of 1,642 self-supporting native woody plant species belonging to 552 genera and 112 families (Appendix S1). The



sampling, covering 32 countries across Africa, was heterogeneous, but comprised a relatively good balance across the Equator, with 146 northern and 152 southern samples (Appendix S2). Management intensity data were not available for most samples, and our data describe present-day woody vegetation for recent samples, and potential vegetation for the older ones. The species lists collated in this study reflect coexisting species in real assemblages for most samples, with the exception of a few checklists and/or compilations of plots (Pendjari National Park in Benin and Hluhluwe-iMfolozi Park in South Africa), for which species do not necessarily coexist within a plot, but at a larger scale, and for which the species list might span multiple habitats.

## 2.2 | Floristic relationships, specificity and turnover

We used unconstrained ordination and clustering methods to identify the major discontinuities and gradual transitions across African savannas. Our approach, first developed for tropical African forest tree species (Fayolle et al., 2014), is comparable to the methodological roadmap for biogeographical regionalization proposed by Kreft and Jetz (2010), with some slight modifications. For instance, we did not work with aggregated floristic data on a grid.

We first examined the concordance between floristic variation at different taxonomic levels using ordinations, comparing the results of correspondence analyses at species and genus levels. We preferred correspondence analysis to other (and perhaps more popular) ordination techniques such as non-metric multidimensional scaling (NMDS) because correspondence analysis successfully ordines samples of different sizes and shapes when they share species. The assumption of normality of the species response curve is acceptable at this continental scale and for this relatively complete coverage of African savannas. Moreover, the sensitivity to species-poor samples and extremely infrequently occurring taxa has been addressed by restricting the floristic analyses to samples with at least 10 species ( $n = 280$  samples), and to species and genera with at least two occurrences ( $n = 989$  species out of 1,642, and  $n = 409$  genera out of 552).

To delineate floristic clusters, we examined several clustering methods at the species level but only presented here the clustering results from Ward's algorithm on the Euclidean distances of the first five axis scores (accounting for 13.5% explained variance and selected according to the decay in eigenvalues). Direct clustering of the presence matrix (using Simpson index of dissimilarity) resulted in a very similar biogeographical regionalization. Once identified, we named the floristic clusters according to their geographical distribution, rather than environmental associations, and tried to avoid using existing terms that might have been defined differently. We also determined indicator species of both individual floristic clusters and combinations of clusters using the procedure developed by De Caceres and Legendre (2009). We used 999 random permutations for computing the significance of the indicator value, i.e. the association of the species with a specific cluster or combination of clusters. In the proposed biogeographical regionalization, we selected eight clusters because the cluster sizes remained interpretable (>10 samples)

and the total number of significant indicator species of individual clusters were found to be the greatest, thus indicating strong floristic specificity. For each cluster, we computed the number of species and the percentage of them being significant indicators. Only non-rare (at least two occurrences) and significant indicator species of the individual clusters, and not in combination with other clusters, were considered here.

For the geographical visualization of species turnover, we followed the approach originally proposed by Kreft and Jetz (2010). The idea is to select specific samples (or grid cells in the original approach) on each side of any well-defined biogeographical transition zone, and then examine the spatial turnover of species from each of these samples with respect to all the other samples, using pairwise dissimilarities. In this study, we used the Simpson index of beta diversity ( $\beta_{sim}$ ) which is known to be richness independent (Baselga, 2010; Koleff, Gaston, & Lennon, 2003). We selected the most species-rich sample for each floristic cluster that was considered to be the most representative of the cluster, i.e. including the largest number of species from the species pool. We then examined the spatial decay in floristic (dis-)similarity between these specific samples with all other samples, using the Simpson index of similarity ( $1-\beta_{sim}$ ) rather than dissimilarity for clarity.

To further examine the floristic specificity among clusters and overall floristic relationships, we also calculated the mean floristic similarity between all pairs of samples within and between clusters as previously proposed (DRYFLOR 2016).

## 2.3 | Environmental correlates

For each of the 298 samples, the value of the 19 climatic variables of the BIOCLIM dataset was obtained from the 'WorldClim' Global Climate database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; <http://www.worldclim.org/download>) and altitude was obtained from the Shuttle Radar Topography Mission (SRTM). The resolution used was 10 min of a degree, which is suitable for continental analyses. To examine the environmental correlates of woody species composition and turnover, environmental vectors were fitted on the sample ordinations. To determine the environmental space occupied by the African savannas, and by each floristic cluster, we located our samples and clusters into the environmental space defined by the mean annual temperature (in °C) and mean annual precipitation (in mm) overlaying the delineation of major biomes. This allowed us to assess how our clusters fit into the temperature-precipitation scheme of Whittaker (1975). We also used the Welch two-sample t-tests to test for significant differences in altitude between two groups of samples.

