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Patterns and Drivers of Phylogenetic Beta Diversity in the Forests and Savannas of Africa

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ABSTRACT

Aim: Studying beta diversity, or the variation in species composition among communities, can give insights into plant community assembly over space and time. If different biomes show contrasting large-scale beta-diversity patterns, this can indicate divergent evolutionary histories or ecological processes that then drive species turnover among communities. Here, we examine phylogenetic beta-diversity patterns across Africa in forest and savanna assemblages, the two most widespread tropical biomes on the continent. We hypothesise that savannas will show lower phylogenetic beta diversity due to their younger evolutionary history.

Location: Tropical Africa.

Taxon: Woody angiosperms.

Methods: We gathered 301,159 occurrences of woody angiosperms representing 1883 forest species and 1302 savanna species. We compared levels of phylogenetic beta diversity between forest and savanna assemblages, analysed spatial patterns of phylogenetic beta diversity using 1° grid cells and modelled their relationship with climate, disturbance and geographical distance.

Results: We found that savannas show greater relative regional phylogenetic beta diversity, whereas forest assemblages show greater relative local phylogenetic beta diversity. The spatial distribution of beta diversity showed strong East–West patterns for both forests and savannas, aligned with a major floristic discontinuity associated with the Albertine rift. Our results also highlighted West Africa as showing a high amount of compositional change for both biomes, arranged along an aridity gradient. Variance partitioning showed that predictors linked to precipitation were the main drivers of compositional change for both forests and savannas, but the importance of individual predictors was different in each biome.

Main Conclusions: Contrary to our expectations, our results indicate that savannas may have a deeper and richer evolutionary history than suggested by previous studies and that individual regions of both forest and savanna have high conservation value. Finally, our results demonstrate that environmental filtering is the dominant force influencing the assembly of these two important biomes at a continental spatial scale.

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1 | Introduction

Understanding the patterns and drivers of biodiversity has been a major goal in ecology and biogeography for over two centuries (Humboldt and Bondpland 1805). Whittaker (1960, 1972) proposed a framework for decomposing the overall diversity of a region (gamma) into separate components, namely alpha and beta diversity. Beta diversity can be thought of as the difference between communities in species composition and, since its inception, has been associated with ecological gradients. As such, analysing compositional patterns along environmental, spatial and temporal gradients has been pivotal in understanding community assembly, functional strategies and biogeographic histories (Condit et al. 2002; Hubbell 2001; Leibold and Chase 2018; Ovaskainen et al. 2019; Tscharntke et al. 2012). Some of the most important forces that shape beta diversity, including biogeographic history, dispersal limitation and environmental filtering, have been intensively scrutinised as to which might better explain compositional variation among communities, yet disagreement often occurs depending on taxonomic/phylogenetic and geographic scales (Condit et al. 2002; Dexter et al. 2012; Guevara Andino et al. 2021; Hardy et al. 2012; Hardy and Sonké 2004; Kraft et al. 2011; Muñoz Mazón et al. 2021; Qian et al. 2024; Ringelberg et al. 2023). Understanding patterns and drivers of beta diversity is important for conservation because changes in community composition and function will influence overall diversity at large scales (Condit et al. 2002; Socolar et al. 2016).

Beta diversity can be defined and calculated in many ways, focusing either on taxonomic, phylogenetic or functional diversity (Anderson et al. 2006, 2011; Chiu et al. 2014; De Bello et al. 2010; Faith et al. 1987; Legendre et al. 2005; Tuomisto 2010a, 2010b). Most methods use either presence/absence data or a form of weighting, by incorporating abundances, for example. Importantly, beta diversity can be quantified as a single metric for a region, or as a pairwise metric between sites. True beta diversity (β_M *sensu* Tuomisto 2010a) is a ratio of gamma/alpha and quantifies the effective number of distinct compositional units in the data set that have an equal effective number of species as the average sampling unit. This measure of beta diversity is not dependent on the alpha diversity of individual sites within the study system, and as such, represents a relative estimate of beta diversity useful for comparing systems that might differ greatly in their alpha and gamma diversities. Other measures of beta diversity, including many pairwise metrics, quantify compositional change and are often correlated with ecologically meaningful covariates to understand the roles of biogeographic history, dispersal limitation and environmental selection in driving variation in species composition (Anderson et al. 2011). This pairwise aspect of beta diversity is at the heart of bioregionalisation, a procedure that involves clustering communities into discrete units based on their pairwise resemblance (Daru et al. 2018; Droissart et al. 2018; Linder et al. 2012; Marshall et al. 2021).

Phylogenetic beta diversity focuses on comparing communities through the lens of evolutionary history. Depending on which metric is used, pairwise phylogenetic beta diversity can give more importance to recent diversification (tip weighted) or ancient diversification events (basal weighted) (Swenson 2011; Tucker et al. 2017) and can also be used to decompose the assembly of communities through time (Rosauer et al. 2014). Phylogenetic beta diversity is particularly useful at large spatial and taxonomic scales, as phylogenetic niche conservatism and phylogenetic clustering become the dominant patterns influencing community assembly, reflecting environmental filtering and dispersal limitations (Cavender-Bares et al. 2006; Swenson et al. 2006, 2007; Webb et al. 2002). The relative importance of dispersal limitation and environmental filtering has implications for conservation and for understanding fundamental drivers of the composition of communities through time (Qian and Ricklefs 2012; Segovia et al. 2020; Tuomisto et al. 2003). Very few studies have looked at phylogenetic beta diversity in Africa (Daru et al. 2018; Davies et al. 2023; Kubota et al. 2018; Qian et al. 2024; van Tiel et al. 2024) and none so far have compared biome-specific patterns and drivers of beta diversity at continental scales. As such, our understanding of the structuring of different biomes in Africa is still incomplete.

Forests and savannas represent the two most productive biomes on Earth, accounting for 34% and 26% of annual gross primary productivity respectively (Beer et al. 2010). Forests are closed biomes dominated by trees where most species are shade tolerant, whereas savannas are open biomes dominated by herbaceous plants (often C4 grasses) where most species are shade intolerant (Bond 2019). Savannas are thought to have originated later in evolutionary history, with a global rise of the major savanna lineages dated to the Miocene (Beerling and Osborne 2006; Cerling et al. 1997; Edwards et al. 2010). The sharp differences in physiognomy, species composition and ecological strategies have led researchers to suggest these biomes represent alternative states within the same environmental setting (Aleman et al. 2020; Bond 2005; Staver et al. 2011; Van Langevelde et al. 2003), although the spatial extent of these alternative states is still debated (Higgins et al. 2023, 2024). As such, it can be expected that the biogeographical histories and ecological drivers of beta diversity will be different for these two biomes. Africa is particularly important for studying these biomes as it is home to the Miombo woodlands, the largest savanna in the world, and the Congo basin, the second largest rainforest in the world, both of which are at risk of losing species through extinction and ecosystem disruption (Trisos et al. 2023). It is also the continent that will experience the fastest population growth this century, with a total population estimated to double by 2050, reaching over 2 billion people (United Nations 2022). In this context, anthropogenic-driven global change and habitat fragmentation will seriously affect how forests and savannas function and exchange species. There is an urgent need to understand how these biomes will be affected and to ensure the conservation of their unique diversity.

Here we combine georeferenced and taxonomically verified occurrence data of woody plants with ecological and phylogenetic information to analyse the patterns and drivers of phylogenetic beta diversity in the forests and savannas of Africa. Specifically, we ask

1. How do forests and savannas compare in overall phylogenetic beta diversity?
2. How is phylogenetic beta diversity spatially distributed across tropical Africa?
3. What are the ecological drivers of phylogenetic beta diversity for savannas and forests?

