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Woody Species Diversity and Diameter Structure of Sacred Forests in the Collines Department, Central Benin (West Africa)

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Abstract

Sacred forests constitute important reservoirs of woody biodiversity in West Africa, yet their floristic composition and structural characteristics across contrasting vegetation types remain poorly documented in central Benin. This study assessed the diversity and diameter structure of woody species in 28 sacred forests distributed across three communes (Glazoué, Savalou, Dassa-Zoumé) of the Collines Department, covering three forest types: woodland (FC), dry dense forest (FDS), and gallery forest (GF). Floristic inventories were conducted in 56 plots of 30 m × 30 m (19 FC, 34 FDS, 3 GF) using Braun-Blanquet phytosociological methods, recording all woody individuals with diameter at breast height (DBH) ≥ 10 cm. Diversity indices (Shannon H′, Simpson D, Pielou evenness, Margalef, Chao1 estimator) were computed per plot and compared across formations using Kruskal-Wallis tests with the plot as the analytical unit. Diameter distributions were fitted to the Weibull model. A total of 58 woody species were recorded. Mean species richness was 15.95 ± 2.03 spp./plot in FC and 15.71 ± 1.77 in FDS, and 8.33 ± 0.88 in GF; no significant differences among formations were detected for any diversity index ($p > 0.05$), but this result is imprecise because GF is represented by only three plots. Biological spectra were exclusively dominated by phanerophytes (100%), which is expected given that only stems with DBH ≥ 10 cm were recorded. All formations showed unimodal, right-skewed diameter distributions dominated by stems of 10 - 30 cm DBH (72% - 85% of stems). Indicator species analysis (IndVal) identified four significant species: *Pterocarpus erinaceus* and *Vitellaria paradoxa* for FDS, *Khaya senegalensis* for FC, and *Diospyros*

mespiliformis for GF. These results are consistent with sacred forests acting as refuges for woody biodiversity and support the integration of traditional conservation mechanisms into formal forest management frameworks.

Keywords

Sacred Forests, Floristic Diversity, Weibull Distribution, Phanerophytes, IndVal, West Africa, Benin

1. Introduction

Sacred forests are culturally protected areas found across sub-Saharan Africa, managed under customary rules enforced by traditional authorities. They represent some of the last remnants of primary vegetation in densely settled agricultural landscapes and function as refuges for woody species that have disappeared from surrounding degraded habitats [1] [2]. In Benin, sacred forests cover an estimated 0.2% of the national territory but provide critical ecosystem services including biodiversity conservation, spiritual and cultural identity, and local pharmacopoeia [3] [4].

Despite their ecological value, sacred forests in West Cameroon experienced a mean decline of 10.9% of their forest cover between 1990 and 2023, driven by agricultural expansion, extraction of non-timber forest products (NTFPs) and fuelwood collection [5]. Yet rigorous quantitative assessments of their floristic diversity and population structure remain scarce, particularly in the Collines Department of central Benin, a transitional zone spanning Sudano-Guinean phytogeographic zones.

Characterising the diversity and diameter structure of woody communities is fundamental for understanding forest dynamics, regeneration capacity, and the ecological role of sacred protection [6] [7]. Diameter distributions fitted to the Weibull model are widely used to describe population structure and infer demographic trends in tropical woody communities [8].

This study addresses three objectives: 1) to inventory and characterise woody species richness and diversity across three forest types (woodland, dry dense forest, gallery forest) in sacred forests of central Benin; 2) to compare diameter and height structures among formations using Weibull modelling and non-parametric tests; and 3) to identify species with significant affinity for specific formation types through indicator species analysis. We tested the null hypothesis that woody diversity does not differ among the three sacred forest types despite their physiognomic differences.

2. Material and Methods

2.1. Study Area

The study was conducted in the Collines Department of central Benin (West Af-

rica), in 28 sacred forests distributed across three communes: Glazoué, Savalou, and Dassa-Zoumé (latitudes 7˚30'N-9˚00'N). The region has a bimodal rainfall regime averaging 1100 - 1300 mm per year. The vegetation forms a mosaic of Sudano-Guinean formations including woodlands (forêts claires), dry dense forests, and gallery forests along watercourses [1]. Three vegetation types were distinguished at the sacred forest sites: 1) woodland (FC), with a seasonally open canopy (25% - 75% cover); 2) dry dense forest (FDS), with a denser, more closed mixed-deciduous canopy; and 3) gallery forest (GF), riparian strips with taller trees along permanent or seasonal streams.

2.2. Plot Design and Floristic Inventory

Floristic inventories were carried out in 56 square plots of 30 m × 30 m (0.09 ha each) distributed across the three forest types: 19 in FC, 34 in FDS, and 3 in GF. The 56 plots were in the 28 sacred forests (2 plots per forest on average). Plot number and location considered the area of each sacred forest; in large forests, plots were set 100 m apart from one another. In each forest, plots were installed in a representative part of the vegetation physiognomy, on homogeneous floristic units, following the phytosociological approach of Braun-Blanquet [9]. For each woody individual with DBH ≥ 10 cm, the following variables were recorded: scientific name (identified using [10]), DBH (measured at 1.30 m using a diameter tape), and total height (m, measured with a Suunto clinometer). Braun-Blanquet abundance-dominance coefficients (+, 1 - 5) were assigned per species. Life forms were classified following Raunkiaer [11].

