

Climate variability in the last 12,500 years has shaped vegetation dynamics differently across West African savannas and forests

Sanusi Camara

s.camara@utg.edu.gm

University of The Gambia, Department of Geography, Division of Humanities and Social Sciences, Faraba campus, The Gambia <https://orcid.org/0009-0006-7722-6827>

Hamada E. Ali

Department of Biology, Sultan Qaboos University, Muscat, Oman

Josep Peñuelas

Global Ecology Unit CREAM-CSIC-UAB, Center for Ecological Research and Forestry Applications (CREAF), National Research Council (CSIC), Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain

Moisés Méndez-Toribio

Instituto de Ecología, A.C., Red de Diversidad Biológica del Occidente Mexicano, Pátzcuaro, Michoacán, México

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Climate variability in the last 12,500 years has shaped vegetation dynamics differently across West African savannas and forests

ABSTRACT

This study examines how climate variability from the Younger Dryas to the present shapes vegetation dynamics across West African savannas and forests using pollen-based compositional and functional analyses. Fossil pollen assemblages were grouped into major ecological domains and harmonised with TRY trait records, retaining defensible matches for key numeric traits, such as specific leaf area, leaf area, wood density, and seed mass. Functional dispersion (FDis), the squared chord distance (SCD), and principal coordinate analysis (PCoA) were used to evaluate regional differences and long-term ecological change. Within the savanna domain, Sahelian and Sudanian assemblages were compositionally distinct but only modestly functionally differentiated, indicating broad overlap in the occupied trait space. Temporal structuring also differed between the two regions: in the Sahel, FDis increased significantly toward the present, whereas no equivalent monotonic trend was detected in Sudan. At the broader biome scale, compared with savanna assemblages, forest assemblages showed substantially greater FDis and compositional turnover. Complementary PCA and NMDS of the harmonised pollen matrix revealed the same broad forest–Savanna split, whereas PERMANOVA confirmed significant biome-scale compositional differentiation ($R^2 = 0.1309$, $p = 0.001$) and highlighted additional regional structuring across the dataset. Trait trajectories further suggested more conservative strategies in savanna communities, with higher wood density and lower specific leaf area, whereas forest assemblages were more variable and structurally complex. The independent proxy variables showed limited direct explanatory power for FDis, with age, South Atlantic SST, $\delta^{13}\text{C}$, and $\delta^{18}\text{O}$ emerging as the dominant predictors for Sahel. Overall, the results demonstrate that Holocene vegetation change in West Africa was biome-specific, regionally uneven, and characterised by stronger compositional differentiation than functional differentiation within the savanna domain.

Keywords: Holocene; West Africa; Vegetation dynamics; Climate variability; Fossil pollen; Plant functional traits; Functional diversity; Proxy analysis

1 INTRODUCTION

West Africa is among the world's major centres of biodiversity, but it has also experienced substantial environmental changes over long timescales (Lézine & Cazet, 2005; Nicholson, 2001; Shanahan et al., 2015). During the late Quaternary and Holocene, vegetation dynamics in the region were shaped by major climatic and hydrological transitions (Grouard & Lézine, 2023), including the rise of sea level to near-modern levels (130 m) by c. 7 ka BP (Fleming et al., 1998) and the persistence of humid conditions during the African Humid Period (AHP) between c. 15.5 and 5.5 ka BP (Hély et al., 2009, 2014; Watrin et al., 2009a). The termination of the AHP contributed to marked landscape alteration, including the contraction and redistribution of woodland and forest formations (Salzmann et al., 2002). Although humid conditions during this interval were not continuous and several studies have reported a dry phase between 11 and 10.2 ka BP associated with the Younger Dryas (Barker et al., 2004; Bonnefille et al., 1992; Gasse et al., 1990; Maley & Brenac, 1998; Salzmann & Hoelzmann, 2005), savanna vegetation communities persisted through these fluctuations (Salzmann, 2000). These long-term changes were expressed through boundary migration (Watrin et al., 2009a),

hydrological buffering (Hély et al., 2014), shifts in community composition (Watrin et al., 2009b), and broader ecological reorganisation (Adeleye et al., 2021, 2022).

Most reconstructions of long-term vegetation change in West Africa have relied on taxonomic or biome-level interpretations of fossil pollen assemblages. These approaches remain valuable, but they provide limited insight into how ecological strategies changed over time. Plant functional traits offer a complementary framework because they capture key dimensions of species' responses to environmental change, including variations in resource use, stress tolerance, dispersal, and competitive ability (Funk et al., 2017). Traits such as plant height, seed mass, leaf area, and specific leaf area are linked to major axes of plant ecological strategy and broader patterns of plant form and climatic adaptation (Díaz et al., 2016; Westoby, 1998; Wright et al., 2004). This approach may be especially relevant in West Africa, where trait–climate relationships may not conform closely to conventional global expectations. The persistent atmospheric humidity of the rainforest zone and the ecological influence of north-easterly trade winds in the savanna may partly modify expected latitudinal trait patterns (Brussel & Brewer, 2021), suggesting that, for Tropical Africa, regional trait–climate relationships require contextual evaluation rather than assumption.

Despite the potential for pollen–trait integration, trait-based analyses of fossil pollen records remain rare or absent in West Africa. Existing studies elsewhere, including North America (Brussel & Brewer, 2021; Lacourse & Adeleye, 2022) and southeast Australia (Adeleye et al., 2023), have shown the value of linking pollen assemblages with plant trait data to reconstruct ecological function through time, but comparable applications in West Africa are still lacking. Accordingly, this study examines how vegetation composition and functional trait structure responded to climatic variability in West Africa from the Younger Dryas to the present. Fossil pollen datasets were grouped into major ecological domains and harmonised with TRY-based records (Kattge et al., 2020) through a transparent taxonomic crosswalk to obtain matched numerical trait information following established procedures (Adeleye et al., 2023). Specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$), leaf area (LA, mm^2), wood density (g cm^{-3}), and seed mass (SM, mg) were retained because they were both ecologically informative and relatively well represented across the matched taxa. Using a multiproxy framework, the analysis then evaluated long-term ecological change, contrasted functional and compositional patterns within and between major biomes, and assessed whether observed functional shifts were associated with broader climatic and environmental processes.

2 MATERIALS AND METHODS

2.1 STUDY DESIGN AND ANALYTICAL FRAMEWORK

This study was designed to test whether Holocene vegetation change in West Africa was expressed more strongly in functional trait structure or in taxonomic composition and whether those signals varied within and between major biomes. The analysis therefore proceeded at two linked scales. First, savanna pollen assemblages were divided into Sahelian and Sudanian groups to test for regional differences within the open-vegetation domain. Second, those savanna assemblages were compared with those of a broader forest group to assess biome-scale contrasts. Across both analytical levels, the workflow combined taxonomic harmonisation, trait matching, functional diversity estimation, compositional dissimilarity analysis, ordination, and age-based statistical testing.

2.2 DATA SELECTION, PREPARATION AND REGIONAL GROUPING

Sixteen pollen datasets (Fig. 1) were obtained from the Neotoma Palaeoecology Database (Neotoma Palaeoecology Database 2024: <https://www.neotomadb.org>) and selected to represent major

environmental gradients across West Africa. In addition to the pollen records, seven other palaeoenvironmental proxies were added for comparison purposes, and the individual samples (Table 1 and Fig. 1) were assigned calibrated ages from the available site chronologies and treated as the primary analytical units. Before analysis, the taxon names were standardised to a consistent nomenclature to reduce duplication caused by spelling variants, synonymy, and mixed taxonomic ranks. Pollen types that clearly represented the same botanical entity were merged, whereas unresolved morphotypes were retained as distinct categories when further taxonomic precision could not be justified.

The samples were then assigned to regional ecological groups on the basis of the modern environmental context of each site and the broader biogeographic framework used throughout the paper. For the savanna-focused analysis, the sites were classified as Sahelian or Sudanian. For broader comparison, samples were grouped into forest and savanna domains, while the savanna category retained its internal Sahelian and Sudanian structure for ordination and interpretation. This grouping strategy allowed the same pollen database to be examined at both the subbiome and the biome scales.

Table 1: Summary of the palaeoenvironmental records used in this analysis.

Dataset ID	Site Name	Dataset Type	Max Age	Min Age	Max. Age Resolution	Min. Age Resolution	Latitude	Longitude	Elevation (m)	Reference
Neotoma59848	Lake Sélé	Pollen	8367.272	-137.146	1295.355	31.875	7.15	2.433333	8	Salzmann, U. (2024)
Neotoma59867	Lake Nokoué	Pollen	8175.657	2330.709	403.544	43.15	6.495	2.388056	47	Tossou, M. G. (2024)
Neotoma53325	Goho	Pollen	7560.034	887.4304	568.955	7.584	6.443056	2.579167	9	Tossou, M. G. (2022)
Neotoma57566	Yéviédé	Pollen	7926.011	1326.842	693.024	35.256	6.535	2.378333	4	Tossou, M. G. (2023)
Neotoma52752	E. Niger Delta	Pollen	35000	0	1444.688	17.1	4.55	6.433333	13	Sowunmi, M. A. (2022)
Neotoma59846	KW31	Pollen	6697	5040	4832.59	20.12	3.516944	5.566944		Cazet, J. P. (2024).
Neotoma54284	Lake Chad	Pollen	6371.441	5593.234	117	44	14.5975	13.0083	326	Amaral, P. (2022)
Neotoma46702	Mare d'Oursi	Pollen	4559	0	222	42	14.65787	-0.47614	259	Ballouche, A. (2021)
Neotoma54266	Bemba Ya	Pollen	2722	205	445	102	16.52513	2.18726	297	Tovar, C. (2022)
Neotoma49261	Lake Tilla	Pollen	13063.98	247.8519	747.08	36.979	10.39556	12.12972	534	Salzmann, U. (2021)
Neotoma49447	Bal Lake	Pollen	10205.17	0	838.099	13.3226	13.30694	10.94944	320	Waller, M. P. (2021)
Neotoma52672	Kuluwu Oasis	Pollen	9682	789	405.678	90.151	13.21722	11.55083	317	Salzmann, U. (2022).
Neotoma54329	Jikarya	Pollen	6890	150.2034	271	8	13.313667	11.077	315	Waller, M. P. (2022)
Neotoma48235	Lake Guiers	Pollen	11587.103	3472	559	221	16.235675	-15.86294	14	Lézine, A.-M. (2019)
Neotoma52387	Lompoul	Pollen	7833.028	355	700.239	82.38	15.35	-16.716667	24	Lézine, A.-M. (2022a).
Neotoma52420	Potou	Pollen	11500	362	660	106	15.75	-16.5	7	Lézine, A.-M. (2022b)
Not Specified	Mboro peat bog	Charcoal	9412	0.004	309	75	15.08	-16.53	17	Ndiaye et al. (2022)