All analyses were performed within the open-source R environment (R Development Core Team, 2017). The 'ade4' package was used for the ordinations (Dray & Dufour, 2007) and the 'indicpecies' package for computing species indicator values and significance (De Caceres & Legendre, 2009). The 'vegan' package was used for the computation of the Simpson index of beta diversity and for the environmental vector fitting (Oksanen et al., 2011).

### 3 | RESULTS

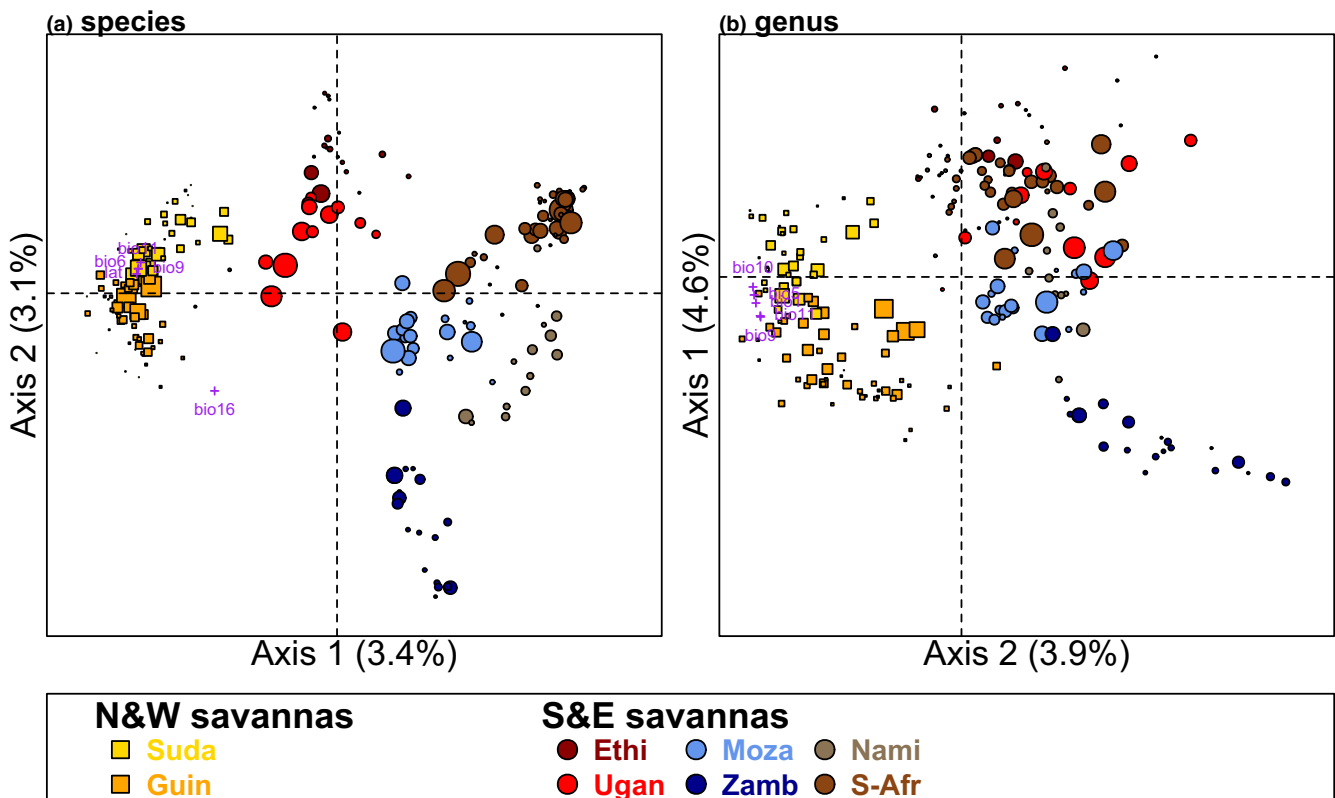
#### 3.1 | Proposed biogeographical regionalization

The ordination and clustering of the woody species composition highlighted a clear floristic differentiation, contrasting the Northern and Western savannas (N&W hereafter) comprising two floristic clusters, with the Southern and Eastern savannas (S&E hereafter) comprising six floristic clusters (Figures 1 and 2).