2.3. Diversity Indices

Species richness S was computed per plot along with four complementary indices: Shannon diversity $H' = -\Sigma p_i \log_2 p_i$ [12]; Simpson index $D = \Sigma p_i^2$, expressed as the inverse Simpson index 1/D (range 1 to S) [13]; Pielou evenness $J = H'/H'\max$ (where $H'\max = \log_2 S$) [14]; and Margalef richness D_mg = (S − 1)/lnN. The Chao1 non-parametric estimator was used to evaluate sampling completeness. Species accumulation and rarefaction curves were generated by random plot permutation (999 iterations). All analyses used R 4.3.2 (vegan package).

2.4. Structural Analyses

Diameter class distributions (10-cm amplitude classes, DBH ≥ 10 cm) were constructed for each forest type. The Weibull two-parameter probability density function was fitted to observed distributions. These distributions describe the size-class structure of stems with DBH ≥ 10 cm only; stems below this threshold were not inventoried. Structural parameters (mean DBH, mean height, mean density) and diversity indices were compared among formations using the Kruskal-Wallis test ($\alpha = 0.05$). The analytical unit of every test was the plot (n = 56), using the plot mean DBH, plot mean height, plot stem density (stems ha^{-1} = number of stems/0.09 ha) and plot-level diversity indices; individual trees were not treated as

independent observations. Effect sizes (epsilon-squared, ε^2) are reported with 95% bootstrap confidence intervals. When significant differences were detected, formations were assigned to statistically homogeneous groups (a, b, ab, c). Floristic similarity among plots was assessed by hierarchical clustering (UPGMA) based on Bray-Curtis dissimilarity.

2.5. Indicator Species Analysis

Indicator species were identified using the IndVal.g index [15] (indicspecies package, R 4.3.2). Species with IndVal ≥ 0.5 and $p \leq 0.05$ (1000 permutations) were considered significant indicators. Because 58 species were tested, these p-values are not adjusted for multiple comparisons and the results are exploratory. Biological spectra (Raunkiaer life forms) were expressed as relative proportions.

3. Results

3.1. Floristic Diversity and Taxonomic Composition

A total of 58 woody species were recorded across the three sacred forest types. Woodland (FC) presented the highest taxonomic breadth with 19 families and 42 genera, compared to 13 families and 20 genera in FDS, and 7 families and 11 genera in GF. Mean species richness per plot was 15.95 ± 2.03 (FC), 15.71 ± 1.77 (FDS), and 8.33 ± 0.88 (GF). Mean richness in GF was about half that of FC and FDS, but Kruskal-Wallis tests detected no statistically significant differences among formations for any diversity index (Table 1); given that GF is represented by only three plots, this comparison has low power and is imprecise (effect sizes with 95% CI in Table 1). Shannon indices were 2.17 ± 0.09 (FC), 2.12 ± 0.10 (FDS), and 1.76 ± 0.11 (GF) ($p = 0.425$). Inverse Simpson (1/D) values were 6.66 ± 0.56, 7.01 ± 0.47, and 4.90 ± 0.73, respectively ($p = 0.396$). Pielou evenness was similar across all types (0.84 - 0.85; $p = 0.858$). Margalef richness corrected for

Table 1. Floristic diversity parameters by forest type in sacred forests of central Benin (Kruskal-Wallis test on plot-level values).

Parameter	Woodland (FC)	Dry Dense Forest (FDS)	Gallery Forest (GF)	p-value (Kruskal-Wallis)	Effect size epsilon2 [95% CI]
Number of plots	19	34	3	-	-
No. of families	19	13	7	-	-
No. of genera	42	20	11	-	-
Inverse Simpson 1/D (mean ± SE)	6.66 ± 0.56	7.01 ± 0.47	4.52 ± 0.67	0.275	0.011 [0.000 - 0.156]
Margalef Dmg (mean ± SE)	3.02 ± 0.28	2.83 ± 0.26	1.86 ± 0.15	0.365	0.000 [0.000 - 0.115]
Pielou J (mean ± SE)	0.84 ± 0.01	0.85 ± 0.01	0.83 ± 0.04	0.703	0.000 [0.000 - 0.114]
Species richness S (mean ± SE)	15.95 ± 2.03	15.71 ± 1.77	8.00 ± 0.58	0.398	0.000 [0.000 - 0.098]
Shannon H' (mean ± SE)	2.17 ± 0.09	2.12 ± 0.10	1.72 ± 0.11	0.269	0.012 [0.000 - 0.117]

FC: woodland; FDS: dry dense forest; GF: gallery forest; SE: standard error. No statistically significant differences were detected among formations for any diversity index (all $p > 0.05$). GF is based on three plots only, so these tests have low power. 1/D is the inverse Simpson index ($1/\Sigma p_i^2$).

