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Local-scale structuration of species-habitat association in the semi-deciduous tropical rainforest in eastern Cameroon

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ABSTRACT

Tropical forests are hyperdiverse, and although broad-scale variation in diversity can be reasonably well explained, local-scale variation in diversity is harder to understand. It has been revealed that species may show species-habitats associations. However, how the assembled species are associated with local habitats and how community-habitat associations vary regarding species abundance and class size remains unclear. Here, we analyzed the community-habitat associations by applying the multivariate regression trees (MRT) technique on data of 22,064 trees distributed across 30 1-ha plots varying in topography and soil conditions in a semi-deciduous tropical rainforest of Cameroon. Further, the indicator species analysis was used to determine the most important species for structuring assemblages.

The MRT divides the whole tree community inventoried into four habitats types: Habitat 1 (H1) sandy loamy, acidic soil with a low Na concentration ($\text{pH} \leq 6.245$ and $[\text{Na}] < 4.535 \text{ cmol kg}^{-1}$); H2 equal to neutral sandy soil with a small Na concentration ($7 \leq \text{pH} < 6.245$ and $[\text{Na}] < 4.535 \text{ cmol kg}^{-1}$); H3 equal to Loamy sandy soil with average Na concentration ($4.535 \leq [\text{Na}] < 6.243 \text{ cmol kg}^{-1}$) and; H4 equal to Loamy sandy soil with high nutrients concentration ($[\text{Na}] \geq 6.243 \text{ cmol kg}^{-1}$). Coincidentally, the same habitat types were also generated for the understorey and large trees classes taken separately, although a difference was somehow recorded for the small stems class. Among investigated environmental variables, soil Na content and, to a lesser extent, soil pH were identified as the primary responsible for the first split for habitat types for understorey and large trees classes. By contrast, the most determinant for discrimination habitat types for small stems was soil cation exchange capacity, followed by soil moisture content. Overall, 29 species were found as indicators characterizing the four habitat types for the whole tree community, with index values varying between 33% and 99%. But specifically, the number of indicators species for large trees was 28. Intriguingly, some indicator species within the large trees class changed to either non-indicator or intermediate indicator species in the understorey trees class that was best represented by as less as 16 species. A comparable species richness was recorded across all plots of the studied area; however, significant variability was found regarding species abundance, with habitats H1 and H4 with higher average abundance values. This study highlights that soil variables adding to topographical habitat filtering were important in shaping the composition of local species.

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1. Introduction

Understanding the importance of niche-assembly processes in shaping community structure is a significant challenge for community ecology. Furthermore, it is of particular interest in species-rich communities such as tropical forests hyperdiverse, where the broad-scale variation in diversity can be reasonably well explained while the local-scale variation in diversity is harder to understand (Pitman et al., 1999, Weiher and Keddy, 1999, Chesson, 2000, Chase and Leibold, 2003).

The classical exclusion principle by Chapman (1935) states that many species competing for the same resources cannot stably coexist because the number of limiting resources often exceeds the number of competing species (Hutchinson, 1961, Connell, 1978). Several hypotheses, such as the classical niche theory (Pimm, 1983) and the neutral theory of biodiversity (Hubbell, 2001), have been developed to resolve this enigma. Depending on the neutral approach, functionally, species are equivalent, and diversity is controlled by stochastic processes such as drift and dispersal limitation (Hubbell, 2001, McGill, 2003). Thus, the functional equivalence of plant species would mean that segregation along environmental niche axes is not the primary driver of species assembly. In contrast, classical niche theory states that competing for plant species can avoid competitive exclusion by relying on different, spatially segregated resources (Harms et al., 2001, Sugihara et al., 2003, Pavoine and Bonsall, 2011, Valladares et al. 2015).

It has been shown that habitat plays an essential role in distributing forest species from the local to the landscape scale. This role comes from non-random associations observed between species distributions and environmental variables (Fayolle et al., 2012, Toledo et al., 2012, Ricklefs and He, 2016, Gonmadje et al., 2017, Gonmadje et al., 2018). However, at local scales, aggregation of seedling and adult populations represents the consequence of the limited dispersal, which also plays a vital role in determining species distribution (Gomez-Aparicio et al., 2007, Mack and Bever, 2014). The inadequacy of the relative importance of niche and dispersal mechanisms with the local community's structure is problematic because both factors contribute to the spatial correlation of species composition at this scale. Dispersion processes lead to spatially aggregated species distributions and, therefore, to spatially structured communities (Pulliam, 2000, Seidler and Plotkin, 2006). Moreover, habitat distribution leads to a spatial community structure because of the strong spatial correlation of environmental variables.