2 | Materials and Methods

2.1 | Herbarium Specimens and Biome Information

We used a combination of two large herbarium data sets (RAINBIO and FLOTROP) to generate a taxonomically verified list of woody plant occurrences across tropical Africa (Dauby et al. 2016; Taugourdeau et al. 2019). The taxonomy was standardised using the African Plant Database, except for *Acacia* names that were assigned to either *Senegalia* or *Vachellia* following Kyalangalilwa et al. (2013). The data were filtered to include only the woody species present in the work of Gorel et al. (2022) which assigned species to a biome (either forest or savanna). To summarise their methods, Gorel et al. (2022) used a data set of georeferenced herbarium specimens (Dauby et al. 2016), complemented with tree species lists in forests (Fayolle et al. 2014) and savannas (Fayolle et al. 2019) and bioclimatic variables (Noce et al. 2020) to build the climatic niches of tropical African woody species through a climatic ordination of Africa. They used hierarchical clustering based on niche similarity to group species. The two major divisions of this hierarchical clustering were interpreted as reflecting forests and savanna groups. This method was shown to be robust to sampling bias and choice of resolution (Broennimann et al. 2012). In addition, there is a large congruence between this approach and an expert-based approach derived from the physiognomic vegetation types in which species predominantly occurred (forest versus savanna), independent of climate data (Aleman et al. 2020; Rees et al. 2023). We also restricted the analyses to the woody species that had been categorised as either 'tree', 'shrub' or 'shrublet' by the RAINBIO database. We deleted all gymnosperms and tree ferns, as these clades are known to add long branches in the phylogeny and potentially bias patterns of phylogenetic diversity (Honorio Coronado et al. 2015).

2.2 | Sampling Units

We used square grid cells of 1 decimal degree (c. 110 × 110 km at the equator) between the Tropic of Capricorn and the Tropic of Cancer as our sampling units. We overlaid the herbarium occurrence with the sampling units using the raster R package (Hijmans 2023). As forests and savannas potentially represent alternative biome states with contrasting ecological requirements, they can both be present in the same sampling unit; therefore, we analysed beta-diversity patterns for each biome separately. We then filtered the data to include only sampling units with at least five forest species or five savanna species, as preliminary analyses indicated stable positioning of assemblages in ordination space if they contained at least this number of species. All collections within the same sampling unit (a 1° grid cell) are further referred to as 'assemblages'. We created three matrices: the first matrix contained only the forest species (457 assemblages containing 1883 species), the second matrix contained only the savanna species (837 assemblages containing 1307 species) and the third matrix combined the two previous matrices into one, resulting in 1294 assemblages containing 3190 species. In this third matrix, the same sampling unit can be represented two times (once by the forest assemblage and once by the savanna assemblage).

2.3 | Phylogenetic Tree

We constructed a synthetic phylogenetic tree based on the megatree of Smith et al. (Smith and Brown 2018) and Magallon et al. (Magallón et al. 2015) as a backbone. About 36% of the species were already present in the tree. We used the V.Phylomaker R package (Jin and Qian 2019) to graft the missing species using scenario three, which consists of binding species to the half-way point of the genus to which they belong. We constructed a single tree for all species, from both forest and savanna, which was later pruned to forest or savanna species for some downstream analyses. Using these, synthetic phylogenetic trees generally does not affect the conclusions drawn from large-scale phylogenetic analyses (Li et al. 2019; Qian and Jin 2021).

2.4 | Environmental Predictors

As climatic variables, we combined the 19 bioclimatic variables from WorldClim 2.0 (Fick and Hijmans 2017) with the Cumulative Water Deficit (CWD) parameter from Chave et al. (2014) and the potential evaporation (PET) from CHELSA 2.1 (Karger et al. 2017). For disturbance predictors, we used summed fire count from MODIS Terra and Aqua combined product (MCD64A1, Giglio et al. 2018) over the period 2001–2020 and estimates of past herbivore biomass (Hempson et al. 2015). We also used a digital elevation model obtained from the Shuttle Radar Topographic Mission and calculated the topographic ruggedness index (TRI) (Table 1). For each predictor, we calculated the mean for each grid cell using zonal statistics in the terra R package (Hijmans 2024). For calculating geographical distances, we used the centroid of each grid cell and calculated the pairwise distances in km with the geosphere R package (Hijmans 2022).

2.5 | Statistical Analyses

To test how forests and savannas compare in their levels of phylogenetic beta diversity, we used the combined matrix of forest and savanna assemblages, and computed an evolutionary PCA (evoPCA) based on Hellinger distance with presence/absence data, implemented in the adiv R package (Pavoine 2020). This method allows the placement in ordination space of communities using the shared branch lengths of the phylogenetic tree. Contrary to using classic floristic ordinations like correspondence analysis (CA) or Non-Metric Multidimensional Scaling (NMDS), the evolutionary ordination approach avoids the saturation of dissimilarity between communities that share no species in common, because all species share some branch length

TABLE 1 | Environmental predictors.

Variable	Code	Source
Mean annual temperature	bio01	WorldClim 2.0 (Fick and Hijmans 2017)
Mean diurnal temperature range	bio02	WorldClim 2.0 (Fick and Hijmans 2017)
Isothermality	bio03	WorldClim 2.0 (Fick and Hijmans 2017)
Temperature seasonality	bio04	WorldClim 2.0 (Fick and Hijmans 2017)
Maximum temperature of the warmest month	bio05	WorldClim 2.0 (Fick and Hijmans 2017)
Minimum temperature of the coldest month	bio06	WorldClim 2.0 (Fick and Hijmans 2017)
Temperature annual range	bio07	WorldClim 2.0 (Fick and Hijmans 2017)
Mean temperature of the wettest quarter	bio08	WorldClim 2.0 (Fick and Hijmans 2017)
Mean temperature of the driest quarter	bio09	WorldClim 2.0 (Fick and Hijmans 2017)
Mean temperature of the warmest quarter	bio10	WorldClim 2.0 (Fick and Hijmans 2017)
Mean temperature of the coldest quarter	bio11	WorldClim 2.0 (Fick and Hijmans 2017)
Mean annual precipitation	bio12	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation of the wettest month	bio13	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation of the driest month	bio14	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation seasonality	bio15	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation of the wettest quarter	bio16	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation of the driest quarter	bio17	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation of the warmest quarter	bio18	WorldClim 2.0 (Fick and Hijmans 2017)
Precipitation of the coldest quarter	bio19	WorldClim 2.0 (Fick and Hijmans 2017)
Total fire count (2001–2020)	fire	MODIS BA Product MCD64A1 (Giglio et al. 2018)
Cumulative water deficit	cwd	Chave et al. 2014
Past herbivore biomass	herbivr	Hempson et al. 2015
Altitude	alt	SRTM (Jarvis et al. 2008)
Topographic ruggedness index	tri	SRTM (Jarvis et al. 2008)
Potential evapotranspiration	pet	CHELSA 2.1 (Karger et al. 2017)

in the phylogenetic tree. We transformed the evoPCA into a dissimilarity matrix using the function dist.dudi(), implemented in the ade4 R package (Dray and Dufour 2007) to obtain a phylogenetic Hellinger distance matrix ($\beta_{\mathrm{Hellinger}}$). We used this Hellinger distance matrix to test for multivariate homogeneity of group dispersions between forest and savanna assemblages with a beta dispersion test using the vegan R package (Oksanen et al. 2022). We assessed the significance of the test using 1000 permutations and calculated the difference between the two groups with Tukey's honest significant difference (HSD). As beta dispersion calculates the arithmetic mean of all distances to the spatial median, we compared this to the maximum a posteriori probability estimate (MAP) using a Bayesian *t*-test with the ggstatsplot R package (Patil 2021).

We complemented our multivariate dispersion tests by calculating beta diversity as a ratio of gamma/alpha diversity (multiplicative beta, β_M) while accounting for sampling completeness using the iNEXTbeta3D R package (Chao et al. 2023). This method implements interpolation and extrapolation curves to calculate diversity using Hill numbers (Hill 1973). Importantly, iNEXTbeta3D allows the calculation of independent alpha and beta components (Chao et al. 2012; Jost 2007, 2010). We chose to analyse only effective diversity numbers of order $q=0$, which represent richness, because we are trying to identify past episodes of differentiation; thus, abundance information is not necessarily relevant except for standardising the coverage (Chiu et al. 2014). We selected the assemblages that had at least five species and 15 occurrences to avoid sampling artefacts from undercollected assemblages ($N=386$ for forest assemblages and $N=738$ for savanna assemblages). This allowed comparison between assemblages with high levels of sampled coverage (80%). We compared beta diversity using sample coverage standardisation of 50%, 60%, 70%, 80% and 90% (the latter of which represents extrapolated estimates). We also performed this analysis at a taxonomic level for comparison. Because beta diversity, when expressed as a ratio of gamma/alpha (multiplicative beta, β_M) represents relative beta diversity, it does not convey information on absolute beta diversity (additive beta, β_A), which can be more important from a management perspective. However, both multiplicative and additive forms of beta are influenced by the number of assemblages. To standardise our measures of beta diversity on a per-assemblage basis, we used the differentiation measures 1-CqN (which represents absolute local turnover per assemblage, or the effective proportion of unique lineages in an average assemblage) and 1-UqN (which represents relative regional turnover per assemblage, or the effective proportion of unique lineages in the pool) (Chao et al. 2023; Chiu et al. 2014).