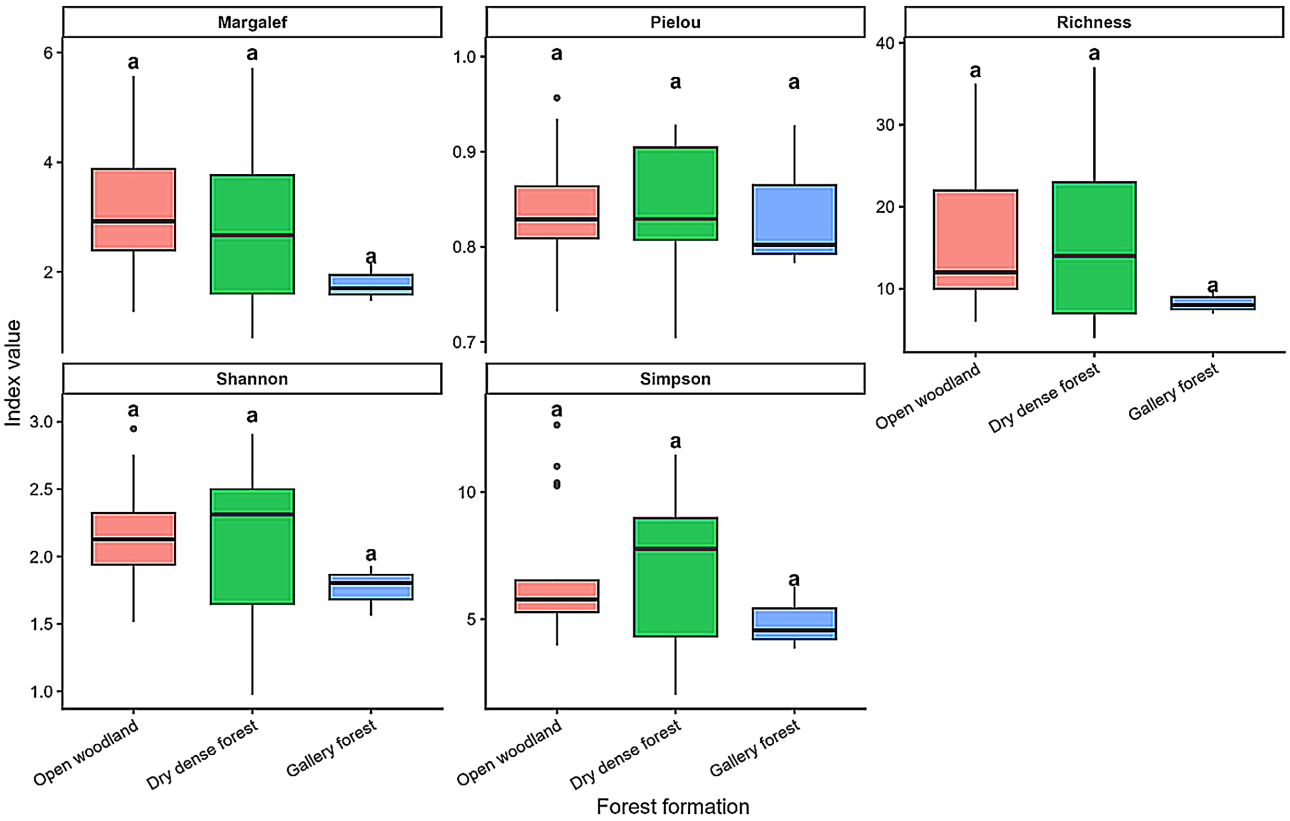


Figure 1. Comparison of woody species diversity indices across the three sacred forest types (FC: woodland; FDS: dry dense forest; GF: gallery forest). Boxplots show median, interquartile range, and 1.5 × IQR whiskers; dots are outliers. Identical letters above the boxes indicate statistically homogeneous groups. The Simpson panel shows the inverse Simpson index (1/D). No statistically significant differences were detected among formations (all $p > 0.05$). n: number of plots per formation (19 FC, 34 FDS, 3 GF).

sampling effort followed the same pattern (FC: 3.02 ± 1.22; FDS: 2.83 ± 1.51; GF: 1.79 ± 0.37; $p = 0.366$). As shown in Figure 1, the boxplots of the five diversity indices overlap widely among the three forest types, and no significant difference was detected for any index (all $p > 0.05$; Table 1). Species richness was similar in FC and FDS (≈15.9 and 15.7 spp./plot, with maxima of 35 - 37 species) and lower in GF (≈8 spp./plot), but the distributions overlap and within-formation variability is high in FC and FDS. Shannon H' followed the same pattern (FC: 2.17; FDS: 2.12; GF: ≈1.7 - 1.8), as did inverse Simpson 1/D, which was highest in FDS (7.01), then FC (6.66) and GF (≈4.5 - 4.9). Margalef richness was slightly higher in FC (3.02) and FDS (2.83) than in GF (≈1.8 - 1.9). Pielou evenness was nearly identical among formations (≈0.83 - 0.85) with narrow dispersion, indicating a comparable distribution of individuals among species. All formations were composed exclusively of phanerophytes (100% of biological spectrum).

3.2. Species Accumulation and Rarefaction Curves

Species accumulation curves showed contrasting dynamics among formations. In FC, the curve approached saturation around 47 species after 12 - 15 plots, suggesting adequate sampling coverage. In FDS, richness continued to increase without

reaching a clear plateau, reflecting high beta-diversity and strong spatial heterogeneity. In GF, 11 species were detected in the three plots; with so few plots, saturation cannot be assessed. The comparative accumulation curve (Figure 2) illustrates the gradient FC ≈ FDS >> GF in total floristic richness (the GF curve is limited to three plots). Rarefaction curves (Figure 3) were consistent with this hierarchy: FC and FDS both reached approximately 35 species at 400 - 550 individuals, while GF did not exceed 11 species at 60 individuals. Chao1 estimates closely matched observed richness in most plots, suggesting high inventory completeness overall, while minor Chao1 surpluses in some rich FDS plots indicated the probable presence of undetected rare species.