Despite substantial evidence of the importance of niche partitioning in structuring communities, the relative influence of different environmental factors is still poorly known, especially for tropical African forests. At the local scale, the niche distribution is mainly based on topographic variation (Chuyong et al., 2011, Kitagawa et al., 2015, Sosa and Loera, 2017, Wang et al., 2017, Jucker et al., 2018). This serves as a valuable indicator of habitat heterogeneity as it is relatively easy to measure and because it influences water availability and biogeochemical processes (Werner and Homeier, 2015). However, integrating edaphic characteristics to topographic variables may reveal the importance of previously unmeasured environmental variation. This assertion was demonstrated by Baldeck et al., (2013b), who found that the proportion of community composition explained by the environment significantly increased when soil conditions were taken integrated with environmental variables.

Furthermore many studies have shown the influence of topography and soil conditions on the structure and composition of tropical forest vegetation globally (Laurance et al., 2010, Baldeck et al., 2013b, Rocha-Santos et al., 2017). Generally, compared to homogeneous landscapes, those with heterogeneous abiotic site conditions offer a greater diversity of soil properties and, therefore, more niches for different plant species (Dufour et al., 2006, Tamme et al., 2010). However, only a few studies (e.g., Chuyong et al., 2011) have investigated the small-scale effects of topography and soil conditions on plant diversity composition and

structure variability in African tropical forests, particularly those of Cameroon that have been only scantily investigated.

The main objective of this study was to assess the relative contribution of topographic and edaphic factors at the local scale in a semi-deciduous tropical rainforest in eastern Cameroon and their relative contribution to the variation in the community composition. We combine topography and soil conditions variation data for 30 1-ha plots within the terra-firme forest of the Doume Communal forest (DCF) belonging to the tropical semi-deciduous rainforest of East Cameroon. Hence, we address three questions. Question 1: Does the forest show distinct habitats, and to what extent variance in local species composition is explained by habitat differentiation? We hypothesize that the terra-firme forest of the DCF would indicate a specific topo-edaphic habitat differentiation, which could be detected because the forest plot emerged with strong fine-scale topography and soil heterogeneity. Question 2: Do the forest plots show habitat driving species association and is invariant with tree size groups? We hypothesize that topo-edaphic habitat types would vary with tree size groups. Question 3: How much variability in local species in the different habitat types explain the composition and whether certain indicator species characterize the habitat types? We hypothesize that local species and indicators did not vary too much between the habitat types.

2. Material and methods

2.1. Study site

The study was conducted in the moist and evergreen forest of the Doume municipality (4°31'0" S, 13°47'5" W). The Doume Council, situated in the Department of Upper Nyong of Cameroon's eastern region, is distant from Abong-Mbang and Bertoua, respectively, at ~58 and 57 km. Spread over an area of 2 500 km², the municipality of Doume is bordered by Ndiang, Abong Mbang, Doumaintang, and Angossas in the north, south, east, and southwest. Two forest blocks constitute the Doume communal forest (DCF) of 45 359 ha (Fig. 1). Topographically, the forest is uneven, with low hills interspersed with small well-marked streams or swampy, sometimes vast depressions (several hundred meters) without a specific watercourse. The altitude varies from 540 to 676 m, with some particularly marked summits culminating at less than 700 m (Anonymous, 2015). Climatically, the DCF is exposed to an equatorial Guinean climate characterized by two seasons: a long rainy season from mid-March to mid-November and a short dry season from mid-November to mid-March. The mean annual temperature is 25 °C, and annual rainfall varies between 1300 and 1800 mm (Anonymous, 2015).

2.2. Plot selection and sample design

Representative and homogeneous vegetation types were selected based on physical features (e.g., topography and altitude) and land use/land cover change analyses in the study area (Zekeng et al., 2019). Thirty 1-ha plots were established within the two blocks of the DCF, avoiding rivers and swampy vegetation types. Each 1-ha plot was subdivided into 25 subplots of 20 m × 20 m. In addition, five sub-quadrats of 5 m × 5 m were also installed at the four corners and the center of the 1-ha plots to identify the small stems (1.0–4.9 cm) and record their diameter data. Please refer to Zekeng et al., (2020, 2021) for additional details on sample selection.

2.3. Botanical inventory

Complete inventories of all vascular plants with a DBH ≥ 10 cm considered as large trees were measured, recorded, and identified within each plot. According to Nascimento and Laurance (2002), the DBH of all vascular plants with DBH between 5.0 and 9.9 cm considered as understorey trees was measured using a DBH tape at 1.3 m or above any buttresses and identified in each second plot of 20 m × 20 m. The