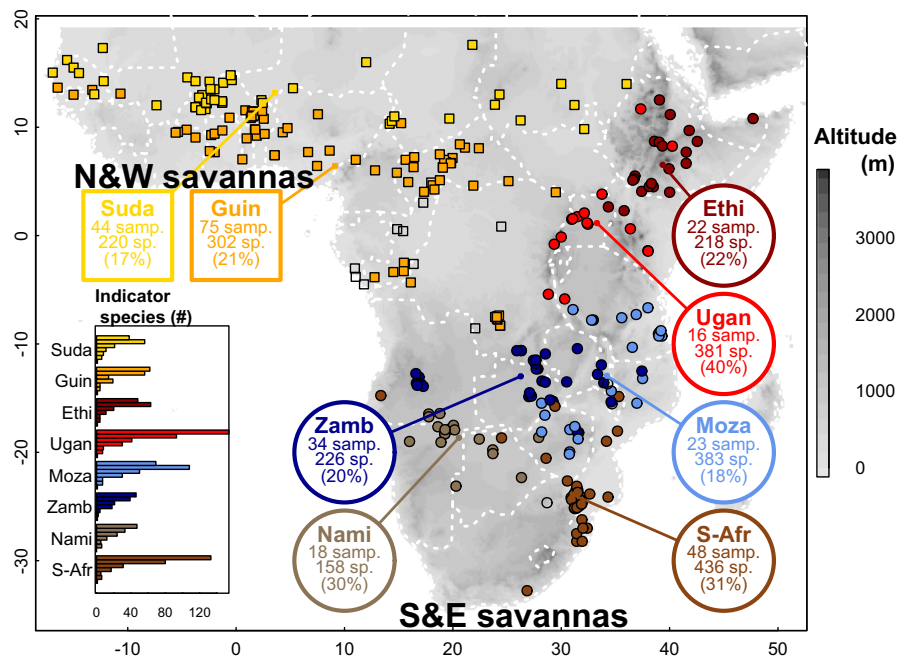
There was a large range of species richness (from 3 to 208 native woody species, with a median and mean of 34 and 44) among our samples of different size and shape. However, we found that short species lists were well ordinated and classified (Figures 1 and 2), although removing poor samples (<10 species) and extremely infrequently occurring taxa improved both ordinations and clustering. Ordinations at different taxonomic levels highlighted strong spatial patterns (Figure 1). Specifically, the first ordination axis at the species level (3.4% of variance explained, Figure 1a) and the second axis at the genus level (3.9%, Figure 1b) highlighted a strong spatial discontinuity, discriminating samples from North and West Africa

(squares) from samples from South and East Africa (circles). This floristic discontinuity closely corresponds to the Low and High division of Africa proposed by White (1983) according to the physical characteristics of the environment. The second axis of the species-level ordination highlighted a gradual transition from more mesic sites (negative scores) towards drier and more arid sites (positive scores, Figure 1a).

In the N&W savannas, we identified two floristic clusters, the Sudanian ( $n = 44$  samples) and the Guinean ( $n = 75$ ) savannas, partitioned along this north–south rainfall gradient (Figures 1 and 2). The Sudanian cluster hosted a moderate number of species ( $n = 220$ ), with 17% of them being significant indicators (Figure 2). Important genera were *Senegalia* and *Combretum* ( $n = 3$  significant indicator species of the individual cluster, Appendix S1). The Guinean cluster hosted a large number of species ( $n = 302$ ) with 21% of them being significant indicators, but the cluster was not clearly associated with any particular genera. It has to be noted that the majority of significant indicator species of the Guinean cluster were also significant indicators of the Sudanian cluster and vice versa.



**FIGURE 1** Floristic variation across African savannas at different taxonomic levels depicted by sample ordination at the species (a,  $n = 989$ ) and at the genus (b,  $n = 409$ ) level. Symbols discriminate the N&W (square) and S&E (circle) savannas and colour of symbols corresponds to different clusters derived by the Ward's clustering following species-level ordination (a). The size of symbols is proportional to the logarithm of species and genus richness, larger symbols corresponding to richer samples. The five most correlated environmental and spatial variables were plotted on the ordinations (in purple), i.e. latitude, bio9 (mean temperature of driest quarter), bio11 (mean temperature of coldest quarter), bio6 (minimum temperature of coldest month) and bio16 (precipitation of wettest quarter) for the species-level ordination (a); and bio1 (annual mean temperature), bio11, bio9, bio10 (mean temperature of driest quarter) and bio16 for the genus-level ordination (b). The BIOCLIM variables were obtained from the 'WorldClim' Global Climate database (Hijmans et al., 2005) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 2** Map of floristic clusters overlaying a base map of altitude. Symbols discriminate the N&W (square) and S&E (circle) savannas and colour of symbols corresponds to different clusters derived by the Ward's clustering following species-level ordination (Figure 1a) and unfilled symbols (<10 species) were not included in the ordinations (Figure 1) and clustering. Number of samples (samp.) among the 280 samples with at least 10 species, number of species (sp.) among the 989 species with at least two occurrences and percentage of them being significant indicators of the single cluster are given for each cluster. The lines from the cluster labels indicate the geographical centroid of each cluster. Country borders are indicated in white. The number of significant indicator species of the individual cluster (first column), and of the cluster in combination with the other 1–7 clusters (succeeding columns) is given for each floristic cluster in the inset histograms [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