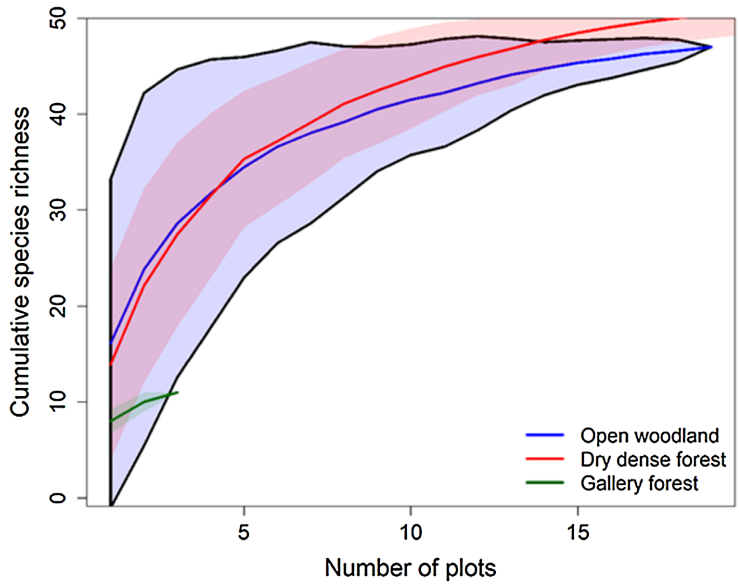


Figure 2. Comparative species accumulation curves for the three sacred forest types, generated by random permutation of plots (999 iterations). Shaded bands represent ± 1 standard deviation. FC: woodland (n = 19 plots); FDS: dry dense forest (n = 34 plots); GF: gallery forest (n = 3 plots).

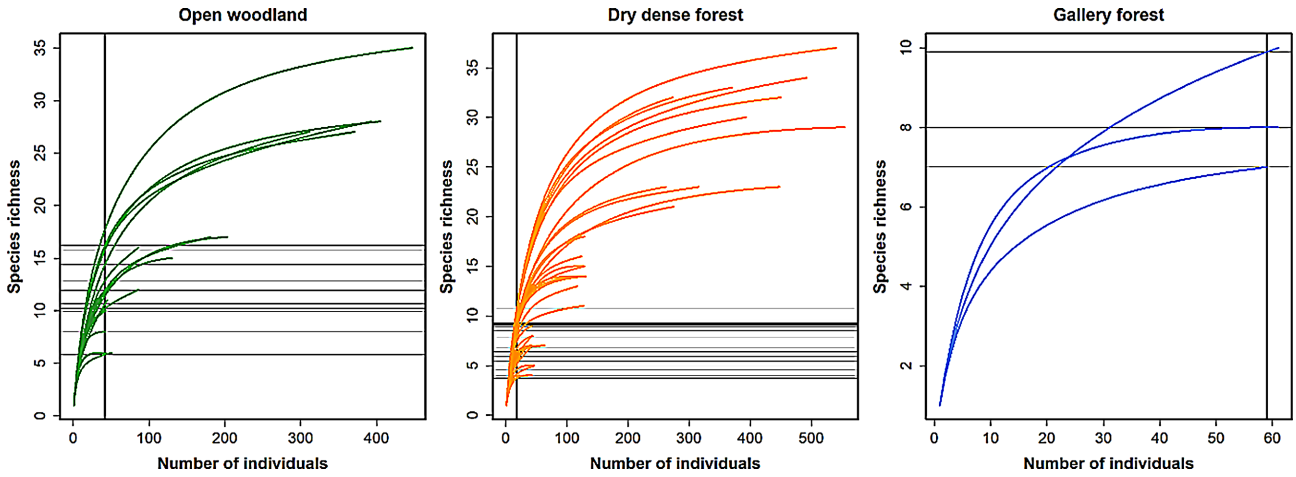


Figure 3. Rarefaction curves for the three sacred forest types, standardised by number of woody individuals (DBH ≥ 10 cm). Shaded bands represent 95% confidence intervals. The GF curves rest on only three plots. FDS does not attain a clear plateau, indicating residual floristic diversity not yet captured by sampling.

3.3. Structural Parameters and Diameter Distributions

Descriptive statistics of stems with DBH ≥ 10 cm are given in Table 2. Kruskal-Wallis tests at the plot level gave: mean DBH, $\chi^2 = 8.376$, df = 2, p = 0.015; mean total height, $\chi^2 = 12.051$, df = 2, p = 0.002; and stem density, $\chi^2 = 4.414$, df = 2, p = 0.110. The tree-level values of the previous version ($\chi^2 = 133.63$ and 80.5, p < 0.001), which treated individual trees as independent observations, have been removed.

Diameter class distributions are shown in Figures 4-6 and Tables 3-5. In all

Table 2. Descriptive statistics and plot-level Kruskal-Wallis results for structural parameters by forest type.