To analyse how phylogenetic beta diversity is spatially distributed across tropical Africa, we used the same evoPCA approach, but this time we analysed forest and savanna assemblages separately. The evoPCA not only allows the representation of continuous gradients (as opposed to hard boundaries defined by hierarchical clustering methods), it also allows identifying specific phylogenetic lineages associated with assemblage positioning in the ordination space and is a powerful tool for analysing phylogenetic patterns along spatial and environmental gradients (Pavoine 2016). Thus, it can serve to test hypotheses about dispersal limitations and environmental filtering (Luize et al. 2024). We fit divergent colour gradients of a red–green–blue spectrum to the points in the ordinations using the first three axes of the ordination, to visualise the compositional phylogenetic distance between assemblages. We used the same colour scheme to map the identity of the points in the ordination back onto the map of Africa with their respective grid cells. As a sensitivity test, we also performed this analysis with a more conservative threshold, using a minimum of 20 species for the inclusion of any assemblage. We compared our evoPCA method with two other common ways of analysing patterns of beta diversity, namely moving window average of pairwise dissimilarities and phyloregionalisation. We transformed the evoPCAs into dissimilarity matrices and calculated a geographic pairwise distance matrix with the geosphere R package (Hijmans 2022). The moving window average was calculated using a 500 km radius around each assemblage and averaging the dissimilarities between the focal assemblage and the neighbour assemblages. The phyloregionalisation was performed by using hierarchical clustering with Ward's minimum variance method (Ward 1963). We varied the number of clusters (k) from two to n, n being the phylogenetic beta diversity value obtained at 90% sample coverage in the iNEXTbeta3D analysis, rounded to the nearest integer. We did not partition the floristic dissimilarity matrix into further components (nestedness and turnover) as is commonly seen elsewhere (Baselga 2010; Carvalho et al. 2012) because we refer to the original idea of Whittaker (1960) in defining beta diversity irrespective of the process that generated it.

Finally, to understand the ecological drivers of phylogenetic beta diversity, we modelled floristic distances using ecological and geographical predictors. We created the environmental dissimilarity matrices using all environmental predictors and built a PCA, then transformed the PCA into a Euclidean distance matrix. We compared the floristic, environmental and geographical distance matrices using distance-decay plots and partial mantel tests in the vegan R package (Oksanen et al. 2022). To visualise how the lineage composition of forests and savannas is related to ecological factors, we used an ad hoc correlation test between the evoPCA axes and the environmental predictors. We then used Generalised Dissimilarity Modelling (GDM) with the gdm R package (Fitzpatrick et al. 2022) to model the main drivers of phylogenetic beta diversity for forests and savanna assemblages. This method is well suited for analysing non-linear relationships between predictors and multivariate response matrices, a case which is common when sampling wide ecological gradients (Ferrier et al. 2007; Fitzpatrick et al. 2013). We first fit the model using all predictors and used the geographic distance between the centre of each grid as a spatial predictor. We then removed all predictors for which the sum of coefficients was zero and, to avoid multicollinearity, we calculated the Pearson correlation coefficients among all pairs of remaining predictors and selected one predictor among any pair with a correlation coefficient > 0.75. We used a variation partitioning framework to determine which of the climate, disturbance or geographic distance predictors contributed the most explained deviance. We then focused on the climatic variables and partitioned the deviance between temperature and precipitation variables.

3 | Results

3.1 | Comparing Levels of beta Diversity

The first two axes of the evoPCA on the combined matrix of forest and savanna assemblages explained 8.2% and 6.4% of the variance respectively (Figure S1). The first axis mainly separated forest assemblages from savanna assemblages, and the second axis emphasised the large variance within savanna assemblages.

The beta dispersion test found a significant difference between the two groups ($F = 8.8$, $p > 0.01$), with forests having a mean distance to the spatial median of 0.763 and savannas 0.756. Tukey's honest significant difference between the two groups was 0.008 ($p < 0.01$). Compared this with the Bayesian t-test, forests had a maximum a posteriori probability estimate of 0.751 and savannas had 0.768. The estimated posterior difference was 0.007 ($BF_{10} = 7.37$, prior scale $= \sqrt{0.5}$) (Figure S2).

The interpolation–extrapolation analysis shows forest assemblages hold higher levels of phylogenetic alpha and gamma diversity than savanna assemblages, but savanna assemblages hold higher levels of relative phylogenetic beta diversity (β_M). When accounting for the number of samples in each group, forests show a higher relative turnover at the local scale (1-CqN) but a lower relative turnover at the regional scale (1-UqN) (Figure 1; Table S1). The analysis using taxonomic information found similar results (Figure S3).

3.2 | Spatial Distribution of Phylogenetic beta Diversity

3.2.1 | Forests

The first three axes of the forest evoPCA explained 17.6% of the variance and showed strong spatial patterns (Figure 2A). A reduced evoPCA, including only assemblages with at least 20 species, found very similar results (Figure S4). The first axis mainly separated Guinean forests from all other forests

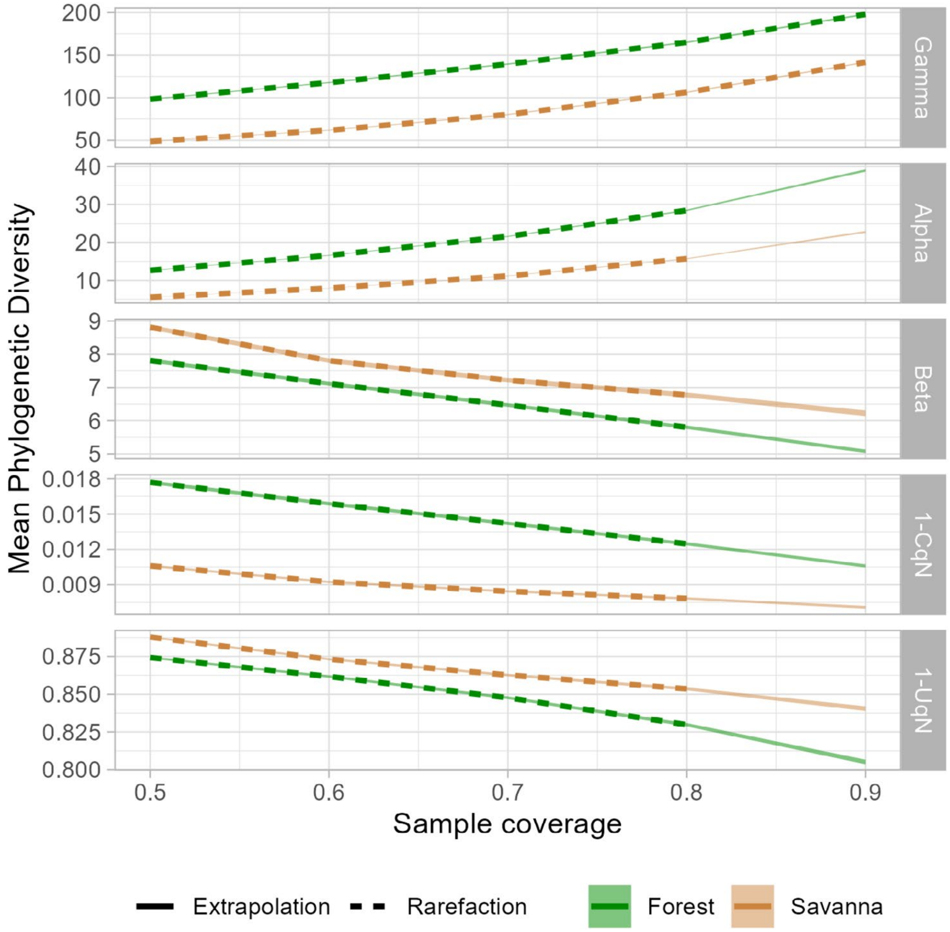

FIGURE 1 | Partitioning of phylogenetic diversity of order $q = 0$. Forests are represented in green and savannas in brown. The ribbon around the line corresponds to the 95% confidence interval from 100 bootstrap replicates. The mean phylogenetic diversity corresponds to the effective number of equally divergent lineages and is calculated by dividing the effective total branch length by the depth of the tree. 1-CqN represents the effective proportion of unique lineages in an average individual assemblage and is a measure of local lineage turnover. 1-Uqn represents the effective proportion of unique lineages in the pooled assemblages and is a measure of regional lineage turnover.