In the S&E savannas, we identified six floristic clusters with a patchy distribution (Figure 2). The Ethiopian cluster ( $n = 22$  samples) hosted a moderate number of species ( $n = 218$ ) with 22% of them being significant indicators. Important genera were *Commiphora* ( $n = 11$  significant indicator species), *Grewia* and *Vachellia* ( $n = 4$  for both). The majority of significant indicator species of the Ethiopian cluster were also significant indicators of another cluster, mostly the Ugandan cluster. The Ugandan cluster ( $n = 16$  samples) hosted a large number of species ( $n = 381$ ) and high floristic specificity, 40% of them being significant indicators. Important genera for the Ugandan cluster were *Ficus* ( $n = 9$  significant indicator species) and *Euphorbia* ( $n = 5$ ). The Zambezian cluster ( $n = 34$  samples) hosted a moderate number of species ( $n = 226$ ) with 20% of them being significant indicators. Most Miombo species, and specifically species of the genus *Brachystegia* ( $n = 6$  species) and *Uapaca* ( $n = 5$ ) but also *Isoberlinia angolensis*, were strongly associated with this cluster. The Mozambican ( $n = 23$  samples) cluster hosted a large number of species ( $n = 383$ ), with 18% being significant indicators. Except for the genus *Diospyros* ( $n = 4$  species), the Mozambican cluster was not clearly associated with any particular genera, but it is worth noting that four Miombo species, *Brachystegia microphylla*, *B. tamarindoides* and *B. bussei*, and *Julbernardia globiflora*, were found to be significant indicators of the individual cluster and that four other Miombo species, *Brachystegia boehmii*, *B. spiciformis*, *B. manga* and *B. stipulata*, were found to be significant indicators of the combination of the Zambezian and Mozambican

clusters. The majority of significant indicator species of the Mozambican cluster were also significant indicators of another cluster. The Namibian cluster ( $n = 18$  samples) hosted a moderate number of species ( $n = 158$ ) with 30% being significant indicators. The Namibian cluster was associated with the *Grewia* ( $n = 5$  significant indicator species), *Combretum* ( $n = 4$ ) and *Vachellia* ( $n = 3$ ) genera, and *Baikiaea plurijuga* that can locally form almost pure stands was also a significant indicator. Finally, the South-African cluster ( $n = 48$  samples) hosted a large number of species (>400), with 31% being significant indicators. Important genera for the South-African cluster were *Grewia* and *Rhus* ( $n = 4$  significant indicator species for both), and *Vachellia* and *Commiphora* ( $n = 3$  for both). *Colophospermum mopane* that can also form almost pure stands was a significant indicator of the combination of the Namibian and South-African clusters.

### 3.2 | Discontinuities and species turnover

The greater number of clusters of the S&E savannas with respect to the N&W savannas reflects the relatively greater floristic heterogeneity in the former. Interestingly, the first ordination axis at the species level highlighted a second floristic discontinuity within the S&E savannas between samples from the Ugandan and Ethiopian clusters (Uganda, Kenya, Somalia and Ethiopia) and samples from the other four S&E clusters (Figure 1a). This sharp discontinuity between East and Southern Africa at the species level was not detected at

the genus level (Figure 1b) probably because of many shared genera such as *Commiphora*, *Grewia*, *Vachellia* and *Albizia*, although represented by different species in East and Southern Africa. Despite these discontinuities, we identified a set of extremely widespread species across African savannas, occurring in both the N&W and S&E savannas, and significant indicators of combinations of clusters (Appendix S1).

The analysis of species turnover showed a lower floristic similarity between than within the N&W savannas and the S&E savannas (Table 1) and a relatively abrupt replacement of species between them (Figure 3). In addition, within the S&E savannas the floristic similarity was lower than in the relatively homogeneous N&W savannas (Figure 3 and Table 1). Specifically, distance decay in floristic similarity was observed within each cluster, with a relatively shorter distance for the S&E clusters (Figure 3c–h) than for the Sudanian and Guinean clusters (Figure 3a,b). In the N&W, the Sudanian and Guinean clusters were relatively similar floristically, although very dissimilar from all other clusters (Figure 3a,b), confirming the major floristic discontinuity (smaller symbols) between the N&W and the S&E savannas, as already identified with the ordinations and clustering (Figures 1 and 2). The Sudanian cluster was also the most homogeneous with the maximum pairwise similarity (Figure 3a). In the S&E savannas, the Ethiopian and Ugandan clusters showed moderate similarity within the cluster (Figure 3c,d). The Ugandan cluster also shared some species with the Guinean cluster (Figure 3c). The Zambezan (Miombo woodland) was highly homogeneous with a high similarity within the cluster (Figure 3f), and distinct floristically from the other clusters, although sharing some species with the Guinean and Mozambican clusters (Figure 3e). In contrast, the Namibian and South-African clusters tended to be relatively distinct from each other.