Parameter	Values (FC | FDS | GF)	Statistic (df = 2)	p-value	Post-hoc groups
Mean DBH (cm)	24.94 | 16.62 | 35.00	8.376	0.015	FC: ab; FDS: b; GF: a
Median DBH (cm)	23.33 | 18.02 | 34.83	5.657	0.059	–
Max. DBH (cm)*	25.83 | 17.88 | 20.83	4.088	0.130	–
Mean height (m)	25.39 | 15.76 | 38.33	12.051	0.002	FC: a; FDS: b; GF: a
Mean density (stems ha^{-1})	77.44 | 73.24 | 100.35	4.414	0.110	–

FC: woodland; FDS: dry dense forest; GF: gallery forest. Distinct letters (a, b, c) indicate statistically homogeneous groups (post-hoc grouping). Density = number of stems with DBH ≥ 10 cm per hectare (stems/(n plots × 0.09 ha)). The previous values (0.54 | 0.41 | 0.42) were removed: they are incompatible with the mean richness in Table 1 (15.95 species per 0.09-ha plot implies at least 177.2 stems·ha^{-1}) and with the class densities in Figures 4-6.

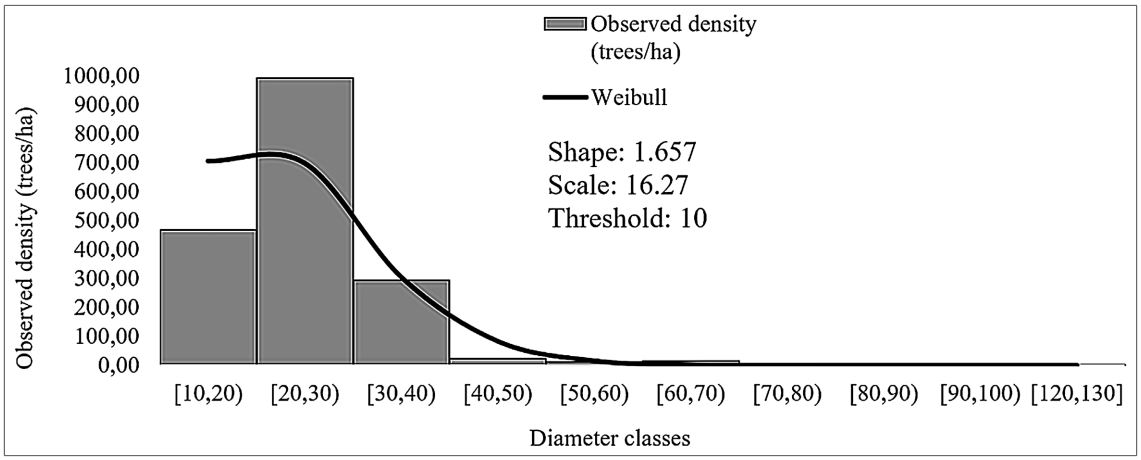


Figure 4. Diameter class distribution of woody species in woodland (FC; n = 19 plots). Bars represent observed density (stems·ha^{-1}) per 10-cm diameter class; solid line shows the fitted Weibull theoretical distribution. The distribution is unimodal and right-skewed (Weibull shape = 1.66), with 80.6% of stems in the 10 - 30 cm classes (see Table 3).

Table 3. Diameter class structure of woody species (DBH ≥ 10 cm) in woodland (FC; 19 plots), with observed and Weibull-predicted densities.

Class (cm)	Number of stems	Mean diameter (cm)	Class centre (cm)	Probability density	Theoretical frequency	Observed density (stems/ha)	Weibull density (stems/ha)
[10, 20)	756	15.27466	15	0.0407193	0.39	466.67	704.64
[20, 30)	1605	24.66475	25	0.0402874	0.39	990.74	697.17

Continued

[30, 40)	474	32.63952	35	0.0176029	0.17	292.59	304.62
[40, 50)	36	44.40423	45	0.0047987	0.05	22.22	83.04
[50, 60)	19	55.80475	55	0.0009007	0.01	11.73	15.59
[60, 70)	24	64.32512	65	0.0001223	0.00	14.81	2.12
[70, 80)	7	73.71148	75	1.238E−05	0.00	4.32	0.21
[80, 90)	3	83.29109	85	9.555E−07	0.00	1.85	0.02
[90, 100)	3	96.6601	95	5.711E−08	0.00	1.85	0.00
[120, 130]	1	127.324	125	2.964E−12	0.00	0.62	0.00

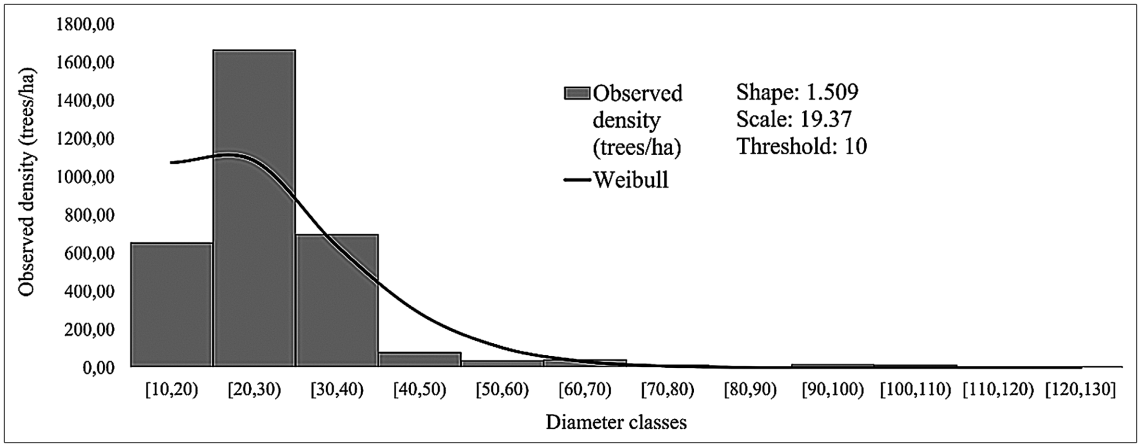


Figure 5. Diameter class distribution of woody species in dry dense forest (FDS; n = 34 plots). Bars: observed density (stems·ha^{-1}); solid line: Weibull fit. The distribution is unimodal and right-skewed (Weibull shape = 1.51), with 71.7% of stems in the 10 - 30 cm classes and a few stems above 60 cm (see **Table 4**).