Global Palaeofire225	Lake Tilla	Charcoal	13128.97	420	333.8	33.01	10.5445 983	12.13137329	4.5	Salzmann et al. (2002)
PANGAEA73719 0	NE Atlantic Ocean	Alkenones- based SST	10406	0.071	0.37	0.07	20.7492	-18.5808	-2273	Leduc et al. (2010)
PANGAEA73699 5	Gulf of Guinea	Mg/Ca ratios	10498	0.362	0.134	0.131	2.502	9.395	-1295	Leduc et al. (2010)
PANGAEA72677 5	GeoB9508-5	Grain size	5712	0.53	0.75	0.04	15.4983 33	-17.948	-2384	Mulitza & Stuut (2009)
PANGAEA72677 6	GeoB9508-5	Carbon-13 Isotope	5721	0.76	0.75	0.04	15.4983 33	-17.948	-2384	Mulitza (2009)
PANGAEA72677 6	GeoB9508-5	Oxygen-18 Isotope	5721	0.76	0.75	0.04	15.4983 33	-17.948	-2384	Mulitza (2009)

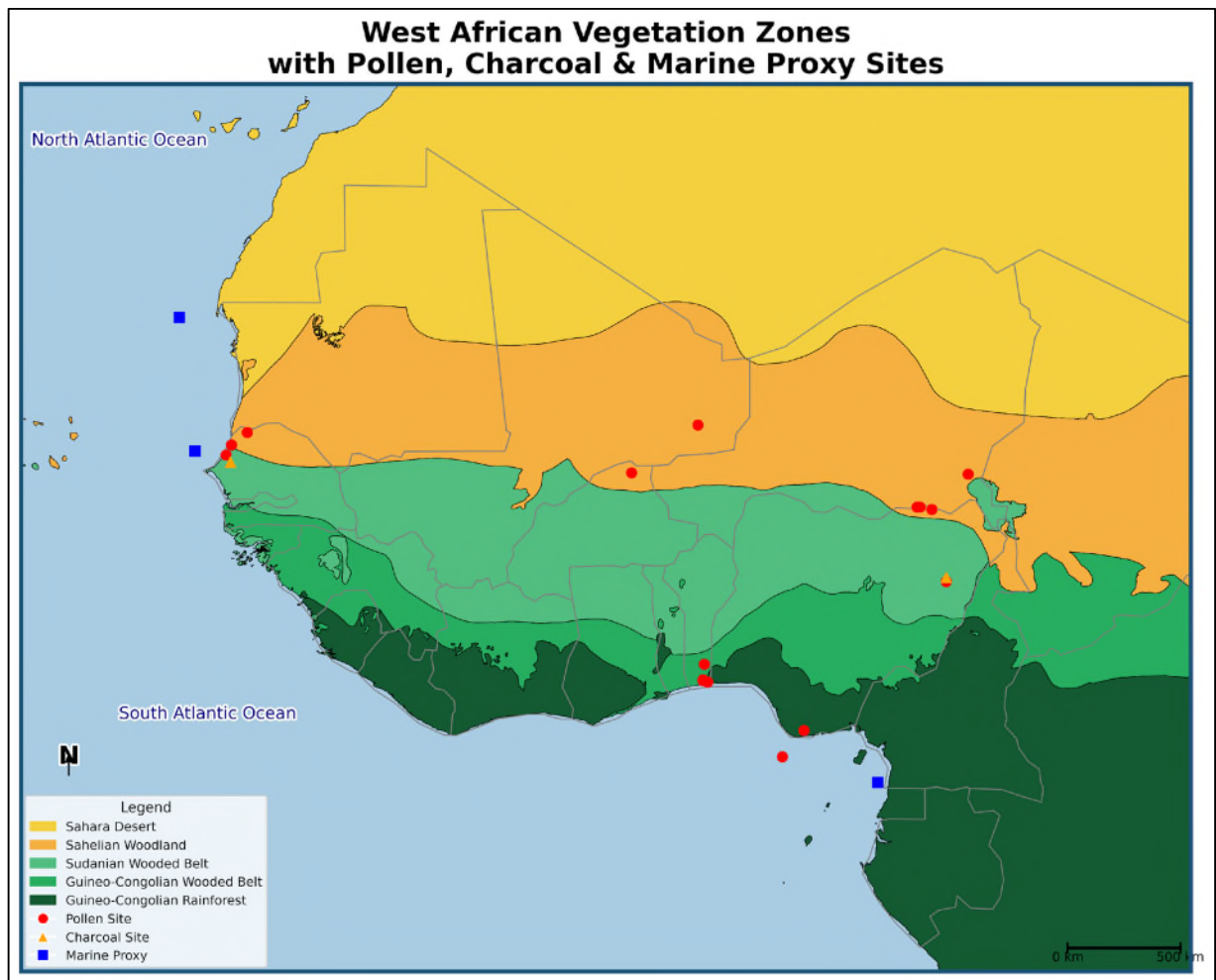


Figure 1. Map of West Africa showing major vegetation zones and the locations of palaeoenvironmental records used in this study. Shaded belts represent the principal biogeographic zones, from north to south: Saharan Desert, Sahelian Woodland, Sudanian Wooded Belt, Guineo-Congolian Wooded Belt, and Guineo-Congolian Rainforest. Symbols indicate site types, including pollen records, charcoal sites, and marine proxy records. The spatial distribution of terrestrial and marine archives used to assess Holocene vegetation dynamics and regional environmental change across West Africa.

For compositional analyses, pollen counts were converted to relative abundances within each sample so that differences among samples reflected assemblage structure rather than raw count totals. Unmatched or taxonomically ambiguous taxa were retained in the compositional dataset where they contributed legitimate pollen information because the purpose of the compositional analysis was to capture the floristic structure of the assemblages as recorded.

To support the complementary biome-scale ordination, forest and savanna composition tables were also merged into a single harmonised master dataset with rows defined at the sample level. Metadata fields were standardised across source tables, structurally absent taxa were coded as zero where justified by the merged matrix structure, and each sample row was renormalised to 100% after taxonomic harmonisation. Taxon labels were retained in both an exact-cleaned form and a more conservative working form that collapsed obvious duplicates, type variants, and mixed taxonomic ranks to a common analytical level suitable for cross-site comparison. These relative abundances

were interpreted as palynological abundance signals rather than direct estimates of plant biomass or vegetation cover because pollen production, dispersal, and preservation differ among taxa. High-pollen producers, such as Poaceae, may therefore be overrepresented relative to some insect-pollinated woody taxa. For this reason, the functional analyses were interpreted as changes in pollen-inferred functional structure, not as absolute reconstructions of biomass. Abundance-weighted FDis was used to evaluate shifts in the functional composition represented within the pollen assemblages, while complementary compositional analyses, including squared chord distance and ordination, were used to assess whether functional patterns were supported by broader assemblage structure.

2.3 TRAIT COMPILATION AND TAXONOMIC HARMONISATION

The functional analyses were based on a TRY-derived plant trait dataset (Kattge et al., 2020), and African taxa were extracted using the West African Functional-Ecological Framework (WAFEC; Supplementary Table S5) (Camara, 2025). Because the identification of fossil pollen varied in terms of taxonomic resolution, a taxonomic crosswalk was performed to link the pollen taxa to the trait database as transparently as possible. Matching prioritised exact species-level correspondence where available. Where pollen identifications were secure only to the genus level or where species-level matching would have implied unjustified precision, genus-level matches were used instead. Pollen categories that could not be matched with sufficient confidence were excluded from the trait-based calculations but retained in the compositional analyses.

Trait records, which initially consisted of more than 15 million rows (29 columns), were cleaned before analysis to remove obvious duplicates, harmonise naming conventions, and collapse repeated entries into a single representative value for each taxon used in the crosswalk. Trait aggregation was conducted at the same taxonomic level as the pollen–trait match. This was to ensure that a pollen taxon linked at the genus level received a genus-level trait summary rather than an artificial species-level estimate. All taxonomic harmonisation, dataset cleaning, and data visualisation were performed in RStudio using various packages (Posit team, 2025; R Core Team, 2026; Wickham et al., 2019; Wickham, 2016), except for the map (Fig. 1), which was developed in Python using Google Colab.

2.4 CONSTRUCTION OF THE FUNCTIONAL TRAIT MATRIX

The cleaned trait table was reshaped from a long to wide format and screened to retain numeric traits with sufficient taxonomic coverage for palaeoecological use. After inspection of missingness and redundancy, the final regional trait matrix emphasised the leaf area (LA, mm²; both leaf and leaflet), specific leaf area (SLA, mm² mg⁻¹), stem specific density or wood density (g cm⁻³), and seed dry mass (SM, mg). For broader forest–savanna comparisons, the same core traits were retained, and additional community-weighted mean summaries were generated for the variables for which coverage was permitted.