Overall, the heterogeneous floristics of the S&E savannas contrasted with the relatively homogeneous floristics of the N&W savannas. This was visible in the ordinations at species and genus levels (Figure 1a,b) and was also confirmed by the pairwise similarity analyses (Table 1). High similarity within the Sudanian, Mozambican, Zambezan, Namibian and South-African clusters can also be observed (Table 1), as can the floristic association between the

Sudanian and Guinean, the Guinean and Ugandan, and between the Mozambican and almost all neighbouring clusters.

### 3.3 | Environmental correlates

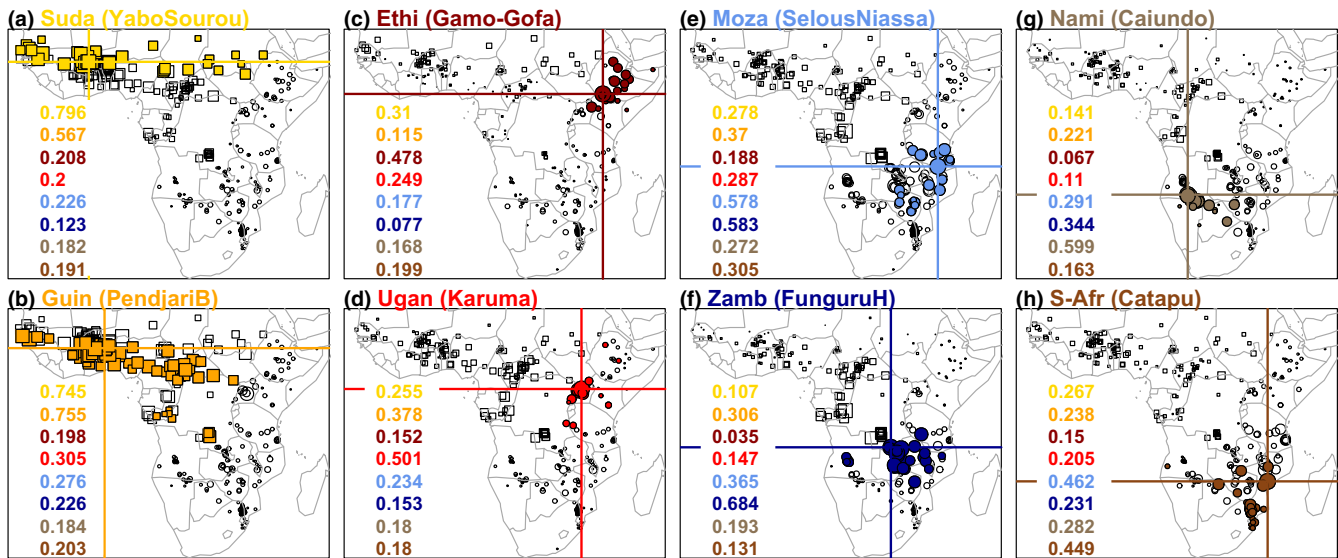
The graphical analysis of environmental variation between clusters showed relatively little overlap between floristic clusters but clear regional differences between the N&W and the S&E savannas, significantly different in altitude and temperature (Figure 4). We found significant differences in altitude between each side of the floristic discontinuity ( $t = 10.76$ ,  $p < 0.001$ ), with means of 431 m for the 134 samples in the N&W savannas and of 921 m for the 164 samples in the S&E, respectively. We found little overlap among floristic clusters along the two major environmental gradients across tropical Africa (i.e. temperature/altitude and rainfall, Figure 4). Particularly in the N&W savannas, the Sudanian and Guinean clusters were clearly partitioned along the north–south rainfall gradient, with some exceptions for high-altitude sites, e.g. the Jebel Marra Massif in Sudan ( $>1,700$  m, Figure 3b). The transition between the two clusters was at  $\sim 1,000$  mm rainfall. In the S&E savannas, temperatures were overall lower than in the N&W savannas. The Zambezan cluster occupied higher altitude, moister and cooler sites, whereas the Namibian and South-African clusters occupied drier sites than the other clusters in the S&E. In particular, the Zambezan cluster (Miombo woodland) showed high environmental consistency offering an environmental explanation for its distinctive floristics while the Mozambican cluster, floristically close, showed a high environmental heterogeneity. The Ugandan and Ethiopian clusters both occurred under a wide range of temperatures but were clearly separated along the rainfall gradient.