(Figure 2B), whereas the second axis separated Congolian + Eastern forests from West Sudanian forests, and the third axis separated Eastern forests from Congolian forests (Figure 2C). Guinean forest composition was driven by Annonaceae, Myristicaceae, Melastomataceae tribe Olisbeoideae (*Memecylon* + *Warneckea*), Lecythidaceae, Pandaceae, *Gilbertiodendron* and *Trichilia*, albeit with low relative contributions. West Sudanian forests were composed of Phyllanthaceae such as *Bridelia*, *Cassia* and members of the order Myrtales, particularly Combretaceae. Congolian forests were strongly defined by members of Magnoliales, Detarioid legumes and members of the family Ochnaceae, such as *Campylospermum*, while east African forests were mainly defined by Rosales, particularly Moraceae. Both Congolian and Eastern forests were strongly associated with lamiids, including Gentianales and, more specifically, Rubiaceae tribe Ixoroideae (Figure 2D,E).

The moving window average showed that Lower Guinean forests hold the lowest levels of pairwise beta diversity with their neighbours, whereas higher levels of pairwise beta diversity were scattered around the Congo basin and in the northern parts of the Dahomey Gap (Figure S5). The phyloregionalisation showed East African forests as being compositionally distinct from all other forests. Upper and Lower Guinean forests were separated from Congolian and Western Sudanian forests (Figure S6).

3.2.2 | Savannas

The first three axes of the savanna phylogenetic ordinations explained 20.4% of the variance and the spatial patterns were less marked than those retrieved from the forest species (Figure 3A). A reduced evoPCA, including only assemblages with at least 20 species, found very similar results (Figure S7). The first axis mainly separated savannas in East Africa versus Sahelian + West Sudanian savannas in West Africa (Figure 3B). The second axis separated Sahelian versus West Sudanian + Somalian savannas, and the third axis separated the moist savannas in Guinea-Congolia + Miombo versus all other savannas (Figure 3C).

East African savanna composition was driven by Rutaceae, Euphorbiaceae, Primulaceae and Campanuliids. Sahelian savannas were composed of Mimosoid legumes such as *Vachellia* and Lamiids, particularly Gentianales. West Sudanian and Somalian savanna composition was driven by Strychnos,

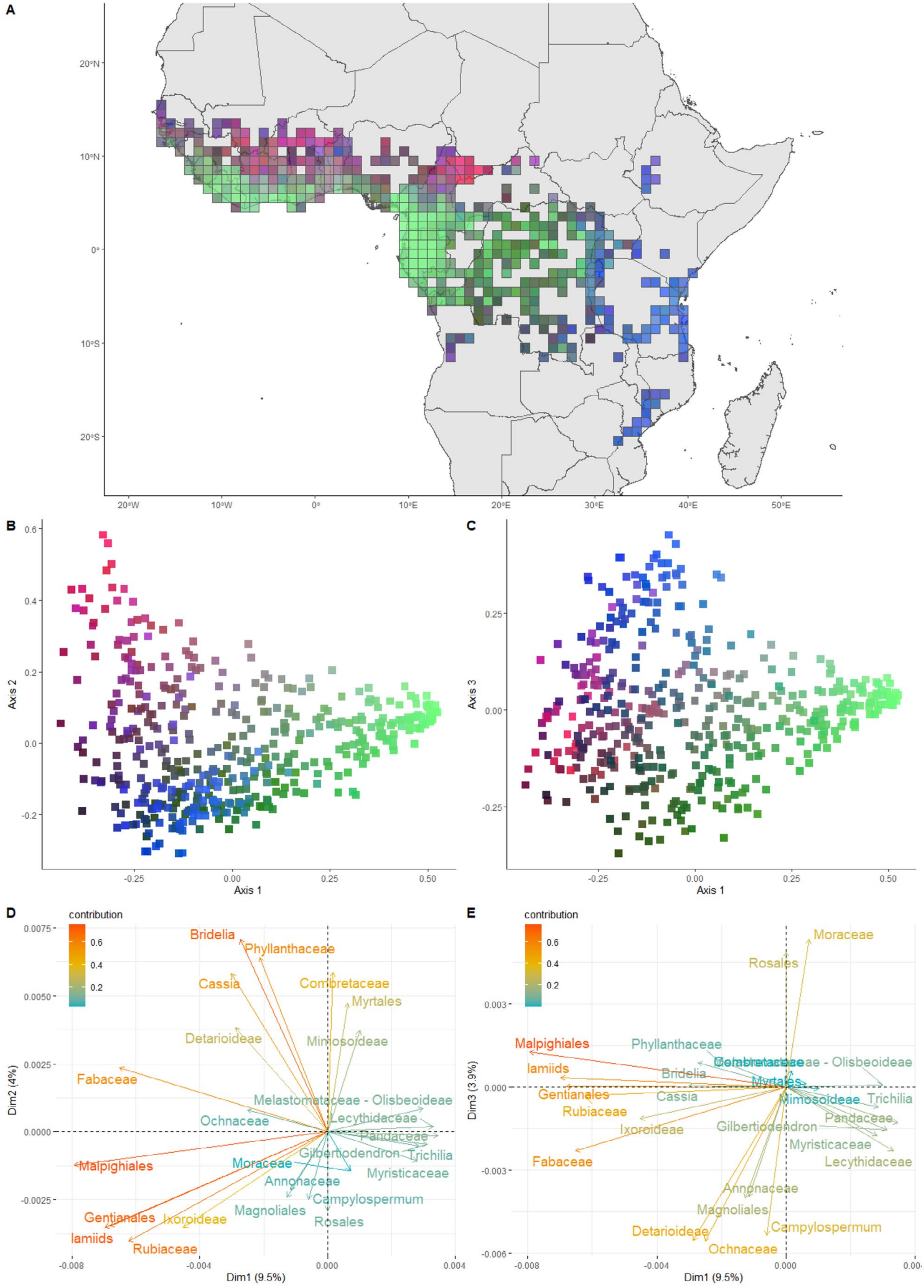

FIGURE 2 | Legend on next page.

FIGURE 2 | Evolutionary composition of African forests. (A) Map of Africa with 1° grid cells coloured in red-green-blue according to the first three axes of the evoPCA on the presence/absence matrix of 1883 forest species over 457 assemblages. Divergent colours represent divergent phylogenetic composition. (B–C) Representation of the first three axes of the evoPCA. (D, E) Lineage contributions to the evoPCA. Arrows show the influence of lineages on the ordination, with length and colour according to how strongly they contributed to each axis.

Annona, *Pterocarpus*, *Piliostigma* and Detarioid legumes. Both Sahelian and West Sudanian savannas shared Combretaceae, Rhamnaceae and Burseraceae and members of the Brassicales such as *Boscia*. Moist savannas in Guinea-Congolia/Miombo were driven by Malpighiales and Rubiaceae, particularly subfamily Ixoroideae (Figure 3D,E).

The moving window average showed that Sahelian and West Sudanian savannas hold the lowest levels of pairwise beta diversity with their neighbours, whereas higher levels of pairwise beta diversity were scattered across Africa with no clear pattern (Figure S8). The phyloregionalisation showed a clear division along White's line between East and West Africa, each with distinct clusters. With a few isolated assemblages, West Africa contained assemblages associated with all clusters (Figure S9).

3.3 | Drivers of Phylogenetic beta Diversity

3.3.1 | Forests

The variables most strongly correlated to Axis 1 were the temperature annual range (bio7) ($R=-0.68$), with high values characterising West Sudanian, Congolian and Eastern forests, and mean annual precipitation (bio12) ($R=0.61$), with high values characterising Guinean forests. The variables most strongly correlated to Axis 2 were the maximum temperature of the warmest month (bio5) ($R=0.65$), with high values characterising West Sudanian forests, and Isothermality (bio3) ($R=-0.44$), with high values characterising Eastern and Congolian forests. The variables most strongly correlated with Axis 3 were past herbivore biomass ($R=0.43$), with high values characterising Eastern forests, and the mean temperature of the coldest quarter (bio11) ($R=-0.38$), with high values characterising Congolian forests (Figure 4A,B).