Table 4. Diameter class structure of woody species (DBH ≥ 10 cm) in dry dense forest (FDS; 34 plots), with observed and Weibull-predicted densities.

Class (cm)	Number of stems	Mean diameter (cm)	Class centre (cm)	Probability density	Theoretical frequency	Observed density (stems/ha)	Weibull density (stems/ha)
[10, 20)	1239	15.62	15.00	0.03	0.33	655.56	1075.75
[20, 30)	3149	24.85	25.00	0.03	0.34	1666.14	1085.32
[30, 40)	1319	33.38	35.00	0.02	0.20	697.88	638.99
[40, 50)	150	43.43	45.00	0.01	0.09	79.37	286.85
[50, 60)	72	54.47	55.00	0.00	0.03	38.10	105.72
[60, 70)	77	64.69	65.00	0.00	0.01	40.74	33.15
[70, 80)	28	73.01	75.00	0.00	0.00	14.81	9.04
[80, 90)	12	85.33	85.00	0.00	0.00	6.35	2.17
[90, 100)	33	95.66	95.00	0.00	0.00	17.46	0.47
[100, 110)	26	102.39	105.00	0.00	0.00	13.76	0.09
[110, 120)	3	113.53	115.00	0.00	0.00	1.59	0.02
[120, 130]	11	125.79	125.00	0.00	0.00	5.82	0.00

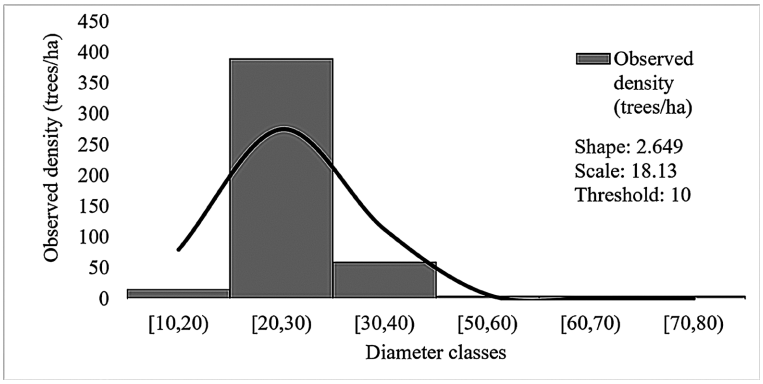


Figure 6. Diameter class distribution of woody species in gallery forest (GF; n = 3 plots). Bars: observed density; solid line: Weibull fit. The distribution is unimodal and right-skewed (Weibull shape = 2.65); 85.2% of stems are in the 10 - 30 cm classes and only three stems reach 50 - 80 cm (see Table 5).

Table 5. Diameter class structure of woody species (DBH ≥ 10 cm) in gallery forest (GF; 3 plots), with observed and Weibull-predicted densities.

Class (cm)	Mean diameter (cm)	Class centre (cm)	Probability density	Theoretical frequency	Observed density (stems/ha)	Weibull density (stems/ha)
[10, 20)	17.26831	15	0.016899	0.17	14.81481	79.67965
[20, 30)	25.08282	25	0.058356	0.58	388.8889	275.1437
[30, 40)	31.05511	35	0.023852	0.24	59.25926	112.4623
[50, 60)	47.74648	45	0.00143	0.01	3.703704	6.74239
[60, 70)	53.79437	55	9.75E−06	0.00	3.703704	0.045976
[70, 80)	63.66198	65	5.58E−09	0.00	3.703704	2.63E−05

three formations, the distribution was unimodal and right-skewed, with the mode in the [20 - 30[cm class (Weibull shape parameter 1.66 in FC, 1.51 in FDS and 2.65 in GF; all > 1, *i.e.* not a reversed J-shape). Stems of 10 - 30 cm accounted for 80.6% of stems in FC, 71.7% in FDS and 85.2% in GF, whereas stems ≥ 50 cm represented only 1.9%, 4.3% and 2.3%, respectively. The [10 - 20[cm class was below Weibull-predicted values (e.g. 466.7 vs 704.6 stems ha^{-1} in FC), while the [20 - 30[cm class exceeded them (990.7 vs 697.2). In FC and FDS, observed densities exceeded Weibull predictions from the [60 - 70[cm class upwards, but these classes hold few stems (stems ≥ 60 cm: 1.3% in FC and 3.1% in FDS), forming a long tail with slight local bumps rather than a distinct secondary peak. In GF (3 plots, 128 stems), 82.0% of stems fell in the [20 - 30[cm class, and only three stems reached 50 - 80 cm, none exceeding 80 cm. Because stems below 10 cm DBH (seedlings and saplings) were not inventoried, this size-class structure cannot demonstrate recruitment or regeneration failure.