## 4 | DISCUSSION

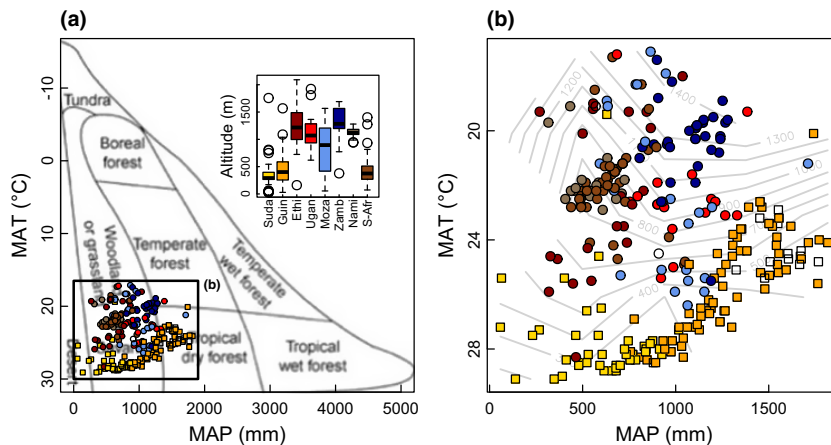
In this study, we propose a biogeographical regionalization of savanna vegetation across Africa based on present-day variation in the beta diversity of native tree and shrub species, using a new collation of data consisting of the so far largest collection of localized woody

**TABLE 1** Floristic relationships and turnover between floristic clusters identified across African savannas. Mean floristic similarity ( $1-\beta_{sim}$ ) between all pairs of samples was computed within and between floristic clusters. Mean pairwise similarities greater than 0.4 and 0.2 are, respectively, shown in bold and italicized

	Sudanian	Guinean	Ethiopian	Ugandan	Mozambican	Zambezan	Namibian	South African
Sudanian	<b>0.529</b>							
Guinean	0.242	0.396						
Ethiopian	0.174	0.034	0.280					
Ugandan	0.158	0.168	0.156	0.303				
Mozambican	0.146	0.159	0.084	0.151	<b>0.401</b>			
Zambezan	0.045	0.128	0.017	0.086	0.292	<b>0.461</b>		
Namibian	0.104	0.082	0.080	0.086	0.209	0.139	<b>0.499</b>	
South African	0.153	0.079	0.108	0.127	0.229	0.073	0.212	<b>0.465</b>



**FIGURE 3** Map of floristic similarity between the richest sample in each floristic cluster and all other samples across African savannas. The most species-rich samples were identified and considered indicative of each floristic cluster: YaboSourou for the Sudanian cluster (a), PendjariB for the Guinean cluster (b), Gamo-Gofa for the Ethiopian cluster (c), Karuma for the Ugandan cluster (d), SelousNiassa for the Mozambican cluster (e), FunguruH for the Zambezan cluster (f), Caiundo for the Namibian cluster (g) and Catapu for the South-African cluster (h). Country borders are shown in background. Symbols discriminate the N&W (square) and S&E (circle) savannas and colour of symbols corresponds to different clusters according to the clustering following species-level ordination (Figures 1 and 2). Size of symbols is proportional to the floristic similarity ( $1-\beta_{sim}$ ) between the richest sample in each floristic cluster (located at the intersection between the two coloured lines) and all other samples, with larger symbols corresponding to greater similarities. Mean similarity within and between floristic clusters are also indicated with corresponding colour codes [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 4** Environmental space defined by the mean annual precipitation (MAP, in mm) and the mean annual temperature (MAT, in °C) as occupied by the 298 sample sites across African savannas in the original Whittaker plot of biome distribution (a) and in the restricted environmental space occupied by African savannas (b). Symbols discriminate the N&W (square) and S&E (circle) savannas and colour of symbols corresponds to different clusters according to the clustering following species-level ordination (Figure 1a). Unfilled symbols (samples with <10 species) were not included in the floristic analyses—the ordinations and clustering (Figures 1 and 2). Altitudinal variation between floristic clusters is shown as inset in (a) and as 100-m-wide contours (in grey) in (b) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

species lists. We identified a major floristic discontinuity across Africa, between the N&W savannas and the S&E savannas, with a relatively abrupt replacement of species between them, and distinct environmental conditions. This floristic discontinuity closely corresponds to the High and Low division of Africa proposed by White

(1983) according to the physical characteristics of the environment, principally rainfall and temperature. White's line, drawn from Angola, then following the Albertine Rift, and then north to the west of Ethiopia, divides Africa into the N&W macro-unit which corresponds to Low Africa, and the S&E macro-unit which corresponds to High



Africa, mostly above 1,000 m. In a previous analysis of the beta diversity of forest tree species across tropical Africa, a similar discontinuity in forest vegetation was also identified between Central and East Africa, and discussed according to the historical, geographical, and environmental factors associated with the uplift of the Albertine Rift (Fayolle et al., 2014). The region around Lake Victoria, in Uganda, corresponds to the area where species characteristic of the two macro-units met. The floristic specificity of the area, recently assigned to a transition zone (Droissart et al., 2018), was already noted by White (1983) as the Regional Mosaic around Lake Victoria.