The remaining missing values for the retained numeric traits were imputed conservatively using the traitwise central tendency values. This allows the final matrix to remain analytically tractable without inflating trait variance. To assess whether the reported FDis patterns were sensitive to the imputation procedure, we conducted a subset-based sensitivity analysis to compare FDis values derived from central-tendency-imputed TRY traits with values calculated using observed-only trait information and pairwise Gower distances. The two approaches produced strongly correlated FDis trajectories (Pearson $r = 0.899$, $p < 0.001$; Spearman $\rho = 0.971$, $p < 0.001$; $n = 128$ comparable samples). These findings suggest that the imputation procedure did not dominate the broad temporal functional signal while allowing taxonomically richer samples to be retained despite isolated missing trait values. The pollen abundance table was then filtered to include only taxa represented in the matched trait matrix.

This produced a reduced abundance matrix suitable for functional diversity analysis while preserving the original assemblage structure as far as the available trait coverage allowed.

2.5 FUNCTIONAL DIVERSITY ESTIMATION

Functional dispersion (FDis) was calculated as the abundance-weighted dispersion of taxa in multidimensional trait space (Laliberté & Legendre, 2010). Because the retained traits differed in units and numerical ranges, pairwise trait dissimilarities among taxa were calculated using the Gower distance prior to FDis estimation. The resulting Gower dissimilarity matrix was supplied to dbFD() in the FD package to calculate FDis for each pollen assemblage. This approach reduces the risk that traits with larger numerical ranges disproportionately influence the resulting functional diversity estimates, following Pavoine et al. (2009).

In addition to FDis, community-weighted means (CWMs) were used to summarise directional changes in selected traits through time. CWM trajectories were examined for major plant axes, such as wood density, SLA, seed mass, and leaf area variables, where coverage was adequate. These summaries were treated not as substitutes for FDis but as complementary descriptors of the ecological strategies dominating forest and savanna assemblages at different times.

Samples that yielded zero FDis because they contained only one functionally singular matched entity were retained for descriptive assessment of the dataset but excluded from inferential contrasts where appropriate because such values can arise from limited trait matching rather than from the ecologically meaningful absence of functional variation.

2.6 COMPOSITIONAL DISSIMILARITY AND ORDINATION

Taxonomic compositional structure was analysed independently of the trait-matched subset so that the full floristic signal of the pollen records could be evaluated. Pairwise dissimilarity among samples was calculated using the squared chord distance. This metric method is well suited to palaeoecological percentage data because it performs well with respect to relative abundance and is less dominated by highly abundant taxa than some alternative measures are. Within the savanna analysis, the squared chord distance was used to compare Sahel–Sahel, Sudan–Sudan, and Sahel–Sudan sample relationships. For broader biome comparisons, adjacent-sample or within-series dissimilarity summaries were used to compare forest and savanna turnover.

Principal coordinate analysis (PCoA) based on the squared chord distance was used to evaluate the latitudinal pollen gradients. The ordination plots were inspected to assess the degree of overlap or separation among the forest, Sahelian, and Sudanian assemblages and to determine whether the regional structure reflected broad ecological grouping, site-level clustering, or both.

A complementary ordination workflow was applied to the harmonised sample-level forest–Savanna composition matrix to test for biome separation using alternative distance structures. After the ultrare taxa were filtered, the rows were restandardised and subjected to Hellinger transformation for principal component analysis (PCA), while the Bray–Curtis dissimilarities, which were determined on the basis of square-root-transformed relative abundances, were used for nonmetric multidimensional scaling (NMDS). PCA was used to summarise the dominant linear gradients in the harmonised matrix, whereas NMDS provided a nonlinear check of the broad biome-scale structure. Because the two-dimensional NMDS solution showed only a moderate fit, it was interpreted conservatively as evidence of broad compositional separation rather than fine-scale intersample geometry. These analyses were complemented by PERMANOVA on Bray–Curtis dissimilarities, as well as Kruskal–Wallis tests and correlation analyses where appropriate.

Rate of Change (ROC) Analysis

To evaluate the temporal dynamics of vegetation shifts, the rate of compositional change (ROC) was calculated for the pollen assemblages using the *RRatepol* package (Mottl et al., 2021). To ensure that the calculated ROC was not biased by uneven temporal sampling density, we employed a standardised binning approach (e.g., 500-year windows) and applied a 'standardisation of pollen sums' across all the samples. This ensures that the detected peaks in compositional turnover represent genuine biological accelerations rather than artifacts of stratigraphic resolution or varying pollen counts. The resulting ROC datasets were subsequently tested for correlations against independent environmental proxy variables (including sea surface temperatures, stable isotopes, charcoal, and dust) to identify potential drivers of accelerated ecological change across the forest and savanna domains. False discovery rate (FDR) corrections were applied to the resulting p values to account for multiple testing.

3 RESULTS

3.1 FUNCTIONAL DIFFERENTIATION WITHIN THE SAVANNA DOMAIN

Functional dispersion (FDis) revealed a modest but statistically significant difference between the Sahelian and Sudanian assemblages (Wilcoxon rank-sum test: $W = 18,441.5$, $p = 0.0073$). The mean FDis (Figure 2A) was slightly greater in Sahel (0.031) than in Sudan (0.026), although the absolute difference remained small. Both regions showed strongly right-skewed distributions with many low-dispersion samples, indicating that a narrow functional trait space characterised much of the savanna dataset. Region-specific temporal analyses (Figure 3B), however, revealed clearer contrasts.

In the Sahel, FDis declined significantly with age (Spearman's $\rho = -0.407$, $n = 158$, $p = 1.15 \times 10^{-7}$), indicating lower values in older samples and a general increase toward the present. In contrast, no significant monotonic relationship was detected in the Sudan ($\rho = 0.060$, $n = 201$, $p = 0.394$). These results suggest that functional dispersion differed not only by region but also in its temporal structure (Figure 2), with a clearer long-term temporal signal in the Sahel than in the Sudan.

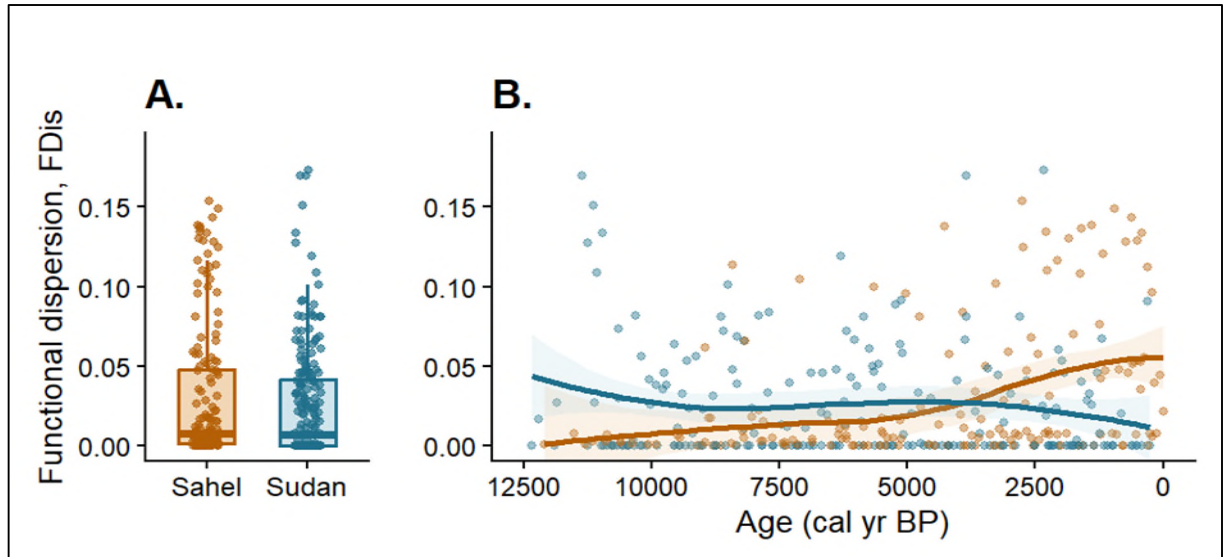


Figure 2. Functional dispersion across Sahelian and Sudanian savanna assemblages during the last 12,500 years. (A) Distribution of FDis values by savanna region, showing generally low dispersion in both Sahelian and Sudanian assemblages. (B) Temporal variation in FDis from 12,500 cal yr BP to the present. Points represent individual pollen assemblages, while fitted curves show loess-smoothed trends with confidence intervals. FDis was calculated from Gower trait dissimilarities among matched taxa and reflects abundance-weighted dispersion in multidimensional trait space.

Holocene phase comparisons supported this interpretation. When all savanna samples were pooled (Fig. 3), the mean FDis increased from the AHP (0.0241) to the late Holocene (0.0356), and these differences were statistically significant overall (Kruskal–Wallis $\chi^2 = 6.72$, $df = 2$, $p = 0.035$). At the regional level, however, phase-related variation was significant in the Sahel ($\chi^2 = 20.21$, $df = 2$, $p = 4.08 \times 10^{-5}$) but not in the Sudan ($\chi^2 = 0.72$, $df = 2$, $p = 0.697$), indicating that the temporal restructuring of functional dispersion was more strongly expressed in the Sahelian assemblages.

Tests of independent environmental proxies showed regionally uneven relationships with corrected FDis. In the Sahel, FDis was negatively associated with South Atlantic SST ($\rho = -0.280$, $pFDR = 0.0031$) and $\delta^{18}O$ ($\rho = -0.236$, $pFDR = 0.0149$), whereas North Atlantic SST, charcoal, dust, and $\delta^{13}C$ were not significant. In the Sudan, none of the tested predictors, including age, showed a significant relationship with FDis. These results suggest that the temporal and environmental structure of savanna functional dispersion was concentrated mainly in the Sahel, while Sudanian assemblages showed weaker and less directionally organised functional change.