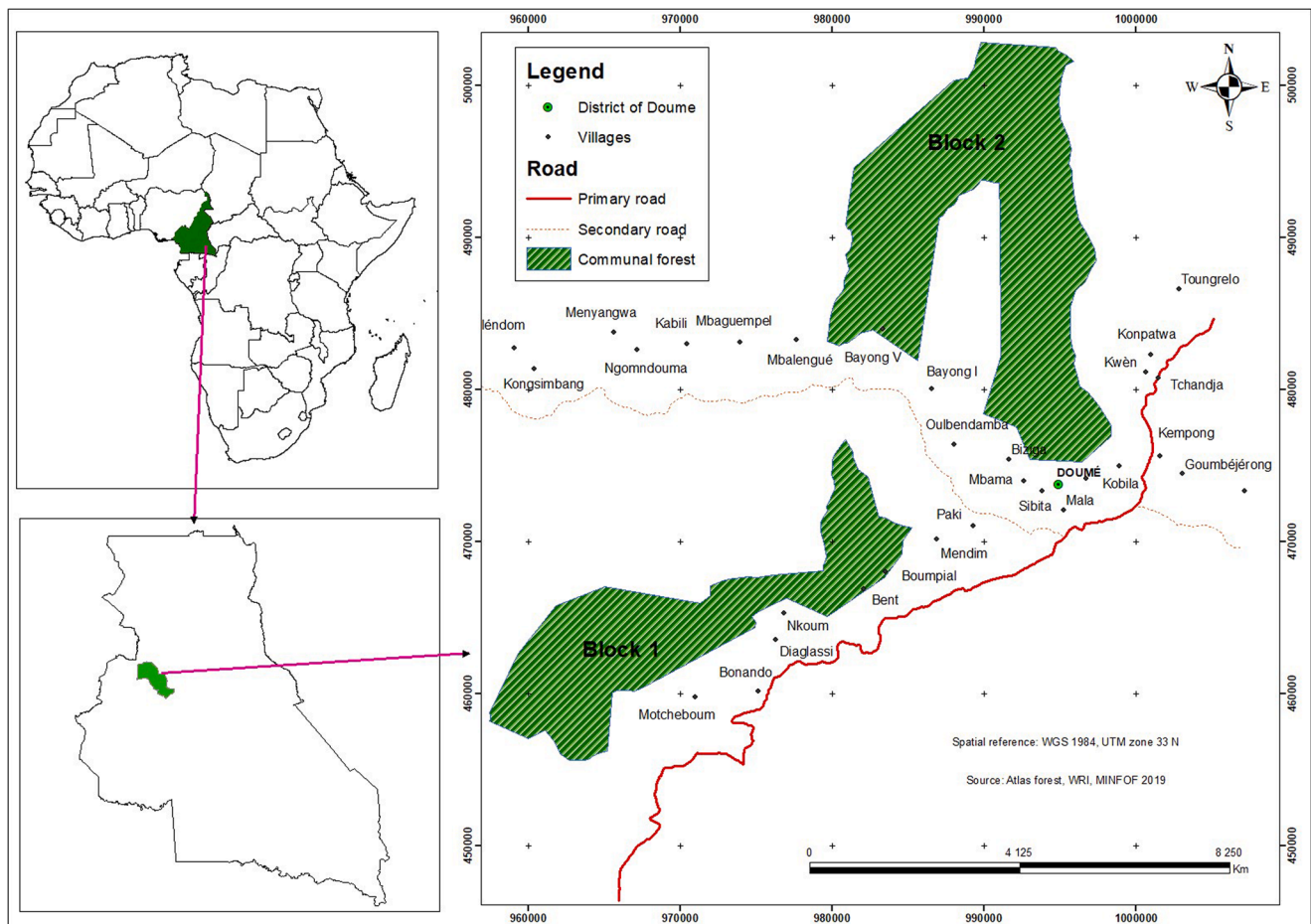


Fig. 1. Map and localization of the Doume Communal Forest, showing its two blocks (FC DOUME block 1 and 2).

diameter of small stems (1.0–4.9 cm) was recorded at 30 cm above-ground level within the five 5 m × 5 m sub-quadrats in the 20 m × 20 m. Within each 1-ha plot, all vascular plants with a DBH ≥ 10 cm were measured using a DBH tape at 1.3 m breast height or, if applicable, above buttresses or deformity (Condit, 1998).

During the fieldwork, a direct identification was performed at tree measurement by observing the leaves, flowers, habit, slash, and other diagnostic characters. In the field, trees were identified by two experienced botanists assisted by local floras and identification guides. Moreover, a unique code was attributed to unidentified species for reuse if encountered later within the plot or locality. A single ecological specimen was also collected for further checking and identification in the National Herbarium of Cameroon. A datasheet of each specimen was filled out, describing its vegetative characters. Each species identified during the fieldwork was homogenized for synonymies and orthographic problems using several plant databases, such as the Plant List database (Hassler, 2018). The Angiosperm Phylogeny Group IV (APG; Byng et al., 2016) was used for families' botanical nomenclature. The new subfamily classification based on a taxonomically comprehensive phylogeny was used for the Leguminosae subfamilies (LPWG 2017).