3.4. Floristic Similarity and Indicator Species

Hierarchical clustering (UPGMA; Bray-Curtis dissimilarity) revealed a dominant group (Group 1) encompassing the majority of plots from all three formation types,

indicating high overall floristic similarity (Figure 7). Two secondary clusters (Groups 2 and 3) isolated a small number of atypical plots (FC_19, FDS_24, FDS_25, FDS_32), suggesting localised disturbance or microhabitat differentiation. The mixing of FC, FDS, and GF plots within the main group suggests floristic continuity rather than sharp floristic boundaries between formation types.

Among the 58 recorded species, only 4 showed statistically significant associations with a specific forest type in the IndVal analysis (Table 6): *Pterocarpus erinaceus* (IndVal = 0.817; p = 0.009) and *Vitellaria paradoxa* (IndVal = 0.797; p = 0.003) were indicators of FDS; *Khaya senegalensis* (IndVal = 0.581; p = 0.046) characterised FC; and *Diospyros mespiliformis* (IndVal = 0.658; p = 0.050) typified GF, at the limit of the significance threshold and based on three GF plots. The proportion

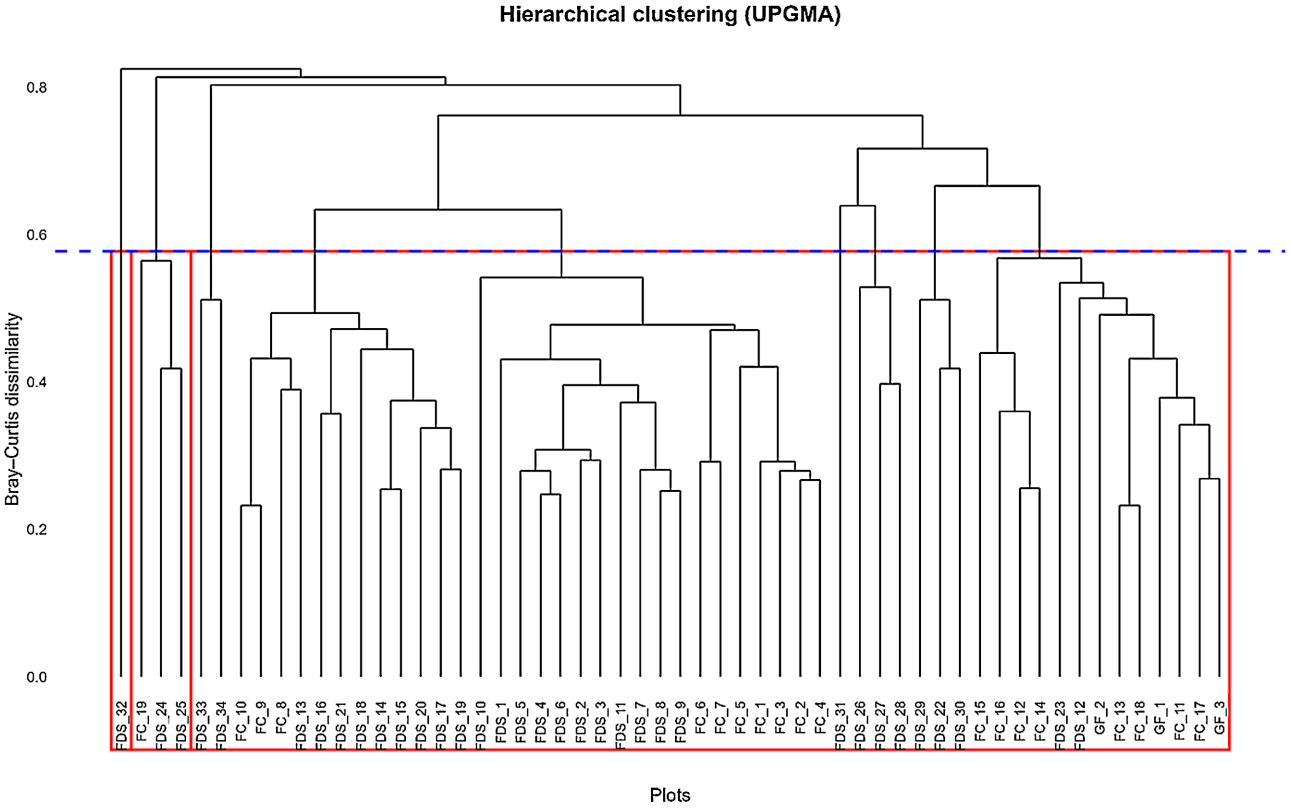


Figure 7. UPGMA dendrogram based on Bray-Curtis dissimilarity among 56 plots. Group 1 (majority of plots) shows high floristic similarity across all three forest types. Groups 2 and 3 isolate a small number of atypical plots (FC_19, FDS_24, FDS_25, FDS_32) with distinct floristic composition, possibly linked to local disturbance or microhabitat differentiation.

Table 6. Significant indicator species by IndVal analysis for each sacred forest type.

Species	Forest type	IndVal	p-value
Pterocarpus erinaceus Poir.	Dry Dense Forest (FDS)	0.817	0.009
Vitellaria paradoxa C. F. Gaertn.	Dry Dense Forest (FDS)	0.797	0.003
Khaya senegalensis (Desr.) A.Juss.	Woodland (FC)	0.581	0.046
Diospyros mespiliformis	Gallery Forest (GF)	0.658	0.050

of significant indicator species (6.9% of total flora) is consistent with broad floristic overlap among formation types.