Fourteen samples of the 18 excluded from our analyses because they had few species were geographically (Figure 2, centred on the equator) and environmentally (Figure 4b, upper right) clearly associated with the Guinean cluster. These included the savannas of the Bateke plateau, the Niari valley and the included savannas in dense forest, and were floristically more associated with northern than southern savannas. Geographically, the Bateke plateau, a vast savanna plateau at the northern limit of the Kalahari sands crossing the borders of DRC, Congo and Gabon, is more connected via a highland belt with the Angolan highlands than northwards. However, over 50% of the flora of the plateau Batéké has been previously classified as Guineo-Congolian, although another 20% of the species have extended distributions into the Zambezan and Sudanian phytochoria (Walters, Bradley, & Niangadouma, 2006). The more recent origin and strong isolation of these savannas might explain their low diversity, but the floristic affinity with the northern savannas is probably linked to the opening of the Congo Basin during the Last Glacial Maximum, which may have facilitated exchange with northern savannas (Maley, 1991).

We found good concordance between our biogeographical regionalization of African savannas and the major phytochoria of Africa proposed by White (1979, 1983) as well as with the more recent biogeographical regionalization of Linder et al. (2012) and Droissart et al. (2018) both based on a quantitative approach. Our N&W macro-unit can be considered as an extension of White's and Linder's Sudanian Region and of Droissart's Guineo-Sudanian Region, whereas our S&E macro-unit encompasses White's, Linder's and Droissart's Zambezan regions and the southern and eastern phytochoria and regions. The number of floristic clusters that we and others identified confirms the great heterogeneity of the S&E savannas. For instance, in East Africa, Linder et al. (2012) recognized the Somali, the Ethiopian and the Kilimanjaro Regions, whereas we found the Ugandan and Ethiopian clusters for savannas, and Droissart et al. (2018) only recognized the East African mountains. Further south, our Zambezan, Mozambican, Namibian and South-African clusters match with Linder's Regions, but unfortunately the RAINBIO dataset used by Droissart et al. (2018) was limited in southern Africa. Among the seven major Regions identified by Linder et al. (2012), the Sudanian and the Zambezan Regions were not subdivided, whereas here the Sudanian Region of Linder et al. (2012) includes samples assigned to our Sudanian and Guinean clusters, and even extends to the West-African forests (Fayolle et al., 2014). Moreover, the Zambezan Region of Linder et al. (2012) includes

samples assigned to our Zambezan, Mozambican and South-African clusters. The discrepancies between our results based on woody species composition and the regionalization based on herbarium specimens (Linder et al., 2012) most probably arose from the different pattern of regionalization displayed by different growth forms (Droissart et al., 2018). Indeed, grasses and forbs, that are a key component of the Savanna flora (Linder, 2014), were not included in our data, although here we assembled the largest collation of trees and shrub species lists across Africa to provide our biogeographical regionalization of savannas.

We also found good correspondence between our floristic clusters and the ecoregions defined by Olson et al. (2001, Appendix S2) that have been widely used for conservation planning, although they lacked any floristic backbone and in fact reproduced what had been delimited by White (1979, 1983) with the addition of faunistic elements. Our Sudanian cluster was composed of two of Olson's ecoregions, the Sahelian Acacia ( $n = 15$  samples) and the West Sudanian ( $n = 23$ ) savannas (Appendix S2). Our Guinean cluster was a bit more heterogeneous, including Olson's East Sudanian Savannas ( $n = 10$  samples), and several Forest-Savanna Mosaics. The transition between our two clusters was at  $\sim 1,000$  mm rainfall, which suggests our Sudanian cluster to be outside the bistability zone where forests and savannas represent alternative stable states (Hirota et al., 2011; Staver et al., 2011) in contrast to our Guinean cluster (Favier et al., 2012). Our Ugandan cluster was associated with Olson's Victoria Basin Forest-Savanna Mosaic ( $n = 4$  samples) and the East Sudanian ( $n = 3$ ), whereas our Ethiopian cluster included Olson's Ethiopian Montane Forest ( $n = 7$ ), the Northern Acacia-Commiphora ( $n = 2$ ) and the Somali Acacia-Commiphora Bushland and Thicket ( $n = 9$ ). We indeed found that *Commiphora* and *Vachellia* were important genera for the Ethiopian cluster. The Zambezan cluster (Miombo woodlands) identified here included Olson's Central Zambezan ( $n = 20$ ) and Angolan ( $n = 9$ ) Miombo Woodlands, but we did not find any further division between samples from Angola and more central samples from DRC and Zambia. The Miombo floristics was relatively homogeneous over quite long distances, and was probably associated with a high environmental consistency of a moist and cool climate with the cluster having the highest mean altitude. The prerequisite of a moist climate for the dominance of the Detarioideae (*Brachystegia* and *Julbernardia* being the dominant genera) in African savannas has been long recognized (White, 1983) and recently revisited (Osborne et al., 2018), but the importance of a relatively cool climate might have been underestimated. Our Mozambican cluster also encompasses several of Olson's ecoregions of Miombo Woodlands and a huge environmental heterogeneity in terms of temperature and altitude that probably explains a substantial part of its high species richness and heterogeneous floristics. Our results suggested the recognition of at least two types of Miombo woodlands at this continental scale (i.e. Zambezan and Mozambican), and perhaps even more Miombo types as recently demonstrated by Daru et al. (2016) using phylogenetic data. Our South-African cluster perfectly matches Olson's Zambezan and Mopane Woodland ecoregion ( $n = 37$  samples). Mopane woodlands