2.4. Topographic variables

Topographic variables consisted of elevation, slope, curvature (the relative altitude of a quadrat concerning its immediate neighbors), and aspect. The altitude was recorded at four corners and the center of the one ha plot and used to calculate topographic variables at the one ha scale. Mean altitude was calculated as the mean of the altitude measurements at the four corners and the center of a one ha plot. The slope

was calculated as the average angular deviation from the horizontal of each of the four triangular planes formed by connecting three of its four corners. Aspect is the direction a slope faces, and $\cos(\text{aspect})$ and $\sin(\text{aspect})$ were calculated to make aspect data usable in linear models. Finally, convexity was the elevation of a quadrat minus the average altitude of all immediate neighbor quadrats (Baldeck et al., 2013b, Wang et al., 2017). Elevation and slope variables were obtained using GPS and lysimeter, respectively, while other topographical variables were obtained using ArcMap 10.5.

2.5. Edaphic variables

During the botanical field survey, five soil samples were taken per plot. One sample was taken from the 20 m × 20 m subplot of the 1-ha plot corner, and one was taken from the 20 × 20 m subplot of the middle of the 1-ha plot. The samples were taken from the top 20 cm of the soil after removing the first organic soil horizon, corresponding to the organo-mineral horizon (Gobat et al., 2004). 500 g per composite soil sample of the 1-ha plots was analyzed at the Environmental Science Department's soil laboratory at the University of Botswana. Soil samples were analyzed for a total of nine physico-chemical characteristics i.e., soil texture, pH, exchangeable cations (Ca^{2+} , Mg^{2+} , K^{+} and Na^{+}), total nitrogen (N), phosphorus content (P), and cation exchange capacity (CEC). The soil texture was determined by estimating the percentage of sand (particle size 0.05 to 2.0 mm), silt (0.002 to 0.05 mm), and clay (<0.002 mm) obtained by using a Malvern Mastersizer 3000E laser particle size analyzer with a Hydro 3000MU pump accessory (Miller and Schatzel, 2012). The pH was determined on a 10 g soil sample, using 50 ml of distilled water and equilibrating for 150 min. The Ca^{2+} , Mg^{2+} ,

K⁺, and Na⁺ concentrations were determined in 1 M ammonium acetate at pH 7 (Westerman, 1990); acidity in 1 M of potassium chloride (KCl). P content was determined using the Ascorbic Acid color development method (Westerman, 1990) and the total N using the micro Kjeldahl method (Cochrane & Barber 1993). The CEC (cmol⁺/kg) was estimated by adding together concentrations of exchangeable K (ppm/390), Ca (ppm/200), Mg (ppm/120), and extractable acids.

2.6. Data analysis

2.6.1. Determination of habitat specificity

Multivariate regression trees technique (MRT) (De'ath, 2002, Larsen and Speckman, 2004) was used to group plots with similar species composition (i.e., species assemblages) according to topographic variables and soil conditions. MRT represents a constrained clustering method exploring the relationships between multispecies and environmental data (De'ath, 2002). It is based on a recursive algorithm, and in this study, the root node consists of all 30 1-ha plots. The MRT is a method that given the dependant variable space makes splits using single independent variables (i.e., environmental variables) that maximizes the deviance between the splits nodes. Indeed, the algorithm determines the environmental factors and its corresponding value threshold that splits the plots into several groups by minimizing the species dissimilarity within groups (Larsen and Speckman, 2004). Then, the same process is repeat on the two groups of samples obtained. It should be noted that it is the algorithm that directly determines the importance of the environmental variables' influence in constructing the tree regression. The regression tree is pruned using cross-validation to an appropriate size. In the framework of this study, tree size was selected by minimizing the cross-validated relative error (CVRE) with 1 SE rule in all the cases, hence avoiding over-fitting of the data (Breiman et al., 1984). This rule takes into account both the complexity of the sample and the size of the error. This tree can be thought of as the "best predictive tree" in the sense that, on average, it should give the most accurate predictions (De'ath, 2002). The MRT analysis was performed using 'mvpart' package in R (R Development Core Team, 2018).

2.6.2. Characterization of the different habitat

It is crucial to investigate which species are most important for habitat classification. Therefore, in this study, indicator species analysis was used to identify statistically significant species of habitats types (Dufrene and Legendre, 1997). The indicator value is defined as the product of the frequency and fidelity for each habitat type, ranging from

0 (species does not occur in a habitat) to 1 (species occurs in all plots of one habitat type and none of the other plots habitat types). Species with high indicator values for particular habitat types are considered indicator species. Indicator species analysis was performed using 'labdsv' package in R.