Partial mantel tests showed that when controlling for ecological distance, geographic distance explained 17.3% of unique variance ($p<0.01$, nperm = 999). When controlling for geographic distance, ecological distance explained 32.3% of unique variance ($p<0.01$, nperm = 999) (Figure S10 for the distance-decay plots). The GDM explained 36.3% of deviance in forest assemblages. The phylogenetic dissimilarity was mainly explained by climate with 9.8% unique deviance, followed by disturbance with 3.1% unique deviance and finally geographic distance with 1.8% unique deviance. Within the climatic factors, precipitation explained slightly more deviance than temperature, with 12.7% and 9.3% respectively. The most important predictor was the mean temperature of the coldest quarter (bio11) which showed that phylogenetic dissimilarity increases almost linearly with an increase in temperature during the coldest quarter. The second most important predictor was the past herbivore biomass, which showed that phylogenetic dissimilarity increases exponentially with herbivore biomass (Figure 4C,D).

3.3.2 | Savannas

The variables most strongly correlated to Axis 1 were the maximum temperature of the warmest month (bio5) ($R=-0.79$), with high values characterising Sahelian and West Sudanian savannas, and the topographic ruggedness index (TRI) ($R=0.58$), with high values characterising East African savannas. The variables most strongly correlated to Axis 2 were fire count ($R=0.44$), with high values characterising West Sudanian savannas, and potential evapotranspiration (PET) ($R=-0.33$), with high values characterising Sahelian and Somalian savannas. The variables most strongly correlated with Axis 3 were cumulative water deficit (CWD) ($R=-0.63$), with high values characterising Western Sudanian, Sahelian and East African savannas and mean annual precipitation (bio12) ($R=0.61$), with high values characterising Congolian and Miombo savannas (Figure 5A,B).

Partial mantel tests showed that when controlling for ecological distance, the geographic distance explained 6.3% of unique variance ($p<0.01$, nperm = 999). When controlling for geographic distance, the ecological distance explained 39.5% of unique variance ($p<0.01$, nperm = 999) (Figure S10 for the distance-decay plots). The GDM explained 31.4% of deviance in savanna assemblages. The phylogenetic dissimilarity was mainly explained by climate with 19% unique deviance, followed by geographic distance with 1.35% unique deviance and finally disturbance with 0.7% unique deviance. Within the climatic factors, precipitation explained almost twice as much deviance as temperature with 10.7% and 6% respectively. The most important predictor was the precipitation of the wettest quarter (bio16) which showed a sharp increase in phylogenetic dissimilarity from 0 to around 500 mm, followed by a slower increase in phylogenetic dissimilarity. The second most important predictor was the cumulative water deficit (CWD) which showed an exponential increase in phylogenetic dissimilarity from −750 until CWD reaches 0 (Figure 5C,D).

4 | Discussion

In this study, we used a large data set of woody plant occurrence records combined with phylogenetic and ecological information to shed light on patterns and drivers of phylogenetic beta diversity in the forests and savannas of Africa. Savannas showed higher levels of relative beta diversity, but lower levels of absolute beta diversity compared to forests. In both forests and savannas, we found strong East–West patterns of phylogenetic composition, which were mainly driven by precipitation.

4.1 | Beta Diversity

Our beta dispersion test found an unequal variance in dispersion between forests and savannas, and that forests had a higher

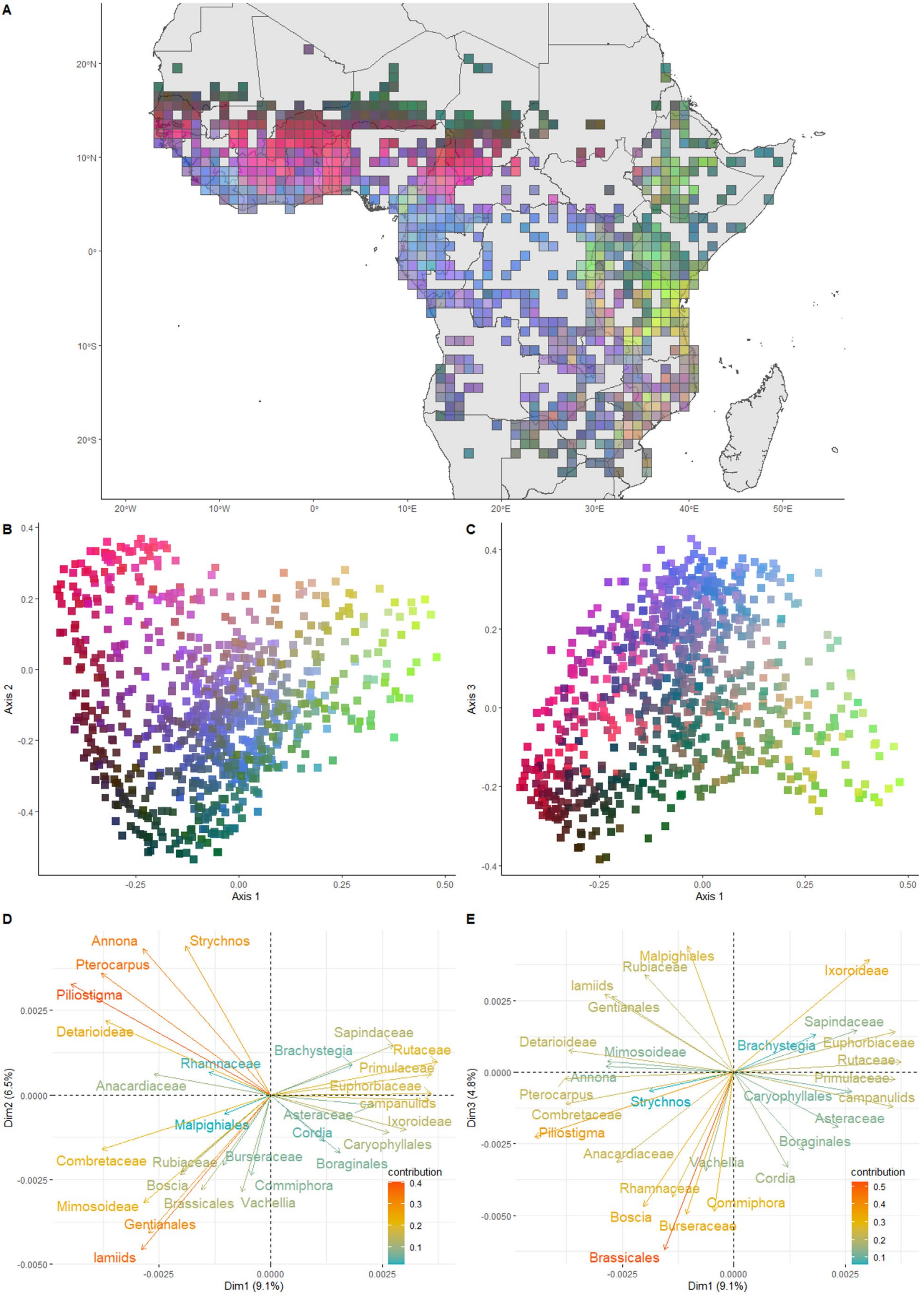

FIGURE 3 | Legend on next page.

FIGURE 3 | Evolutionary composition of African savannas. (A) Map of Africa with 1° grid cells coloured in red–green–blue according to the first three axes of the evoPCA on the presence/absence matrix of 1307 savanna species across 837 assemblages. Divergent colours represent divergent phylogenetic composition. (B, C) Representation of the first three axes of the evoPCA. (D, E) Lineage contributions to the evoPCA. Arrows show the influence of lineages on the ordination, with length and colour according to how strongly they contributed to each axis.