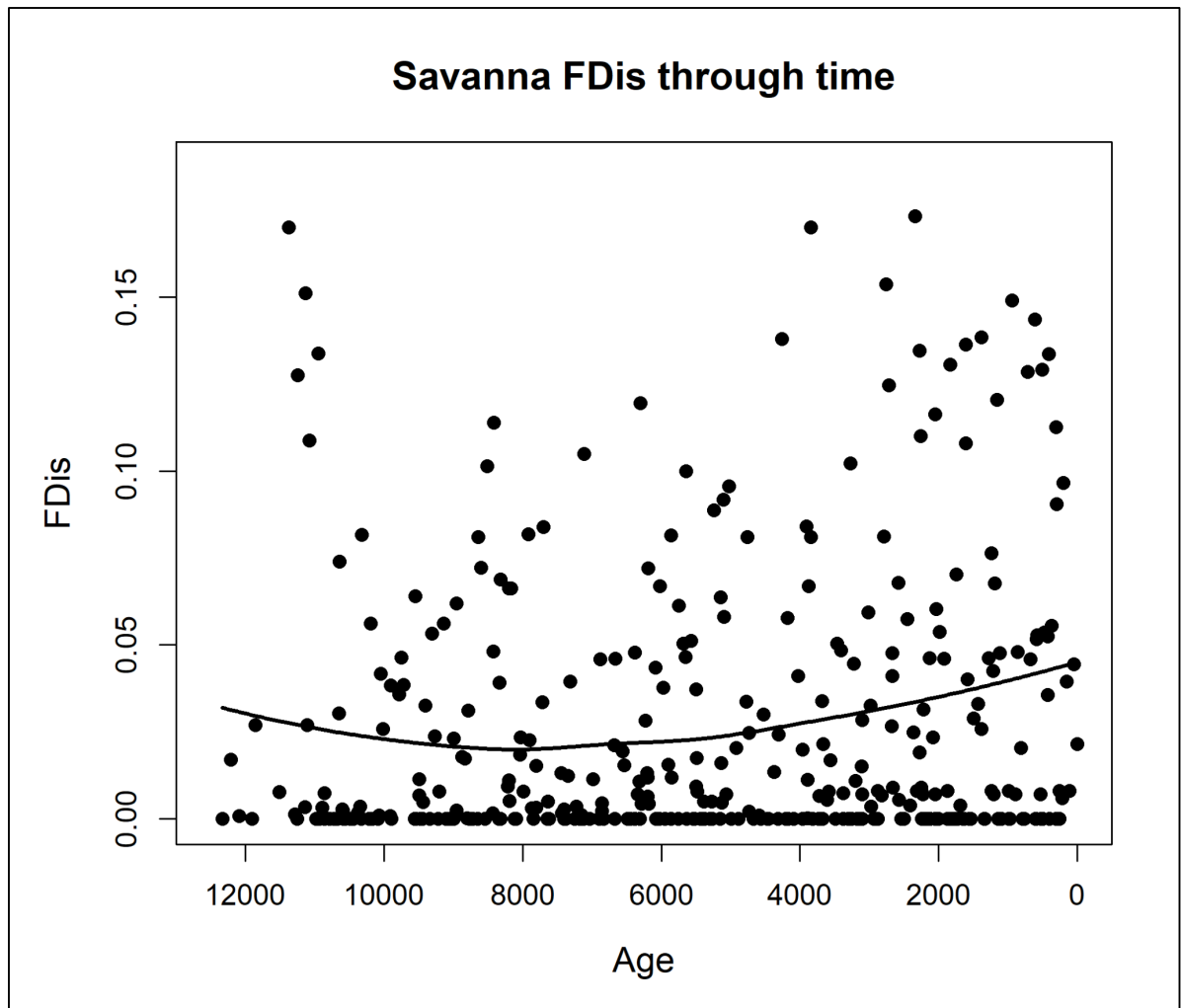


Figure 3. Temporal pattern of functional dispersion (FDis) in West African savanna records. Points represent individual FDis values plotted against age, while the fitted trend line shows the overall temporal trajectory. The distribution indicates high variability throughout the record, with only a weak long-term temporal trend despite intermittent peaks.

3.2 COMPOSITIONAL DIFFERENTIATION WITHIN THE SAVANNA DOMAIN

Compositional analyses produced a much stronger regional signal than functional metrics did. Squared chord distance was greatest for comparisons between Sahelian and Sudanian samples (mean = 1.958), lower for Sahel–Sahel comparisons (mean = 1.664), and lowest for Sudan–Sudan comparisons (mean = 1.414) (Fig. 4). These differences were highly significant (Kruskal–Wallis $\chi^2 = 10881$, $df = 2$, $p < 2.2 \times 10^{-16}$), and all pairwise comparisons remained significant after multiple-testing correction. Sudanian assemblages were therefore more internally cohesive, whereas Sahelian assemblages showed greater internal heterogeneity.

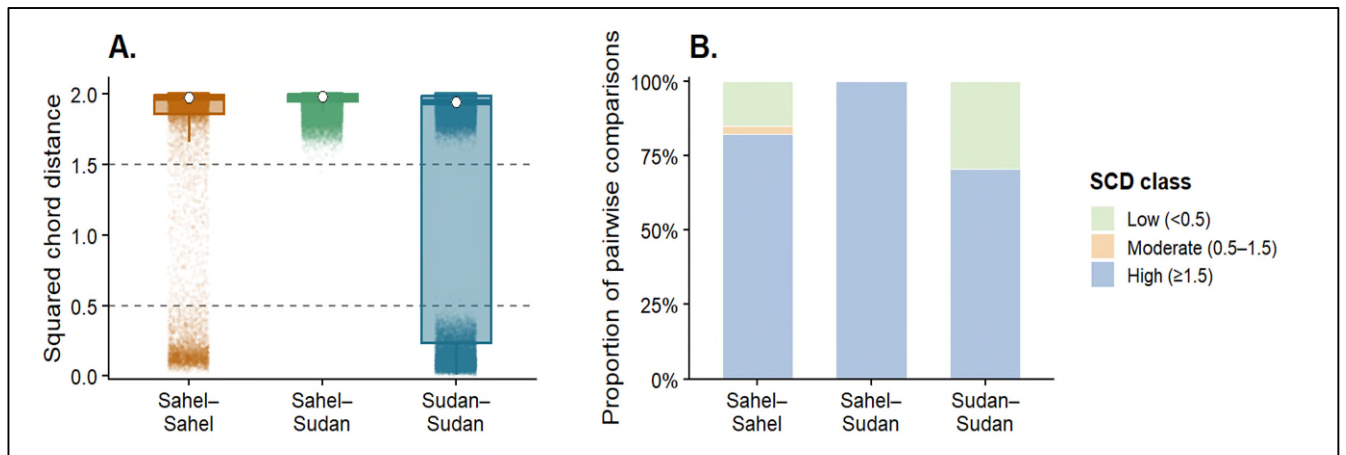


Figure 4. *Pairwise squared chord distance among Sahelian and Sudanian savanna assemblages.* (A) *Distribution of squared chord distance values for within- and between-region comparisons.* (B) *Proportion of comparisons in low, moderate, and high dissimilarity classes. Sahel–Sudan pairs are dominated by high dissimilarity, indicating strong compositional separation.*

Principal coordinate analysis (PCoA) based on the squared chord distance confirmed this separation. The first two axes explained 23.9% and 16.1% of the positive variation, respectively, accounting for approximately 40% of the ordination structure (Fig. 5). The samples formed regionally distinct groupings with limited overlap. Sahelian samples clustered more compactly, whereas Sudanian samples occupied a broader and more continuous ordination space. When site identity was incorporated, much of the within-region structure reflected site-level clustering, indicating that the local ecological context contributed substantially to assemblage composition.

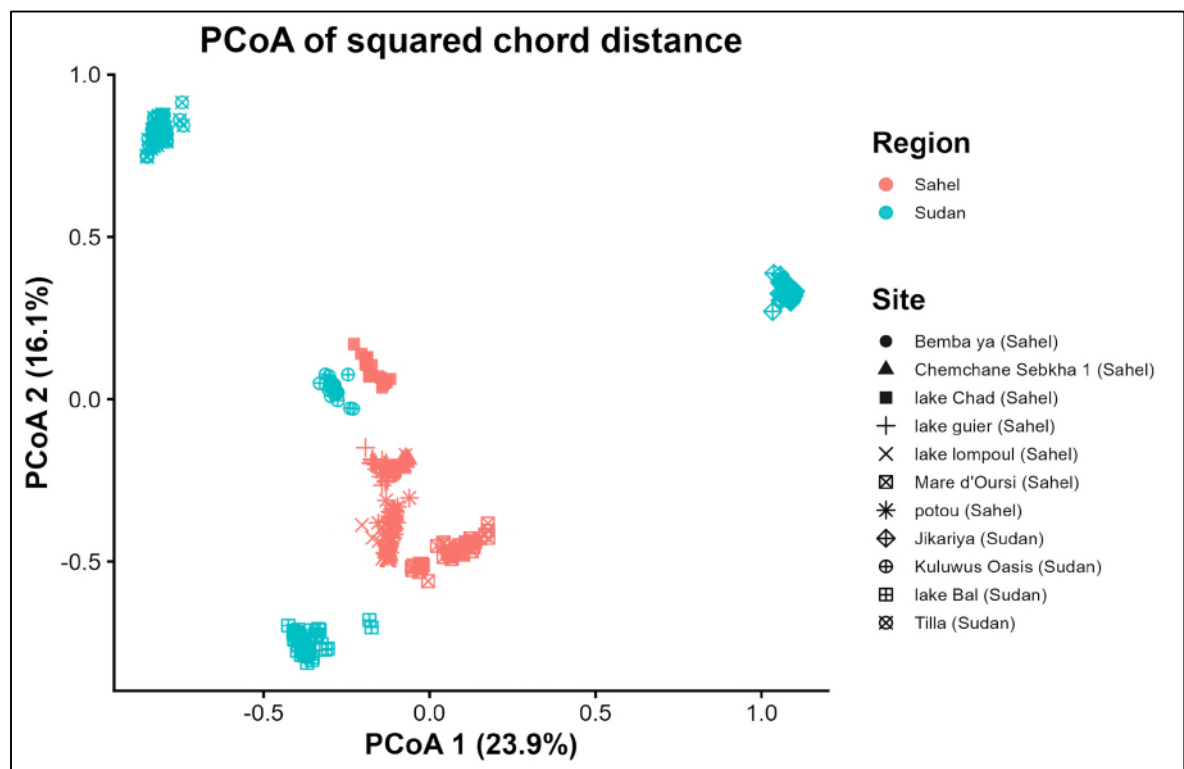


Figure 5. *Principal coordinate analysis (PCoA) of the squared chord distance among the pollen assemblages from the Sahel and Sudan regions. The samples are ordinated along the first two axes, with PCoA 1 explaining 23.9% of the variance and PCoA 2 explaining 16.1%. Regions are*

distinguished by color, and individual sites are identified by symbols. The plot clearly shows clustering by region and site, indicating strong differences in assemblage composition between the Sahel and the Sudan alongside marked within-region site-level structure.