3. Results

3.1. Species association and habitat across the whole tree community

A total of 22,100 stems distributed in the three size classes (1.0–4.9 cm, 5.0–9.9 cm, DBH ≥ 10 cm) was recorded in 30 1-ha sample plots. A total of 22,064 trees were identified to belong to 307 species classified into 194 genera and 72 families. >89 % of morphospecies were identified at the species level, 6 % at the generic level, 2 % at the family level, and 3 % unidentified.

The MRT divides the whole tree community inventoried of the DCF plots into four habitats types, based on soil parameters such as pH and sodium (Na) concentration (Fig. 2; Table 1). The four types of habitat defined are as follow: (i) Habitat 1 (H1) sandy loamy, acidic soil with a low concentration of Na (pH ≤ 6.245 and [Na] < 4.535 cmol kg⁻¹); (ii) Habitat 2 (H2) neutral sandy soil with a small concentration of nutrients (7 ≤ pH > 6.245 and [Na] < 4.535 cmol kg⁻¹); (iii) Habitat 3 (H3) loamy sandy soil with average nutrients concentration (4.535 ≤ [Na] < 6.243 cmol kg⁻¹); (iv) Habitat 4 (H4) Loamy sandy soil with high nutrients concentration ([Na] ≥ 6.243 cmol kg⁻¹). The soil Na contents determined the first node for habitat types (breakpoint = 4.535 cmol kg⁻¹), explaining 19.53 % of the standardized species variance (Fig. 2). The soil pH and Na concentration determined the second node (breakpoint = 6.245). The third node (breakpoint = 6.243 cmol kg⁻¹) forms the four habitat types, explaining 12.10 and 5.61 % of the total standardized species variance. Therefore, 50% of inventoried plots in the DCF were covered by Loamy sand soil with high nutrients concentration habitat and 30% of the plots were cover by acidic sandy soil with a small concentration of nutrients.

The three nodes constituting the MRT explained 37.23 % of the total standardized species variance of the whole tree community species inventoried (Table 2). However, only 17.71% of 37.45% of the total standardized species variance was explained by the second and third nodes, forming the four habitats in the DCF plots (Table 3). While for the second node, which splits, includes habitats one and two, twenty-four species explained 69.72 % of its species variance. Among the twenty-four species, *Annickia chlorantha* (Oliv.) Setten & Maas (Annonaceae),

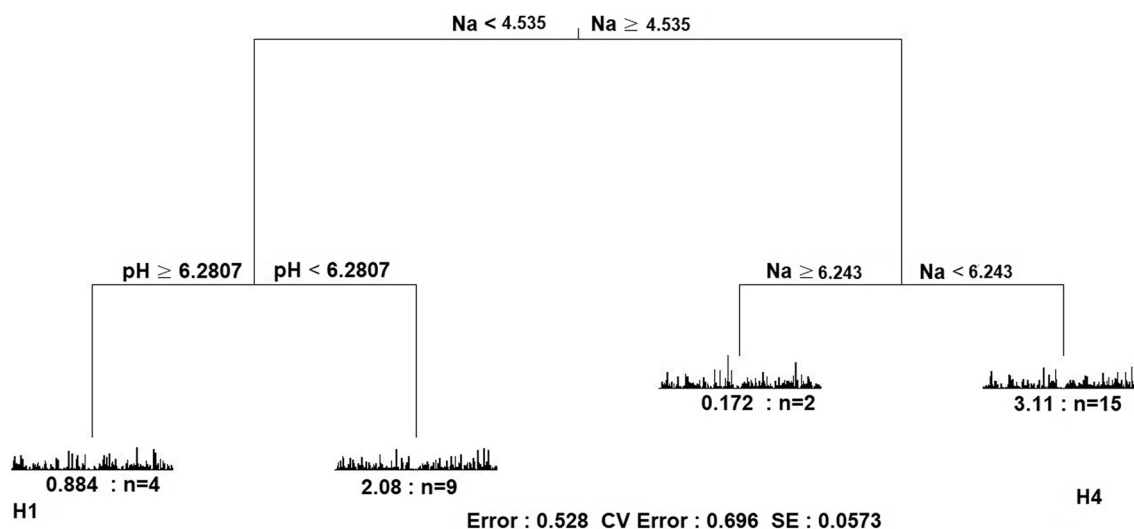


Fig. 2. Community habitat associations of the whole tree community. H1-H4 represents the four habitats given by the Multivariate regression tree; SE = standard error; CV Error = Error coefficient of variation; the bar graphs show the species abundance in each habitat; n = number of plots belonging to that habitat.

Table 1

Results of MRT analyses and identified indicators species for the whole tree community, tree size classes (i.e., large trees, understorey trees and small stems) in the 30 1-ha plots of Doume Forest Communal plot, Eastern Cameroon. CRVE: cross-validated relative error; Breakpoint for whole tree community, Large and Understorey trees: $pH \leq 6.245$, $Na < 4.535$ (H1), $pH > 6.245$, $Na < 4.535$ (H2), $4.535 \leq Na < 6.243$ (H3) and $Na \leq 6.243$ (H4); for Small stems: $CEC < 6.49$, $MC < 33.64$ (H1), $CEC < 6.49$, $MC \geq 33.64$ (H3), $CEC \geq 6.49$, $A < -0.82$ (H3), $CEC \geq 6.49$, $A \geq -0.82$ (H4).