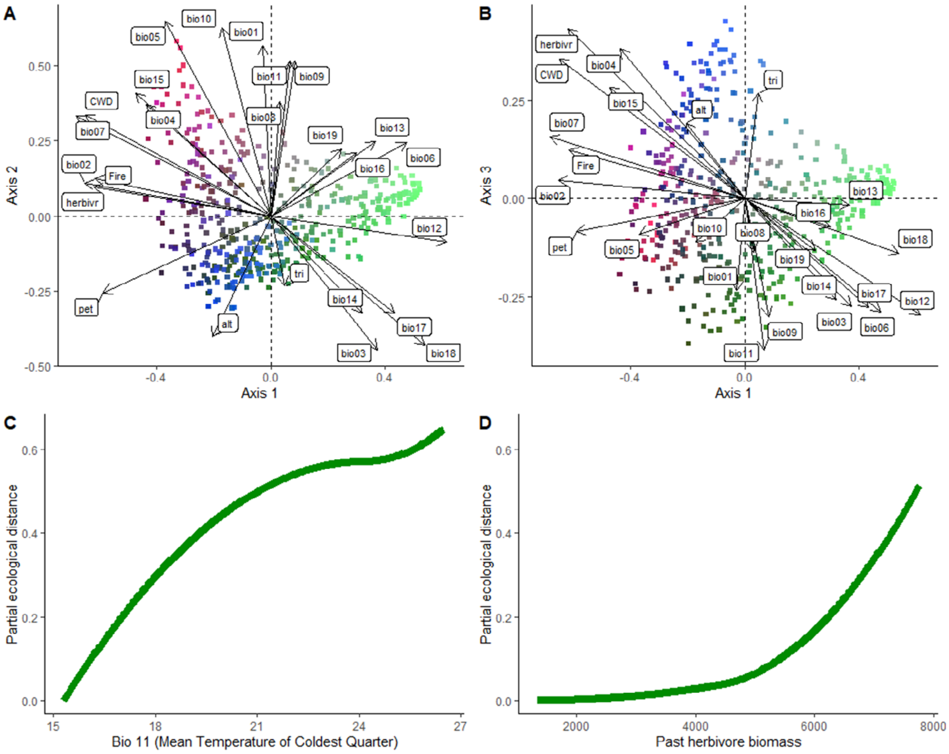

FIGURE 4 | Ecological drivers of forest phylogenetic beta diversity. (A, B) Correlations with phylogenetic ordination axes. Colour scheme follows that of Figure 2. The direction and length of the arrow represents the Pearson correlation coefficient with the portrayed axes. Codes for variables are provided in Table 1. (C, D) Phylogenetic dissimilarity as a function of ecological distance for mean temperature of the coldest quarter (C) and past herbivore biomass (D). The maximum height of the curve shows the predictor's effect on dissimilarity holding all other variables constant, while the slope shows the rate of change along the predictor's gradient.

mean distance from the spatial median. However, the difference between forests and savannas was small and, in fact, our Bayesian *t*-test showed an opposite pattern, suggesting that savannas had a higher maximum a posteriori probability estimate from the spatial median, again with a very small difference between the two groups. This indicates that both forests and savannas have a similar amount of compositional change over large spatial scales. Our result is surprising, given the much higher species richness found in forests, as one would expect two forest assemblages to have more unique species than savannas, thus increasing compositional change. When applied in a phylogenetic context, this might suggest that forest assemblages share as many or as few lineages *inter se* as do savanna assemblages. In addition, savanna lineages are thought to be younger than forest lineages (Beerling and Osborne 2006; Edwards et al. 2010), and thus we expected that forest assemblages would contain lineages with longer branches in the phylogenetic tree and show higher levels of compositional change. However, compositional change is strongly influenced by patterns in alpha diversity (Ives and Helmus 2010), such that assemblages with more species will naturally share more lineages than assemblages with fewer species, thus reducing compositional change.

Our interpolation–extrapolation analysis of beta diversity allowed us to account for sampling coverage, number of assemblages and levels of alpha diversity. We find that both forests and savannas have a high proportion (over 80%) of unique lineages across the whole pool (1 – UqN), meaning there is a high amount of phylogenetic beta diversity that is pure turnover in both biomes. From a conservation perspective, this highlights the importance of having multiple protected areas that cover the entire spread of phylogenetic composition, in order to successfully capture and preserve the unique diversity held in individual regions of both the forest and savanna biomes. We confirm the results of diversity found in Murphy et al. (2016) and Rees et al. (2023): that forests have on average more species and more phylogenetic alpha diversity than savannas. However, the analysis highlighted savannas as having a higher relative regional phylogenetic beta diversity than forests, both before and after standardising for the number of assemblages (β_M and 1 – UqN), but that forests had a higher relative local phylogenetic beta diversity per assemblage (1 – CqN). In other words, forests have a higher number of unique lineages in a single average assemblage, but savannas have a higher proportion of unique lineages across the whole pool. This could be due to

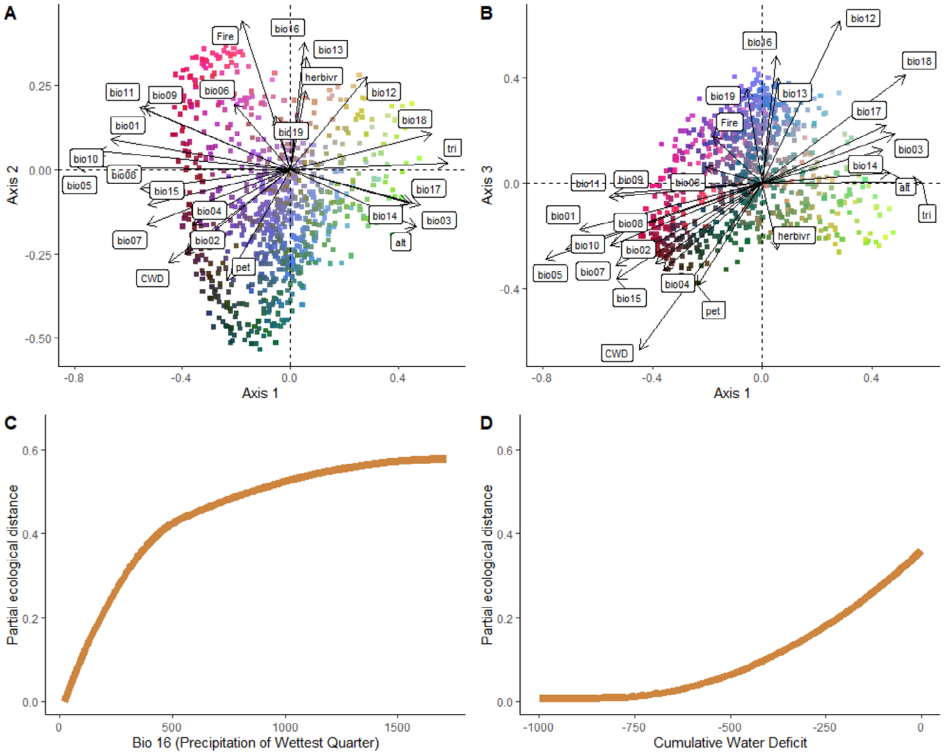

FIGURE 5 | Ecological drivers of savanna phylogenetic beta diversity. (A, B) Correlations with phylogenetic axes. Colour scheme follows that of Figure 3. The direction and length of the arrows represent the Pearson correlation coefficient with the portrayed axes. Codes for variables are provided in Table 1. (C, D) Phylogenetic dissimilarity as a function of ecological distance for precipitation of the wettest quarter (C) and Cumulative Water Deficit (D). The maximum height of the curve shows the predictor's effect on dissimilarity holding all other variables constant, while the slope shows the rate of change along the predictor's gradient.

savannas occupying larger physical space than forests, reducing the exchange of lineages among communities through dispersal limitation or by occupying larger ecological space, with specific clades being selected through environmental filtering. Alternatively, this might be due to savannas having evolved multiple times independently. For example, spiny lineages are thought to have evolved prior to fire-adapted lineages (Charles-Dominique et al. 2016) and molecular phylogenies show that savanna species are found across the angiosperm tree of life (Gorel et al. 2022). Phylogenetic diversity is often used as a proxy for functional diversity when functional traits would be difficult to gather for all species (Swenson 2019). Our results invite us to ask whether these differences in phylogenetic diversity between forests and savannas could also be reflected in functional diversity. With the gradual increase in functional trait data available to plant scientists, answering this question could be imminent (Scheiter, Dushyant, et al. 2024).