4. Discussion

4.1. No Detected Differences in Diversity across a Physiognomic Gradient

The absence of statistically significant differences in diversity indices across the three forest types (all $p > 0.05$) is the most striking finding of this study. This should be read as "no differences were detected", not as evidence that diversity is equivalent: mean richness in GF was about half that of FC and FDS, the GF comparison rests on only three plots, and the confidence intervals of the effect sizes ($\varepsilon^2 = 0.000$ - 0.012, with 95% CI upper limits of up to 0.156; **Table 1**) leave room for substantial differences. Despite clear physiognomic contrasts from the open canopy of woodlands to the dense dry forest and the riparian gallery, woody communities in these sacred forests showed overlapping levels of species richness, evenness, and floristic composition. This result aligns with [16], who reported strong overlap of floristic profiles between forest types within the same sacred complex, and contrasts with studies in unprotected landscapes where physiognomic type typically predicts strong floristic differentiation [7]. One possible explanation is the homogenising role of customary protection, which restricts selective logging and land conversion uniformly across all vegetation types within a sacred perimeter; this study did not sample unprotected sites and cannot test this explanation.

The exclusive dominance of phanerophytes (100% of biological spectra) is expected because only woody stems with DBH ≥ 10 cm were inventoried, which excludes herbaceous and small-stature life forms by design; it therefore cannot by itself indicate forest integrity. It is consistent with findings for wooded zones of Togo by [17], where phanerophyte prevalence signals intact forest cover as opposed to degraded formations where therophytes become proportionally more abundant.

4.2. Structural Differentiation and Diameter Dynamics

While diversity metrics showed no detectable differences, structural parameters differed among formations at the plot level (mean DBH, $p = 0.015$; mean height, $p = 0.002$; stem density did not differ, $p = 0.110$; **Table 2**).

Diameter distributions were unimodal and right-skewed in all formations (Weibull shape > 1), with most stems (72% - 85%) between 10 and 30 cm and few large trees (≤4.3% of stems ≥ 50 cm). Relative to the Weibull model, the [10 - 20[cm class was under-represented and the [20 - 30[cm class over-represented; since stems < 10 cm were not inventoried, this cannot distinguish a recruitment bottleneck from an inventory-threshold effect [6]. The excess of observed over predicted densities in the largest classes of FC and FDS involves few stems and reflects a long tail of large trees not captured by the two-parameter Weibull model [8].

4.3. Indicator Species and Conservation Implications

The very low proportion of significant indicator species (4 of 58, 6.9%) and the dominance of a single mixed-composition floristic cluster suggest that these sacred forests harbour a shared pool of woody species spanning all three physiognomic contexts. Given 58 tests at $\alpha = 0.05$, about three false positives are expected by chance, so the four indicators are treated as exploratory. The four significant indicators nonetheless reflect ecologically meaningful habitat preferences described in West African literature: *Pterocarpus erinaceus* and *Vitellaria paradoxa* are characteristic of seasonally dry, well-drained soils typical of FDS; *Diospyros mespiliformis* is closely associated with gallery habitats throughout the Sudano-Guinean zone; and *Khaya senegalensis* shows higher fidelity to the dappled, semi-open conditions of woodlands [18]. The presence of *K. senegalensis* in the woodlands studied supports the argument that sacred forests provide important refugia for commercially threatened woody species [19]. These findings advocate for the formal recognition of sacred forests in national biodiversity conservation frameworks and their inclusion in forest landscape restoration plans [16].

4.4. Limitations

The results should be read with the following limitations: (i) the gallery forest is represented by three plots, so its comparisons are imprecise; (ii) plots are nested within sacred forests and communes, which limits their independence; (iii) only stems with DBH ≥ 10 cm were recorded, so seedlings, saplings and non-woody life forms are not covered and regeneration cannot be assessed directly; and (iv) no unprotected control sites were sampled, so the effect of customary protection cannot be tested.

5. Conclusion

This study provides the first comparative assessment of woody species diversity and diameter structure across three sacred forest types in the Collines Department of central Benin. Despite physiognomic differentiation, no significant differences in diversity were detected among the three formation types (all $p > 0.05$), although the gallery forest comparison is imprecise (three plots). All stems with DBH ≥ 10 cm were phanerophytes, and floristic similarity among plots was high. Structural analyses at the plot level showed significant differences in mean DBH ($p = 0.015$) and mean height ($p = 0.002$) but not in stem density ($p = 0.110$); diameter distributions were unimodal and right-skewed in all formations, dominated by stems of 10 - 30 cm (72% - 85%), with few stems ≥ 50 cm; regeneration itself was not assessed. Only four of 58 woody species were significant formation-type indicators, consistent with broad floristic overlap among formations. These results are consistent with the role of sacred forests as refuges for woody species, including *Khaya senegalensis*. Future work should integrate inventories of seedlings and saplings, long-term demographic monitoring and dendrochronological analyses of annual growth rings in key indicator species to assess recruitment dynamics

and climate sensitivity across sacred forest formation types.

Author Contributions

J.Z. Kpogniwe: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing—original draft. F.Y. Assongba: Funding acquisition, Project administration, Supervision, Writing—review and editing. P. Tobada: Resources, Validation, Writing—review and editing. J. Djego: Supervision, Validation, Writing—review and editing.

Data Availability Statement

The floristic inventory dataset used in this study will be deposited in a publicly accessible data repository (Zenodo) upon acceptance. The data are available upon reasonable request to the corresponding author.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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