Taken together, the savanna results show that functional differentiation between the Sahel and the Sudan was present but modest, whereas compositional differentiation was strong and consistent. The functional dispersion in the Sahel also showed clearer temporal structuring than that in the Sudan, while the strongest compositional signal arose from between-region dissimilarity and site-level clustering in ordination space.

3.3 FUNCTIONAL AND COMPOSITIONAL CONTRASTS BETWEEN FOREST AND SAVANNA ASSEMBLAGES

The broader forest–savanna comparison yielded a much stronger functional contrast (Fig. 6). Corrected FDis differed significantly between the forest and savanna assemblages (Wilcoxon rank-sum test: $W = 33,204$; $p = 1.71 \times 10^{-10}$), with the FDis values of the forest samples being substantially greater (median 0.06) than those of the savanna samples (median 0.03). The effect size was moderate (rank-biserial correlation = 0.351) on the basis of 211 forest and 233 savanna samples with FDis > 0. Within the matched TRY-based dataset, this finding indicates that forest assemblages occupied a broader functional trait space than savanna assemblages did, although the revised Gower-based effect was less extreme than it was in the original calculation.

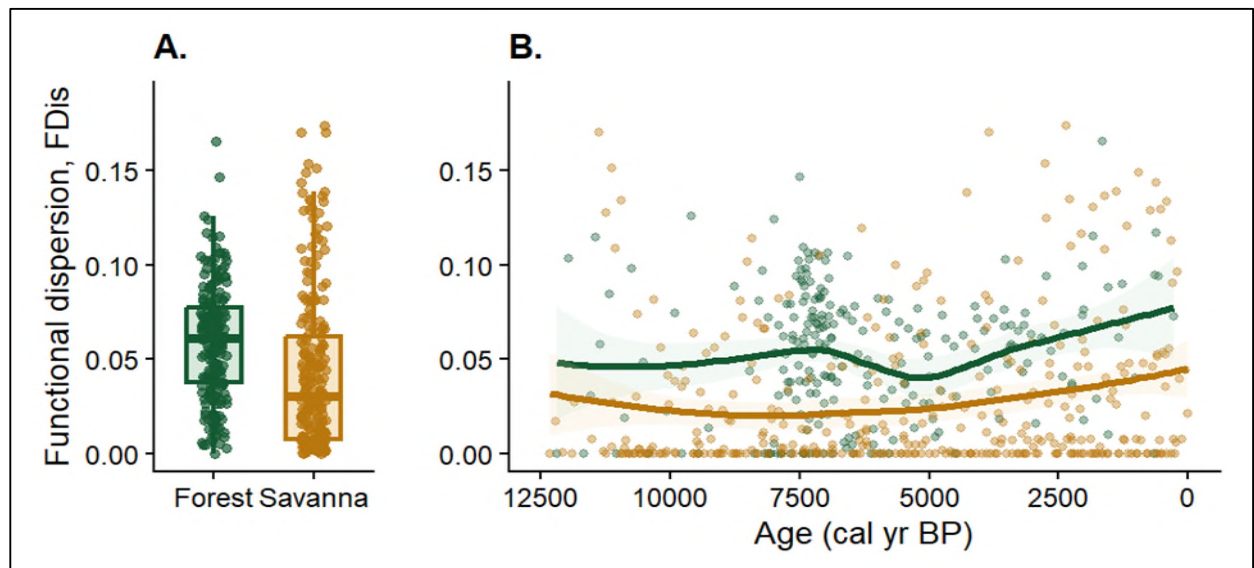


Figure 6. Functional dispersion across forest and savanna assemblages over the last 12,500 years. (A) FDis distribution by biome. (B) Temporal variation in FDis from 12,500 cal yr BP to the present. Points represent pollen assemblages, and curves show loess-smoothed trends with confidence intervals. FDis was calculated from Gower trait dissimilarities among matched taxa.

Squared chord distance (Fig. 7) also differed significantly between the forest and savanna assemblages (Wilcoxon rank-sum test: $W = 81870$, $p < 2.2 \times 10^{-16}$). Compared with the savanna samples, the forest samples presented higher mean and median SCD values (mean = 0.318, median = 0.180) (mean = 0.093, median = 0.061), with a moderate-to-strong effect size (rank-biserial correlation

= 0.467). This finding indicates higher adjacent-sample compositional turnover in forest records than in savanna records.

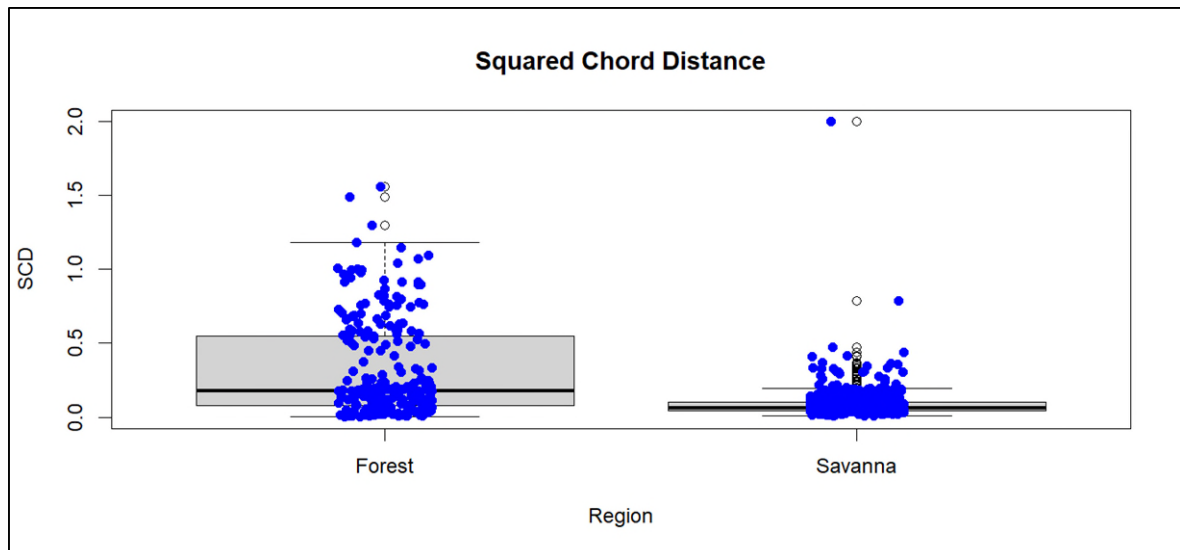


Figure 7. Comparison of squared chord distance (SCD) between forest and savanna regions. Boxplots show the distribution of SCD values for each region, with points representing individual observations. The forest samples display a higher median SCD and a broader spread, indicating greater compositional turnover and variability, whereas the savanna samples are more tightly clustered at low SCD values, with only a few extreme outliers.

A PCoA of the squared chord distance (Fig. 8) further revealed clear separation among the forest, Sahel, and Sudan assemblages. The forest samples clustered mainly in the lower portion of the ordination, the Sahel samples occupied the central band, and the Sudan samples were more dispersed across the upper and lateral portions of the plot. This pattern indicates that the three regional groupings occupied distinct pollen compositional spaces rather than forming a single continuum of overlap. Complementary ordinations based on the harmonised pollen composition matrix supported the same broad biome split. PCA separated the forest and savanna samples primarily along PC1, with Axis 1 and Axis 2 explaining 17.4% and 14.9% of the variance, respectively, and revealed that the forest samples were concentrated toward negative PC1 values and that the savanna samples were centered toward central-to-positive scores. Two-dimensional NMDS recovered the same broad forest–Savanna

structure (Fig. 9), although the relatively high stress (0.2341) indicated that the configuration was more reliable for broad compositional separation than for fine-scale distances.