4.2 | Change in Composition Across Space

Our phylogenetic ordinations of gridded forest and savanna assemblages reveal striking motifs of how beta diversity is distributed across Africa. West African forests displayed the most variation, occupying the entire spectrum of phylogenetic composition, with Upper Guinean Forest and Western Sudanian forests very close in geographic space but very distant in phylogenetic space. This contrasts with East African forests, which were represented by a distinct but more homogeneous phylogenetic composition. Savannas also showed clear patterns in West Africa, with a clear change in composition along a south–north aridity gradient, a result that was previously highlighted by Fayolle et al. (2019). East African savannas were more heterogeneous in the way compositional change was distributed due to the high topographic diversity in the region. The phyloregionalisation approach mirrored these results and broadly matched up with previously defined biogeographic regions (Droissart et al. 2018; Fayolle et al. 2014, 2019; Linder et al. 2005, 2012; Marshall et al. 2021; White 1983).

The results from the moving window average were similar to those of Qian et al. (2024) who found that botanical countries in West Africa had very low levels of phylogenetic beta diversity (as quantified by the Sorenson index β_{Sor}) relative to their neighbours. This contrasts with the results from our ordinations and phyloregionalisation, which suggest that West Africa holds the highest levels of change in composition both for forests and savannas. We interpret this apparent contradiction as a difference between the scales of the analyses, even though the spatial resolution is the same (comparing 1° grid cells across the whole continent in the evoPCA and phyloregionalisation versus comparing only close neighbours in the moving window). This is because the moving window average cannot take into account the patterns of co-occurrence among more than two sites (Baselga 2013). This suggests that using local moving window averages when looking at large-scale patterns should be interpreted with caution, as they might give the false impression that West Africa is phylogenetically depauperate relative to the rest of the continent, when in fact this is where large changes in composition occur, mainly along an aridity gradient. By extension, methods that correlate environmental predictors to these averaged values of beta diversity might provide misleading answers (Melo et al. 2009; Pinto-Ledezma et al. 2018; Qian et al. 2024). It is unclear if similar methods that try to circumvent this issue by taking the dissimilarity between multiple neighbouring cells into account will perform any better (Xu et al. 2023). For continental or global analyses, it is likely more informative to take into account the entire matrix. Further splitting of our assemblages into distinct clusters (East vs. West for example) and comparing the levels of phylogenetic beta diversity between each cluster might help understand these patterns.

4.3 | Savannas, Lineages and Ecology

Early studies distinguished two types of savannas: moist and dry savannas (Irvine 1941; Pole Evans 1936), explicitly highlighting that the major ecological driver was precipitation. Further refinement on the ecology of savannas included soil components, such that savannas were split along an aridity and soil nutrient gradient, with moist-dystrophic savannas at one end and arid-eutrophic savannas at the other end (Cole 1956, 1986). The interest in disturbance, including herbivory and fire, was present early on (Phillips 1930), mainly for land management purposes (Aubreville 1953; Scott 1947), adding to the dichotomy by characterising dry-eutrophic-browser (brown savannas) and moist-dystrophic-fire (black savannas) (Bond 2005; Huntley 1982; Scholes and Archer 1997). At the local scale, soil properties and disturbance (including frost, fire and herbivory) are the main drivers of savanna physiognomy and composition (Bond 2022; Finckh et al. 2021; Hoffmann et al. 2019; Lloyd et al. 2015; Veenendaal et al. 2018), whereas at the regional scale, precipitation gradients are the major driver of taxonomic and phylogenetic alpha and beta diversity (Davies et al. 2023; Fayolle et al. 2019). Our GDM results support the original idea that differences among African savannas are mainly driven by precipitation, showing that dissimilarity increases strongly until around 500 mm of precipitation during the wet season and from −750 mm to 0 mm of CWD. The variance partitioning exercise also found that combined precipitation predictors explained the most deviance in the model. Surprisingly, disturbance was the least influential. This could be because all savannas are partly driven by disturbance; hence, increases in disturbance do not produce as much change as increasing or decreasing precipitation, where adaptations to moist or dry conditions might mediate the coordination of functional strategies.

As well as these functional characteristics of savannas, floristic aspects have also been documented, particularly concerning the lineages of legumes. The lack of nodulation in Detarioid legumes in moist and nutrient-poor savannas has often been contrasted with that of Mimosoid and Papilionoid legumes in phosphorous rich soils in drier climates (Högberg 1986; Huntley 1982; Pellegrini et al. 2016). Osborne et al. (2018) provided a simple floristic generalisation for savannas dominated either by Combretaceae, Detarioid legumes or Mimosoid legumes. Fayolle et al. (2019) delimited eight floristic clusters (two in north-west and six in south-east) and used an indicator analysis to associate certain genera with these clusters. In the north-west, they were not able to identify distinct genera for Sudanian and Western-Guinean savannas. In the south-east, they identified *Commiphora*, *Grewia* and *Vachellia* as being significantly associated with Ethiopian and South African savannas. *Ficus* and *Euphorbia* were significantly associated with Ugandan savannas. The genera *Uapaca* and *Isoberlinia* were associated with the Miombo of Zambia, and the genus *Brachystegia* was associated with both Zambian and Mozambican savannas.

Here we show additional patterns and associate different savannas with climatic conditions. For example, in West Africa, there is a clear environmental gradient shaping savanna composition, from wet savannas in Upper Guinea dominated by members of Rubiaceae and the order Malpighiales, a clade known for its forest affinities (Gorel et al. 2022), through pyrophytic West Sudanian savannas with clades such as Detarioid legumes, Phyllanthaceae, *Piliostigma*, *Pterocarpus*, *Annona* and *Strychnos*, to the arid Sahelian savannas dominated by Mimosoids Legumes, Lamiids, Burseraceae and Brassicales (like *Boscia*). Combretaceae did show some association with all savannas across the north-west.

East African savannas were made up of montane savannas in Ethiopia, the Eastern Arc Mountains, the Albertine rift in eastern DRC, and lowland savannas along the coast of Kenya and Tanzania (also referred to as the Zanzibar-Inhambane coastal forest–savanna mosaic). Parts of the Cameroon volcanic line also showed some level of association with these montane savannas. All shared Rutaceae, Primulaceae, Euphorbiaceae and Campanuliids and were mainly influenced by topography and isothermality. Interestingly, the genus *Brachystegia*, often associated with the moist pyrophytic savannas of the Miombo, was more associated with the East African savannas, a result that highlights this region as being a centre of diversification for the genus (Boom et al. 2021, 2022).

4.4 | Forests, Lineages and Ecology

Despite forests of Lower Guinea and Congolia being connected today, paleoclimatic reconstructions, fossil records and population genetic studies reveal a long history of separation and re-unification following climatic cycles, from as early as the Miocene (Axelrod and Raven 1978; Couvreur et al. 2021; Hardy et al. 2013). Here we find that forests in Upper and Lower Guinea share more lineages with each other than they do with Congolia or East Africa.

Guinean forests are the wettest forests in Africa and, being the richest in number of species and phylogenetic alpha diversity, they are also the forests with the least amount of defining lineages, as they served as refugia during dry periods of interglacial cycles, accumulating many different lineages (Maley 1996). Instead, they could be better defined by the lineages for which they have fewer species, such as Fabaceae, Rubiaceae and Malpighiales, which were more strongly associated with West Sudanian and Eastern forests. Interestingly, these Guinean forests host fewer large herbivores than Eastern or West Sudanian forests and instead are inhabited by many small non-social browsers and primates (Fonteyn et al. 2023; Hempson et al. 2015). This was reflected in our GDM results, which highlighted past herbivore biomass being a strong predictor of forest phylogenetic dissimilarity. The largest animals in these forests, which are also shared with some parts of Western Congolia, are the forest elephants (*Loxodonta cyclotis* Matschie) which have been found to increase carbon stocks by reducing competition among saplings and small trees, and by increasing the relative abundance of species with higher wood density (Berzaghi et al. 2019, 2023; Terborgh et al. 2016a, 2016b). These elephants have also been suggested to modulate the boundaries between forests and savannas, facilitating the coexistence of both biomes in tropical landscapes (Cardoso et al. 2020). This highlights the ancient and important role of disturbance in tropical forests, with a general decrease in diversity as disturbance increases (Alroy 2017; Maicher et al. 2020). In contrast, in savanna systems, disturbance can either have a positive or negative effect on diversity. For example, increases in fire intensity have been found to reduce species richness, whereas herbivory can have a positive effect on species richness and phylogenetic diversity (Davies et al. 2023; Buramuge et al. 2023).