Trees size groups	Habitat index	Total number of stem	Total stems in habitat	Total no species	No species per habitat	CRVE	No of sites	Stems per ha	Number indicator species
Whole tree community	1	22,064	3353	307	203	0.696	4	5547	12
	2		5695		169		9	5710	03
	3		1351		236		2	7281	09
	4		11,665		255		15	7248	05
Large trees	1	15,395	22,427	271	178	0.750	4	551	11
	2		4080		202		9	453	04
	3		953		152		2	477	08
	4		7935		228		15	529	05
Understorey trees	1	4567	654	242	117	0.786	4	314	06
	2		1012		154		9	216	01
	3		254		67		2	244	04
	4		2647		199		15	339	05
Small stems	1	2102	691	167	118	0.925	12	4607	1
	2		126		44		2	5040	0
	3		328		73		4	6560	0
	4		957		132		12	6380	1

Table 2

Percentage of species variation explained from two components for the whole tree community and the tree size classes (i.e., large trees, understorey trees, and small stems). MRT: multivariate regression trees

Variance explained by	Whole tree community	Large trees	Understorey trees	Small stems
MRT	37.23	37.45	25.68	26.76
Unexplained by MRT	62.77	62.55	74.32	73.24

Anthocleista schweinfurthii Gilg (Gentianaceae), *Elaeis guineensis* Jacq. (Arecaceae), *Ficus exasperata* Vahl and *F. mucoso* Welw. ex Ficalho (Moraceae), *Mallotus subulatus* Müll.Arg. (Euphorbiaceae) *Margaritaria discoidea* (Baill.) G.L.Webster (Phyllanthaceae), *Trichilia dregeana* Harv. & Sond. (Meliaceae) and *Uapaca guineensis* Müll.Arg. (Phyllanthaceae) contribute to 41.27 % of splits that form H1 and H2 (Fig. 2; Table 3). For node two, a contrario to node one, which splits defined H3 and H4, eleven species explained 63.97 % of its species variance, with 53.62 % explained by *Berlinia* sp. (Leguminosae-Caesalpinioideae), *Drypetes* sp. (Putranjivaceae), *Grossera macrantha* Pax (Euphorbiaceae), *T. dregeana* (Meliaceae), *Streblus usambarensis* (Engl.) Berg (Moraceae) etc. Among the species mainly contributing to the split that form the four habitats of the DCF plots, only *T. dregeana* (Meliaceae) and *Thomandersia hensii* De Wild. & T. Durand (Thomandersiaceae) were common to both nodes (Table 3).

3.2. Community-habitat associations across tree size groups

The habitats types generated for the different understorey and large trees classes were similar to the habitat types generated for the whole tree community described in the previous section. The MRT generated four different habitats types based mainly on soil parameters such as CEC, MC and A for the small stems class (Fig. 3; Table 1), while Na's concentration was responsible for the first split for habitat types for understorey and large trees classes (Fig. 4a-b, Table 1). In contrast, CEC was responsible for the first split for habitat types for small stems. For small, understorey, and large trees classes, the total species variance explained by the three nodes of the MRT were 26.76, 25.68, and 37.45 %, respectively, and CRVEs were 0.925, 0.786, and 0.750, respectively (Table 1-2).

Total species variance explained by the two node splits from the four habitats in the understorey, and large trees of the MRT represent 16.95, 13.75, and 17.43 %, respectively (Table 4-6). Twenty-two percent of the

total species variance of the large trees class was explained by the species *Annickia chlorantha*, *Anthocleista schweinfurthii*, *Ficus exasperata*, *F. mucoso*, *Mallotus subulatus*, *Margaritaria discoidea*, *Terminalia superba*, *Trichilia dregeana*, *Uapaca guineensis*, *Berlinia* sp., *Drypetes* sp., *Grossera macrantha* and *Streblus usambarensis* (Table 4). Additionally to these species for large trees class, *Annona* sp. (Annonaceae), *Anthonotha macrophylla* P.Beauv (Leguminosae-Caesalpinioideae), *Aptandra zenkeri* Engl. (Aptandraceae), *Celtis mildbraedii* Engl. C. *philippensis* Blanco (Cannabaceae), *Funtumia elastica* (Preuss) Stapf (Apocynaceae), *Hylodendron gabunense* Taub. (Leguminosae-Caesalpinioideae), *Monodora tenuifolia* Benth. (Annonaceae), *Myrianthus arboreus* Beauv. (Urticaceae), *Polyalthia suaveolens* Engl. & Diels (Annonaceae), *Pycnanthus angolensis* (Welw.) Exell (Myristicaceae) and *Staudtia kamerunensis* Warb. (Myristicaceae) explained 36 % of the species variation for nodes two and three in the understorey trees class (Table 5).