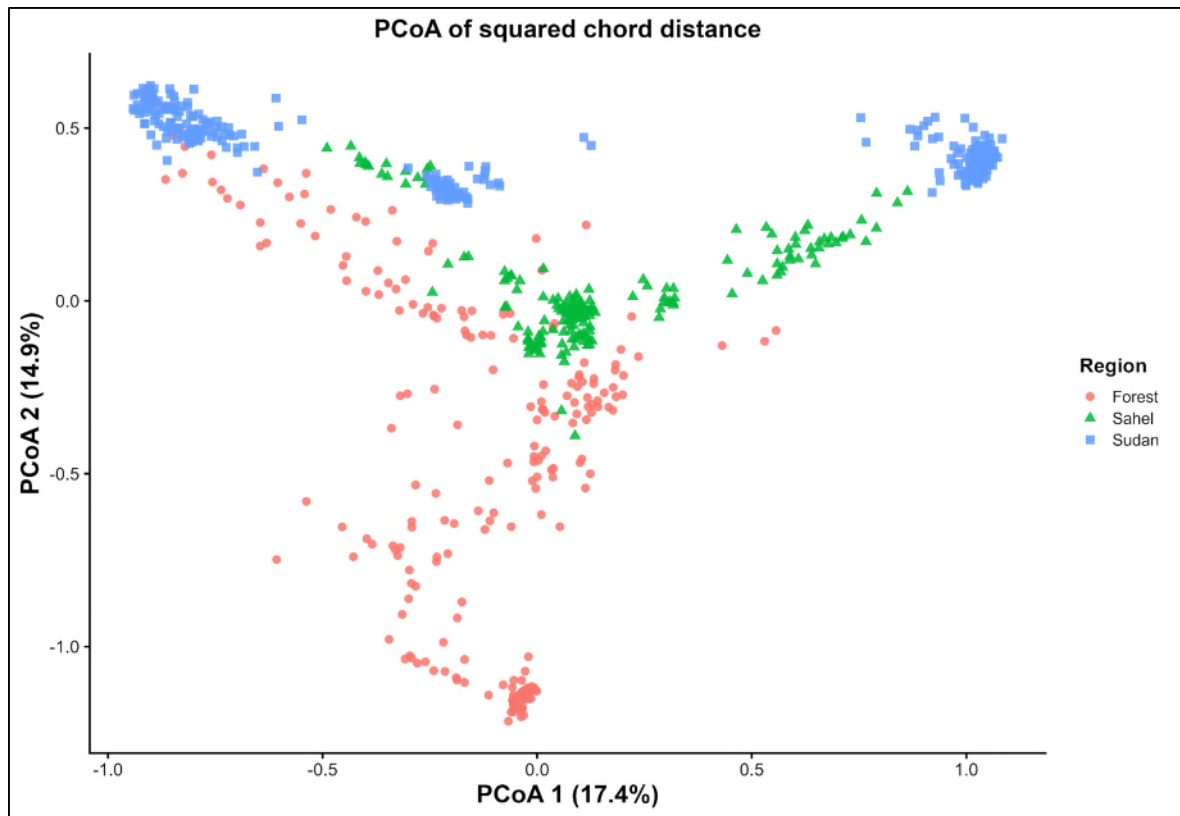


Figure 8. Principal coordinate analysis (PCoA) of squared chord distance among forest, Sahel, and Sudan pollen assemblages. The samples are ordinated along the first two axes, with PCoA 1 explaining 17.4% of the variance and PCoA 2 explaining 14.9%. The colors distinguish the three regions. The ordination reveals clear compositional separation among the forest, Sahel, and Sudan assemblages, with the Sahel occupying an intermediate position between the forest and Sudan.

PERMANOVA based on Bray–Curtis dissimilarities confirmed that the pollen assemblage composition differed significantly between the forest and savanna samples ($R^2 = 0.1309$, $F = 108.11$, $p = 0.001$). A model including biome and age explained 14.6% of the variance, whereas a model including region and age explained 22.1%, indicating substantial regional structure in addition to the broad biome effect. When permutations were constrained within sites, the biome term was not significant ($p = 1$), reflecting the fact that biome membership is largely fixed by site in this dataset and therefore cannot be meaningfully permuted within strata.

Table 2. PERMANOVA results for differences in pollen assemblage composition between biomes.

	Df	SumOfSqs	R ²	F	Pr(>F)
Model	1	38.942	0.130	108.11	<0.001
Residual	718	258.633	0.869		
Total	719	297.576	1.000		

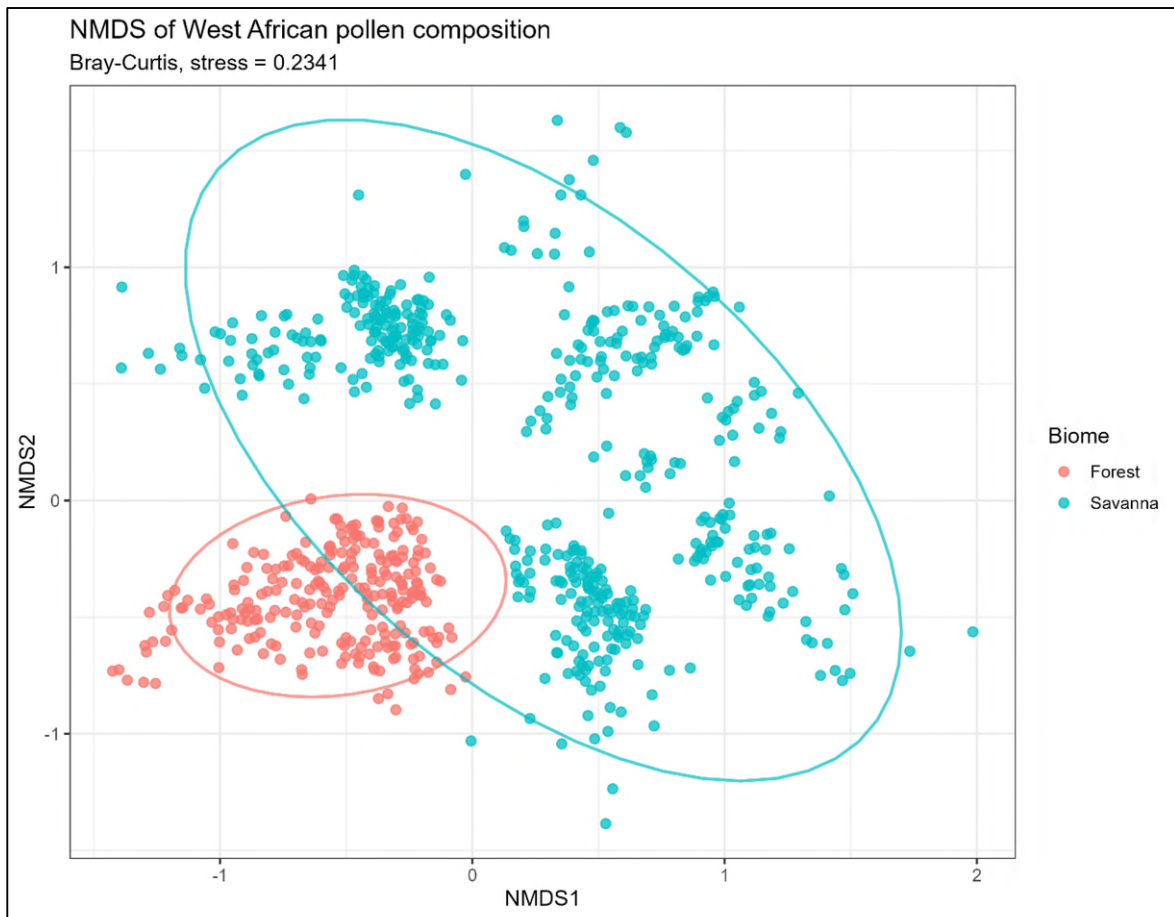


Figure 9. Nonmetric multidimensional scaling (NMDS) ordination of West African pollen composition based on Bray–Curtis dissimilarity. Points represent individual samples coloured by biome, with ellipses showing the overall spread of forest and savanna assemblages in ordination space. The ordination indicates clear compositional separation between the forest and savanna pollen communities. Note: Given the relatively high stress value (0.2341), this 2D configuration should be interpreted as evidence of broad compositional separation rather than fine-scale pairwise distances.

The community-weighted mean trait trajectories revealed persistent functional differentiation between the forest and savanna assemblages over time (Fig. 10). The savanna samples generally exhibited higher wood density and lower SLA, which is consistent with more conservative and stress-tolerant strategies. In contrast, the forest samples presented greater variability and generally greater leaf area traits, indicating more mesic and structurally complex vegetation. Seed mass was more variable in the forest, suggesting episodic contributions from larger-seeded taxa. Overall, the trait trajectories point to nonlinear Holocene reorganisation rather than simple monotonic change.

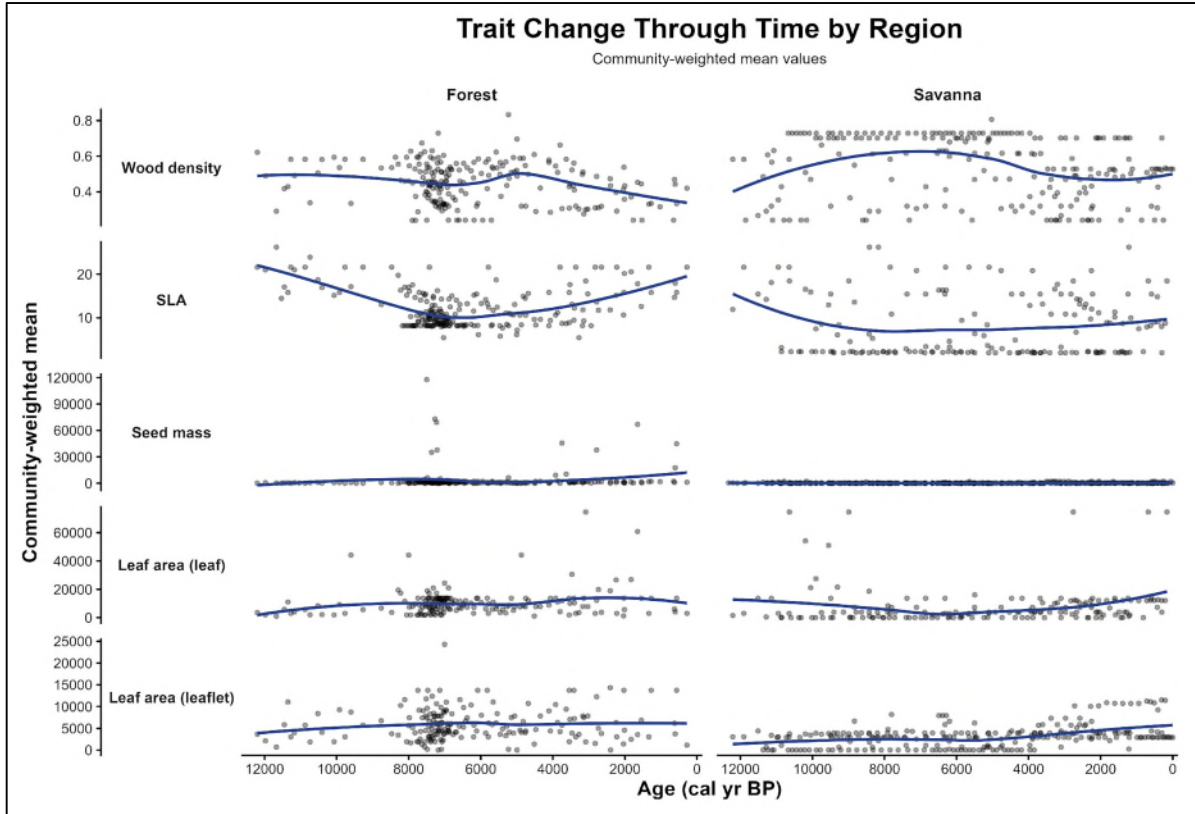


Figure 10. Temporal trends in community-weighted mean trait values across forest and savanna regions. The gray points represent individual sample values, and the blue curves show smoothed temporal trends for each trait against age (cal yr BP). In both regions, wood density, SLA, seed mass, leaf area (leaf), and leaf area (leaflet) displayed distinct long-term trajectories, indicating region-specific changes in trait composition over time.