Congolian forests were found in moist, isothermal climates defined by the clades of Ochnaceae (primarily *Campylospermum*) and Detarioid legumes, species of which are known to form monodominant stands, such as *Gilbertiodendron dewevrei* (Heimpel et al. 2024). Congolian forests also tend to have a higher proportion of deciduous species compared to Guinean forests (Réjou-Méchain et al. 2021). The two main predictors highlighted by our GDM (temperature of the coldest quarter and herbivore biomass) correspond to the two predictors driving the third axis of the evoPCA that separates Eastern from Congolian forests along the Albertine rift, implying that some of the highest changes in composition are found on either side of this line, as previously highlighted by Fayolle et al. (2014). This major biological barrier located along White's line is ecologically similar to the major division between forests in Western Amazonia located on geologically young and relatively nutrient-rich substrate and those located in the Guiana Shield on geologically old and nutrient-poor substrate (Luize et al. 2024). Soils in East Africa tend to be younger and of higher nutrient content than the old ferrasols in the Congo basin (Dewitte et al. 2013).

Eastern forests were composed of montane forests in the highlands of Ethiopia, the Eastern Arc Mountains, and the Albertine rift in eastern DRC, along with lowland forests along the Zanzibar-Inhambane coastal forest mosaic, all of which were defined by members of the Rosales, such as Moraceae and were considerably drier and had more herbivores than Congolian forests. Levels of alpha diversity are generally lower for these forests than for other forests in Africa (Rees et al. 2023), despite the high endemism linked to orogenic activity and long climatic stability (Couvreur et al. 2021; Fjeldså and Lovett 1997; Lovett et al. 2005). However, these forests do show higher alpha phylogenetic diversity than expected given their species richness (PD_{ses}) (Rees et al. 2023). Given the higher concentration of herbivores in these regions, it is possible that these forests might have played an important role in promoting biome shifts from forest to savanna, leading to the diversification of browser-adapted savanna lineages which predate fire-adapted lineages (Charles-Dominique et al. 2016; Donoghue and Edwards 2014).

Finally, the Western Sudanian forests, occupying the transition zone between the wet Guinean forests and the Sahel, are the hottest and driest forests in Africa, defined by many Fabaceae, members of the order Myrtales such as Combretaceae and Phyllanthaceae such as *Bridelia*. Dry forests tend to have increased resistance to disturbance, as they shift their functional strategies towards regeneration through resprouting (Poorter et al. 2010; Swaine 1992). The main bioclimatic variable associated with these forests was the maximum temperature of the warmest month (bio5), a variable that was also found to explain large variance in floristic composition in the Amazon basin (Tuomisto et al. 2019). In general, our variance partitioning exercise and the correlations with the axes of the phylogenetic ordinations show that variables linked to precipitation play a strong role in defining compositional change across African forests.

4.5 | Ecological Drivers

We found a consensus between our GDM, partial mantel test and distance-decay plots, which highlighted environmental filtering as having a stronger role than dispersal limitation for both forests and savannas. This result is in line with other studies at smaller spatial scales in African forests (Parmentier et al. 2014) and the Amazon basin (Baraloto et al. 2012; Guevara Andino et al. 2021; Tuomisto et al. 2003) and large spatial scales between continents (Cai et al. 2024; Hardy et al. 2012), which found that environmental filtering was the dominant force influencing the assembly of tropical forest communities. To our knowledge, there are no similar studies in tropical savanna systems. Many lineages are widespread across Africa, and evidence of long-distance dispersal events is found repeatedly throughout the angiosperm phylogeny (Pokorny et al. 2015). The fact that savannas along the Cameroon volcanic line shared a similar phylogenetic composition with montane savannas in East Africa shows that dispersal is not an issue, but that lineages adapted to montane conditions were selected across both regions. This could suggest that most lineages have been able to spread throughout Africa over evolutionary timescales, but that local diversification and environmental preferences shape which lineages establish in specific regions, a similar process to what was hypothesised in the Amazon (Dexter et al. 2017). However, the evoPCA analyses do show strong geographic patterns, suggesting that there is an important effect of biogeographical contingencies on community composition.

In a recent study, Qian et al. (2024) found that geographic distance and climatic distance had similar unique contributions in explaining phylogenetic beta diversity (β_{Sor}). The reason for the difference between our study and that of Qian et al. (2024) might stem from our focus on biome-specific questions rather than a general approach, which uses all taxa across all biomes in very large botanical regions as sampling units. Alternatively, the result might stem from our study focusing on woody species, which usually disperse further than herbaceous species (Thomson et al. 2011), dispersal limitation would be expected to be less important than environmental filtering (biogeographical signal according to plant life-form, Droissart et al. 2018).

Concerning which climatic factors have the most influence over beta diversity, Xu et al. (2023) found that, from a global perspective, mean annual precipitation and temperature seasonality were the best predictors of phylogenetic beta diversity (β_{Sor}) and had similar effects, while Ringelberg et al. (2023), focusing on the ecologically important mimosoid clade, found that phylogenetic turnover (β_{Sim}) was best explained by mean annual precipitation in Africa. Interestingly, Qian et al. (2024) found that the best predictors of phylogenetic beta diversity in Africa were linked to temperature and its seasonality, although it is important to note that their study also included temperate regions of Africa. In any case, their result reflects what we found for forests, where the temperature range (bio7) was the variable most strongly associated with the first axis of the evoPCA, and the mean temperature of the coldest quarter (bio11) was the best predictor in the forest GDM. However, this does not completely reflect the results we found for savannas. We did find some evidence that the maximum temperature of the warmest month (bio5) was a strong driver of the first axis of the evoPCA, but the precipitation of the wettest quarter (bio16) and CWD were the best predictors in the savanna GDM, confirming the results of Davis et al. (2023) which highlighted precipitation as the main driver of phylogenetic beta diversity for savannas. This reflects that continental/global studies are at risk of confounding drivers of diversity based on which biomes are being studied, with biomes that have more alpha or gamma diversity potentially dominating the signal. It is also likely that different drivers might be affecting specific regions in different ways. For example, Taplin and Lovett (2003) found that West African plant species richness was best predicted by absolute maximum annual temperature, whereas mean monthly potential evapotranspiration was the main predictor for East Africa. This underlines the importance of biogeographic and evolutionary legacies for understanding the lasting effects of historical contingencies on modern and future biome responses to ongoing global change (Scheiter, Wolf, et al. 2024; Yguel et al. 2016).

5 | Conclusions

Rapid ongoing change in natural ecosystems has been documented around the world and will continue to increase pressure on African biomes. In this study, we show that (1) savannas hold more relative phylogenetic beta diversity than forests, but less absolute phylogenetic beta diversity, (2) forests and savannas show strong geographic patterns of phylogenetic composition, (3) phylogenetic composition is mainly shaped by environmental filtering and (4) individual environmental predictors have different effects in each biome. Individual conservation areas are important to cover the breadth of phylogenetic composition in both forest and savanna biomes.

Further work on the functional differences between forests and savannas is warranted. We suggest that studies at the community scale, using permanent sample plots and mechanistic models will bring further insight into the processes shaping the lineage composition of African biomes.

Author Contributions

M.R.: conceptualisation, methodology, formal analysis, investigation, data curation, writing – original draft, visualisation. A.F., A.P.G.: writing – review and editing. J.L.G., D.J.H.: writing – review and editing, supervision. K.G.D.: conceptualisation, writing – review and editing, supervision. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No new data were generated in this study. Occurrence data were compiled from RAINBIO (Dauby et al. 2016) and FLOTROP (Taugourdeau et al. 2019). Fire data were gathered from MODIS MCD64A1 Burnt Area product (Giglio et al. 2018), available on Google Earth Engine. Cumulative Water Deficit came from Chave et al. (2014). Potential evapotranspiration was gathered from CHELSA 2.1 (Karger et al. 2017). Past herbivore biomass was obtained on request from Gareth Hempson (Hempson et al. 2015). The digital elevation model was downloaded from the Shuttle Radar Topography Mission (SRTM), available on Google Earth Engine.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.