Forty-three percent of species variance for the small stems class was explained by the species *Memecylon* sp. (Melastomataceae), *Ochna* sp., *Rinorea* sp., *Sorindeia grandifolia*, *Strychnos* sp. and *Thomandersia hensii* (Table 6). Two species contributed mostly to explain this variance per node.

3.3. Indicator species analysis

Twenty-nine species were found as indicators that characterized the four habitat types within the whole species trees. The index value varies between 33 and 99 % within the four habitats, with few species per habitat type with index values above 75 %. Moreover, some species had a low index value and strongest significance than others with a high index value (Table 7). For the whole tree community, only *Antidesma membranaceum* Müll.Arg. (Phyllanthaceae), *Elaeis guineensis* Jacq. (Arecaceae) and *Occhthocosmus* sp. (Ixonanthaceae) species were found as strong indicators that are not common to the three size classes.

The number of indicators species for large trees was twenty-eight, while the understorey trees class has sixteen species. Only two species were strong indicators for habitats one and four for small stems. With an index value of 33 % ($p < 0.01$), *Microdesmis puberula* Hook.f. Ex Planch (Pandaceae), is the only strong indicator species characterizing the first habitat, while *Thomandersia hensii* (Thomandersiaceae) characterize the fourth habitat with an index value of 75 % ($p < 0.01$). Among the indicators species for the large trees class, *Anthocleista schweinfurthii*, with a highly significant ($p < 0.001$) and strong index value of 98 %, is one of the best species strongly characterizing the first habitat. For habitat two, *Aptandra zenkeri* Engl. (Aptandraceae) with a highly significant ($p < 0.001$) index value of 76 % is one of the best species indicators, while for

Table 3
Variance explained by splits nodes and the total tree of the whole tree community

Species	Species variance (%) explained by tree splits and the total tree						
	pH ≤ 6.245	7 ≤ pH > 6.245	Species node 2	Na ≥ 6.243	Na < 6.243	Species node 3	Total tree
<i>Albizia glaberrima</i>	0.15	0.08	1.20	0.00	0.00	0.00	0.23
<i>Albizia zygia</i>	0.12	0.02	2.17	0.00	0.00	0.00	0.14
<i>Annickia chlorantha</i>	0.03	0.15	3.25	0.00	0.00	0.00	0.18
<i>Annona</i> sp.	0.00	0.00	0.00	0.02	0.08	1.24	0.10
<i>Anthocleista schweinfurthii</i>	0.16	0.00	5.80	0.00	0.00	0.00	0.16
<i>Anthonotha macrophylla</i>	0.11	0.02	2.10	0.00	0.00	0.00	0.13
<i>Aptandra zenkeri</i>	0.04	0.10	1.77	0.00	0.00	0.00	0.14
<i>Barteria fistulosa</i>	0.01	0.11	2.27				0.12
<i>Berlinia</i> sp.				0.13	0.01	4.25	0.14
<i>Bridelia micrantha</i>	0.07		1.12				0.07
<i>Celtis adolfi-friderici</i>	0.05	0.13	1.55				0.18
<i>Drypetes</i> sp.	0.00	0.00		0.20	0.08	4.31	0.29
<i>Duboscia macrocarpa</i>	0.03	0.10	1.10				0.12
<i>Elaeis guineensis</i>	0.20	0.02	7.60				0.22
<i>Ficus exasperata</i>	0.12	0.00	3.05				0.12
<i>Ficus mucuso</i>	0.14	0.01	3.86				0.15
<i>Grossera macrantha</i>	0.00	0.00		0.36	0.08	25.02	0.44
<i>Hylo dendron gabunense</i>	0.00	0.00		0.04	0.10	1.15	0.13
<i>Lasiodiscus marmoratus</i>	0.00	0.00		0.12	0.06	1.13	0.17
<i>Macaranga hurifolia</i>	0.15	0.06	1.92	0.00	0.00		0.29
<i>Mallotus subulatus</i>	0.14	0.01	3.73	0.00	0.00		0.15
<i>Margaritaria discoidea</i>	0.18	0.01	6.13	0.00	0.00		0.19
<i>Milicia excelsa</i>	0.08	0.01	1.28	0.00	0.00		0.09
<i>Monodora tenuifolia</i>	0.00	0.00		0.06	0.13	1.63	0.19
<i>Myrianthus arboreus</i>	0.04	0.12	1.55	0.00	0.00		0.16
<i>Octolobus spectabilis</i>	0.00	0.00		0.12	0.04	2.05	0.17
<i>Polyalthia suaveolens</i>	0.05	0.15	2.24	0.00	0.00		0.19
<i>Psidium guajava</i>	0.07	0.00	1.02	0.00	0.00		0.07
<i>Pycnanthus angolensis</i>	0.24	0.16	1.27	0.00	0.00		0.40
<i>Rhizophora racemosa</i>	0.00	0.00		0.08	0.01	1.65	0.09
<i>Streblus usambarensis</i>	0.00	0.00		0.28	0.05	16.37	0.33
<i>Strombosia scheffleri</i>	0.02	0.12	2.27	0.00	0.00		0.14
<i>Terminalia superba</i>	0.18	0.08	2.61	0.00	0.00		0.26
<i>Thomandersia hensii</i>	0.07	0.00	1.01	0.00	0.07	1.50	0.14
<i>Trichilia dregeana</i>	0.12	0.23	3.19	0.12	0.23	3.67	0.70
<i>Uapaca guineensis</i>	0.07	0.21	4.66	0.00	0.00		0.09
Other species	7.58		30.28			36.03	10.81
Total species variance	12.10		100	3.13		100	17.71
				5.61			