4 DISCUSSION

4.1 REGIONAL HETEROGENEITY IN SAVANNA FUNCTIONAL DYNAMICS

The results indicate that functional differentiation within the savanna domain was real but limited in magnitude. Although the mean FDis of the Sahelian assemblages was slightly greater than that of the Sudanian assemblages, the small absolute difference suggests substantial functional overlap between the two regions. The stronger signal lies in the temporal structure. In regional bivariate analyses, the Sahelian pattern was associated with South Atlantic SST and $\delta^{18}\text{O}$, suggesting that long-term functional reorganisation in the Sahel may have been linked to broader ocean–climate and hydroclimatic variability. In contrast, the Sudanian assemblages showed no equivalent monotonic trend and instead appeared more variable over time. This implies that long-term environmental filtering may have operated more strongly in the Sahel, while more nonlinear ecological dynamics shaped the vegetation history of Sudanian.

The phase-based results reinforce this interpretation. Pooled savanna samples showed a significant overall phase effect, with FDis differing among Holocene intervals and reaching its highest mean and median values in the late Holocene. At the regional level, this pattern was driven mainly by the Sahel, where FDis showed significant phase-related restructuring, whereas Sudan showed no significant phase effect. This suggests that temporal ecological reorganisation within the savanna domain was not spatially uniform but was more strongly expressed under Sahelian conditions. This

may be associated with long-term environmental filtering, in which droughts, desertification, and recent regreening due to soil–water conservation (Claussen et al., 2020; West et al., 2017) contribute to greater, predictable functional and compositional changes in the Sahel. The Sudanian wooded belt, on the other hand, has been found to respond to frequent fires, grazing, and anthropogenic activity through farming (Savadogo, 2007; Touboul et al., 2018), leading to episodic, nonlinear responses. The significant increase in Sahelian FDis toward the present likely reflects the transformation of the region from a relatively uniform humid biome during the AHP into a highly seasonal, heterogeneous 'tension zone.' As the Saharan boundary shifted southwards, the Sahel became an ecological crossroad, incorporating a wider variety of both desert-hardy and Sudanian-refugee taxa. This 'diversification of stress' expanded the occupied trait space, creating the monotonic increase in dispersion that is absent in the more climatically buffered Sudanian wooded belt. This nonlinear temporal structure, especially in the late Holocene, where climate proxies show limited explanatory power for functional shifts, likely reflects the increasing 'anthropogenic overprint' on West African landscapes. The expansion of metallurgy and subsistence agriculture during the past 3,000 years introduced a novel disturbance regime that likely decoupled vegetation dynamics from purely oceanic-atmospheric forcing. Our observation of FDis peaks toward the present in the Sahel may therefore represent 'artificial' functional diversification driven by the expansion of synanthropic and pioneer taxa rather than a purely natural response to aridification. Although the pooled savanna analysis did not identify any single predictor that consistently explained the overall FDis changes, remote-sensing studies by Zeng et al. (2023, 2024) revealed that rainfall variability, land use/cover change, and fire regimes are interacting drivers of savanna vegetation change. This interpretation is further supported by the pollen rate-of-change (ROC) results but not the FDis results. When the ROC curve was tested against the independent environmental proxies, the following corrected associations were obtained:

Table 3: Summary of correlation results between ROC and independent proxies: forests respond significantly to South Atlantic SST, $\delta^{13}\text{C}$, and $\delta^{18}\text{O}$, whereas savannas are sensitive to North Atlantic SST and fire, with dust signals remaining weak.

Region	Proxy	<i>N</i>	<i>r</i>	<i>p_fdr</i>
Forest	SA SST	100	-0.379	<0.001
Forest	carbon-13	113	0.200	0.033
Forest	oxygen-18	113	-0.423	<0.001
Savanna	NA SST	103	0.279	0.008
Savanna	Sahara Dust	115	-0.069	0.462
Savanna	Fire	117	-0.301	0.003

Note: NA SST = North Atlantic sea surface temperature; SA SST = South Atlantic sea surface temperature; bold values indicate that the correlation is statistically significant; p_fdr = false discovery rate (FDR) correction

4.2 COMPOSITIONAL DIFFERENTIATION EXCEEDED FUNCTIONAL DIFFERENTIATION

A striking feature of the dataset is that compositional differentiation was far stronger than functional differentiation. Sahelian and Sudanian assemblages were sharply separated in squared chord distance space and in ordination space, yet the difference in FDis remained modest. This suggests that compared with the limited set of TRY-based numeric traits, floristic turnover and site-level clustering produced stronger regional contrasts. In other words, assemblages could be compositionally distinct while still occupying broadly overlapping regions of functional trait space. This pattern is ecologically plausible in open tropical systems, where different taxa may converge on similar drought-tolerant or disturbance-tolerant strategies. One of the associated causes is selective

pressure (aridity, disturbance regimes), which leads to taxa maintaining similar functional adaptation strategies even if they are taxonomically unrelated (Aleman et al. 2020; Dendoncker et al. 2023; Geißler et al. 2024; Hähn et al. 2025; Kapinga et al. 2023; Menegat et al. 2019). This convergence suggests that functional trait space is relatively constrained, while species composition varies widely because of plant latitudinal gradients (see Brussel & Brewer, 2021). This striking decrease, where high floristic turnover masks functional stability, suggests a state of high 'functional redundancy' in West African savannas. This implies that the harsh environmental filters of the Sahel and Sudan (i.e., seasonal aridity and fire) have forced taxonomically unrelated lineages to converge upon a narrow set of 'conservative' trait optima. Consequently, while Holocene climate fluctuations triggered significant species migrations and local extinctions, the 'biophysical blueprint' of the savanna remained remarkably resilient, maintaining a consistent suite of stress-tolerant strategies despite shifting floristic identities.

4.3 FOREST–SAVANNA CONTRAST AS A STRONGER FUNCTIONAL DIVIDE

In contrast, the forest–savanna comparison revealed a much sharper functional divide. Compared with savanna assemblages, forest assemblages exhibited substantially greater FDis, which is consistent with broader trait dispersion in more mesic-to-hydric and structurally complex vegetation. This interpretation is supported by the trait trajectories, which show larger leaf area values and greater variability in the forest, whereas savanna assemblages were shifted toward higher wood density and lower SLA. Together, these patterns support a contrast between more functionally heterogeneous forest systems and more conservative, stress-tolerant savanna systems.

Low SLA is commonly associated with thicker or denser leaves, slower resource acquisition, longer tissue persistence, and more conservative ecological strategies (Brussel & Brewer, 2021; Wright et al., 2004). In savanna settings, this is consistent with drought tolerance and persistence under seasonal water limitation. In contrast, higher SLA and greater leaf area in forest assemblages suggest more acquisitive strategies, with faster resource capture and growth under more humid and shaded conditions. Such acquisitive strategies may support rapid colonisation and productivity (Jiao et al., 2022; Ren et al., 2022), although they can also increase vulnerability to drought, pathogens, and mechanical damage (IPCC, 2023; Poorter et al., 2016; Saatchi et al., 2021). Additionally, this functional divide reflects a fundamental shift in the regional carbon–nutrient–water nexus. The higher FDis and acquisitive strategies (high SLA and LA) of the forest assemblages indicate a 'high-throughput' biogeochemical state, which is capable of rapid carbon sequestration under the humid conditions of the African Humid Period. In contrast, the transition to savanna-dominated landscapes represents a shift toward “biogeochemical buffering”, where conservative trait syndromes (high wood density) stabilise carbon stocks against the increasing metabolic volatility of the late Holocene. Our ROC results (Table 3) support this, showing that forest communities were hypersensitive to oceanic-driven moisture pulses (SSTs), whereas savannas were primarily regulated by the internal disturbance filter of fire.

The higher forest SCD values extend this interpretation by suggesting stronger adjacent-sample compositional turnover in forest records. This may reflect the greater sensitivity of forest assemblages to shifts in the Holocene moisture balance, canopy restructuring, or episodic disturbance (Adeleye et al., 2021, 2022; Ametsitsi et al., 2020; Atsri et al., 2018; Camara, 2025; Ngomanda et al., 2009). On the other hand, savanna communities may have remained more compositionally constrained across shorter stratigraphic intervals. The clear separation of forest, Sahel, and Sudan in ordination space indicates that these contrasts were not merely statistical artifacts of summary metrics but reflect genuine differences in assemblage structure (Adeleye et al., 2021, 2022).

Ordination and PERMANOVA reinforce this interpretation, but they also show that the forest–savanna contrast is nested within strong site- and region-structured variation. PCA and NMDS both revealed broad biome-level separation, and PERMANOVA confirmed that this split was highly significant; however, the stronger region-plus-age model indicated substantial regional structure in addition to the biome effect. The nonsignificant site-stratified test reflects the fact that the biome and site are strongly confounded in the present sampling design. Accordingly, the forest–savanna signal should be interpreted as a robust broad-scale pattern across the compiled records rather than as an effect that can be cleanly separated from local site identity in constrained permutations.