have long been recognized as one of the dominant savanna forms in Southern Africa, extending across much of south-western Angola, north-western Namibia, northern Botswana, through southern Zimbabwe/north-east South Africa and into central Mozambique (Stevens, Swemmer, Ezzy, & Erasmus, 2014; White, 1983). Finally, our Namibian cluster corresponds to Olson's Kalahari *Acacia-Baikiaea* woodlands ( $n = 13$  samples). Although confined to the more moist parts of the cluster, *Baikiaea plurijuga* was a significant indicator of our Namibian cluster. Unlike the other *Baikiaea* species that are forest species, *Baikiaea plurijuga* is a deciduous tree often occurring on Kalahari sands (White, 1983) with several other co-dominant species such as *Pterocarpus angolensis* (an indicator of the Namibian, Mozambican and Zambeian clusters combined), *Schinziophyton rautanenii* and *Guibourtia coleosperma* (both indicators of our Namibian cluster).

Although we believe that true coexistence is a key advantage of our approach, in our study we relied on identifications provided by individual study authors, with no possibility of checking identifications, which is a strength of herbarium-based studies. For an exact spatial delineation of the clusters and identification of the transition zones, modelling studies, additional samples and most probably field studies would be needed, specifically in under-sampled areas such as southern DRC, northern Angola and northern Tanzania (Stropp et al., 2016). Despite local discrepancies, we found a relatively good concordance between the floristic variation at the species and genus levels, highlighting strong spatial patterns highly correlated with environmental factors. Generic differences therefore also displayed strong spatial patterns, representing a much older evolutionary signal than that of the species level, in line with the strong insights in the evolution of African plant diversity, including that of the savanna flora recently provided by a genus-level approach (Linder, 2014). At even a higher taxonomic level, the contrasted dominance of different lineages in different floristic regions of African savannas has been highlighted, with the dominance of Mimosoideae at low rainfall, of Combretaceae at intermediate rainfall and of Detarioideae at high rainfall (Osborne et al., 2018; White, 1983). The new pan-African classification proposed here might assist in the development of management and conservation policies for African savannas. Our results highlighted the high diversity of savannas across Africa potentially under threat due to human impacts (Osborne et al., 2018; Veldman et al., 2015). The clusters that we found here for the most part spanned multiple ecoregions, and adjusting conservation planning to these larger clusters might facilitate conservation efforts.

Finally, the data collated in this study and the recent contribution of the DRYFLOR group in the Neotropics (DRYFLOR 2016) open the door for cross-continental analyses, necessarily at the genus level. Indeed, a tentative cross-continental analysis of the floristics and biogeography of seasonally dry tropical vegetation formations has been recently published (Dexter et al., 2015), although with a limited sampling across Africa. The integration of phylogenetic information will also most likely provide valuable insight to ecological and historical interpretations of the floristic variation (e.g. Daru et al., 2016 in Southern Africa).

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#### DATA ACCESSIBILITY

The occurrence data have been made available on the repository of the University of Liège under the following reference <http://hdl.handle.net/2268/227793>.

#### BIOSKETCH

**Dr Adeline Fayolle** (Gembloux Agro-Bio Tech, Liège University, Gembloux, Belgium) and **Dr Michael D. Swaine** (Aberdeen University, Aberdeen, United Kingdom) have broad research interests in the biogeography, ecology and management of tropical ecosystems. They are interested in the relative influence of environmental and historical factors on vegetation structure, composition and functioning, especially in Africa.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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