4.4 DIVERSITY, RICHNESS, AND EVENNESS

In addition to ordination and PERMANOVA, relationships among pollen richness, diversity, and evenness were evaluated to characterise the taxonomic structure more directly. Pollen richness reflects the number of taxa present in a sample or time bin, whereas evenness captures how evenly abundance is distributed among those taxa. Together, these metrics provide a complementary view of community organisation that is not fully captured by ordination alone.

The combined diversity plots (Fig. 11) show that the forest and savanna pollen assemblages differed not only in composition but also in taxonomic structure. Compared with the savanna samples, the forest samples generally displayed higher Shannon diversity and Pielou’s evenness, whereas the observed richness overlapped more strongly between the two biomes. The forest assemblages also exhibited a broader range of values, suggesting greater heterogeneity in the diversity structure. Temporal trends indicate that these contrasts persisted through the Holocene: forest assemblages maintained higher mean richness, Shannon diversity, and evenness across most time bins, whereas savanna assemblages remained lower and more constrained. Although both biomes fluctuated through time, the smoothed trajectories suggest that the forest assemblages were consistently more diverse and more evenly distributed, whereas the savanna assemblages were more dominated. This pattern implies that forest systems supported broader and more balanced pollen taxon representation, whereas savanna systems were more frequently shaped by stronger dominance of a smaller subset of taxa.

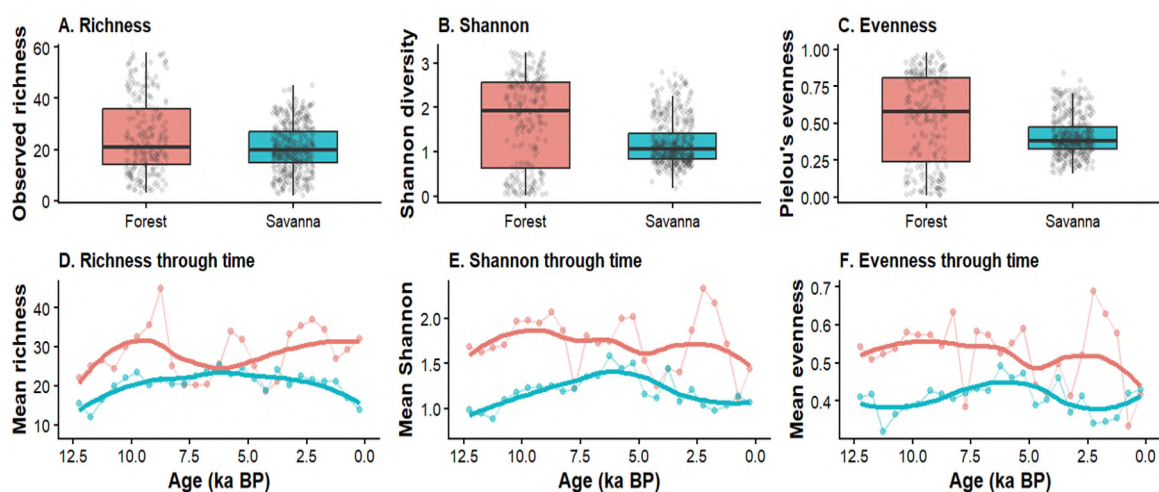


Figure 11. Pollen taxon diversity in West African forest and savanna assemblages. The upper panels compare observed richness (A), Shannon diversity (B), and Pielou’s evenness (C) between biomes using boxplots with overlaid sample points. The lower panels show smoothed temporal trends in mean richness (D), Shannon diversity (E), and evenness (F) from 12.5 to 0 ka BP. Compared with savanna

assemblages, forest assemblages generally exhibit higher Shannon diversity and evenness, while richness shows broader overlap between the two biomes.

Correlation analysis using Spearman's rank correlation (Fig. 12) showed that pollen taxon richness, Shannon diversity, and evenness were all positively related across the dataset, but they did not capture exactly the same aspect of community structure. Observed richness was strongly positively associated with Shannon diversity across all samples ($r = 0.670$, $n = 720$, $p = 3.64 \times 10^{-95}$), indicating that assemblages containing more taxa generally had higher overall diversity. This relationship was similarly strong in both forests ($r = 0.677$, $n = 247$, $p = 1.69 \times 10^{-34}$) and savanna samples ($r = 0.657$, $n = 473$, $p = 1.13 \times 10^{-59}$). In contrast, the relationship between richness and evenness was only moderate across the full dataset ($r = 0.389$, $n = 720$, $p = 2.28 \times 10^{-27}$), and was notably weaker in the savanna ($r = 0.211$, $n = 473$, $p = 3.71 \times 10^{-6}$) than in forest samples ($r = 0.368$, $n = 247$, $p = 2.46 \times 10^{-9}$). This suggests that increases in taxon number did not necessarily result in more evenly structured assemblages, particularly in savanna settings where communities more often remained dominated by a smaller subset of taxa. Shannon diversity and evenness showed the strongest relationship overall ($r = 0.913$, $n = 720$, $p < 0.001$), with similarly strong associations in forest ($r = 0.894$, $n = 247$, $p < 0.001$) and savanna samples ($r = 0.787$, $n = 473$, $p < 0.001$), although this is partly expected because evenness is derived from Shannon diversity.



Figure 12. Relationships among pollen taxon richness, Shannon diversity, and Pielou's evenness across West African forest and savanna samples. Panels show correlations between observed richness and Shannon diversity (A), richness and evenness (B), and Shannon diversity and evenness (C). Points represent individual samples, and colours distinguish forest and savanna assemblages; fitted lines show biome-specific trends.

5 CONCLUSION

Our study revealed that Holocene vegetation change in West Africa was regionally uneven. Within the savanna domain, compositional divergence between the Sahel and the Sudan exceeded functional divergence, whereas the forest–Savanna comparison revealed strong compositional separation and a sharper functional divide. The stronger temporal structuring of FDis in the Sahel further suggests that responses to climatic variability depend on regional moisture stress, landscape structure, and functional redundancy. Additionally, the ordination results, diversity metrics, and functional analyses support a robust biome-scale signal despite substantial regional and site-level structuring.

The community-weighted mean trajectories suggest that both forest and savanna assemblages underwent nonlinear functional reorganisation across the Holocene. In the forest, SLA and leaf area traits showed greater variability and higher overall values, which is consistent with shifts among more acquisitive and more mesic canopy strategies. In the savanna, higher mean wood density and lower SLA indicate more conservative ecological strategies associated with drought tolerance, tougher tissues, and persistence under open, seasonally stressed conditions. The seed mass patterns were noisier in both regions, but the forest displayed greater spread and more pronounced spikes, which is consistent with the intermittent contributions from larger-seeded woody taxa. These trajectories do not support a simple linear trend from one ecological state to another; rather, they point to repeated episodes of adjustment, mid-Holocene reorganisation, and late-Holocene reconfiguration. Environmental predictors showed limited explanatory power for corrected FDis. In the pooled savanna model, no predictor remained significant, and the full model was not significant. Regional bivariate correlations revealed that Sahelian FDis was associated with age, South Atlantic SST, and $\delta^{18}\text{O}$, whereas Sudanian FDis showed no significant proxy relationships. In the forest, the multiproxy model was marginal but nonsignificant, and no individual predictor remained significant in the full model. These results suggest that the available independent proxies explained only a limited proportion of functional dispersion, with clearer proxy associations restricted mainly to Sahelian FDis.

Despite these insights, our findings were not without constraints. Trait matching between the pollen taxa and modern plant trait datasets was constrained by the taxonomic resolution. Many taxa were matched only at the genus level, and some remained unmatched. In the savanna analyses, the TRY matrix was reduced to a small set of numeric traits, and missing values were imputed, meaning that the final functional metrics captured broad functional structure rather than the full multidimensional ecological variation of the original assemblages. In the forest comparison, further restrictions were imposed by reduced matched taxa, complete-case filtering, and genus-level TRY fallback. These constraints do not, however, invalidate the analysis, but they do mean that the results are not exhaustive reconstructions of total ecological function. Furthermore, the reliance on genus-level trait matching, necessitated by the taxonomic limits of pollen morphology, likely imposes a “precision ceiling” on our estimates of functional dispersion. Because interspecific trait variation within a genus is ‘averaged out’ in our framework, our results should be interpreted as a conservative baseline. It is highly probable that the true functional differentiation during the Holocene was even more pronounced than reported here. Nevertheless, the fact that significant biome-scale signals were detected despite this taxonomic smoothing underscores the fundamental strength of the functional reorganisation that occurred across West Africa.

In summary, our functional trait-based reconstruction highlights a fundamental asymmetry in biome sensitivity: West African forests exhibited high metabolic volatility and low functional redundancy, making them hypersensitive to oceanic moisture pulses. Conversely, the savanna domain,

particularly the Sudanian belt, exhibited high functional redundancy and adaptive convergence, suggesting a “biophysical resilience” that buffered the ecosystem against Holocene fluctuations. Understanding these divergent functional trajectories is essential for predicting which West African biomes will act as stable carbon reservoirs and which will become volatile carbon sources under future climate change. Therefore, future studies should aim to expand trait coverage, refine taxonomic resolution, and integrate multiple proxies to reconstruct ecological function more exhaustively.

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DATA AVAILABILITY

The datasets generated and analysed during this study are available in public repositories. Fossil pollen records are accessible via the Neotoma Palaeoecology Database (<https://www.neotomadb.org>). Plant functional trait data were obtained from the TRY Plant Trait Database (<https://www.try-db.org>). Additional ecological datasets were sourced from WAFEC, available on request from the corresponding author. All R scripts used in this study are openly available at: <https://github.com/Sanusi1994cam/West-African-savannas-and-forests->

AUTHOR CONTRIBUTION

SC designed the study, performed analyses, and wrote the manuscript. HA contributed to ecological interpretation and provided detailed revisions. JP provided global ecological expertise, strategic framing, and critical revisions. MMT contributed to the contextual ecological synthesis. All took part in reviewing and approving the final version of the manuscript.

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