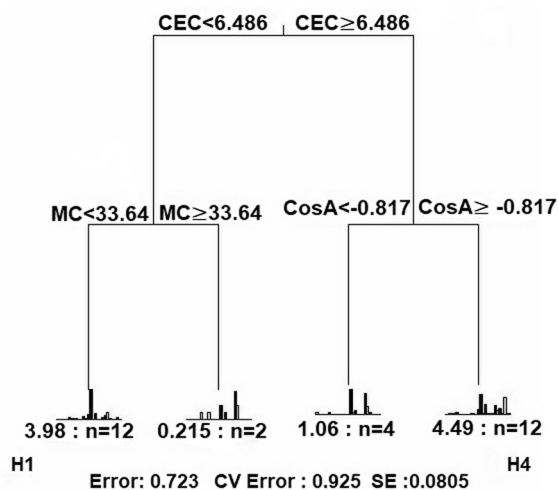


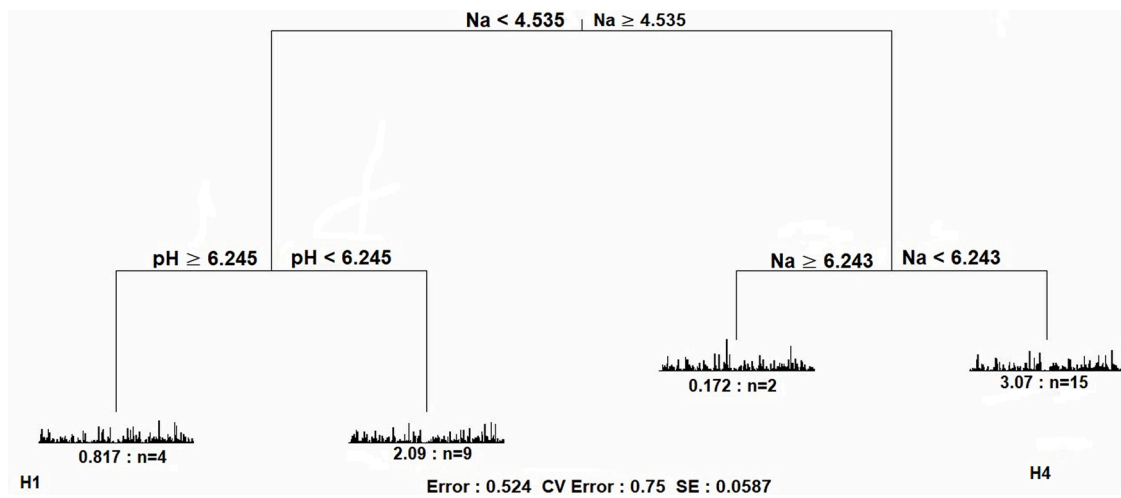
Fig. 3. Community habitat associations of the small stems. H1-H4 represents the four habitats given by the Multivariate regression tree; CEC = Cation Exchange Capacity; MC = moisture content; cosA = cosinus Aspect; SE = standard error; CV Error = Error coefficient of variation; the bar graphs show the species abundance in each habitat; n = number of plots belonging to that habitat.

habitat four, *Khaya grandifoliola* (Welw) C.DC. (Meliaceae) with a highly significant ($p < 0.001$) index value of 80 % were found to be among the best indicators. Within the third habitat, *Berlinia* sp. (Leguminosae-Caesalpinioideae) associate with *Rhizophora racemosa* G.F.W. Meyer (Rhizophoraceae) and *Chrysophyllum perpulchrum* Mildbr. Ex Hutch. & Dalziel (Sapotaceae) are among the best species characterizing this habitat (index values > 89 %, $p < 0.001$).

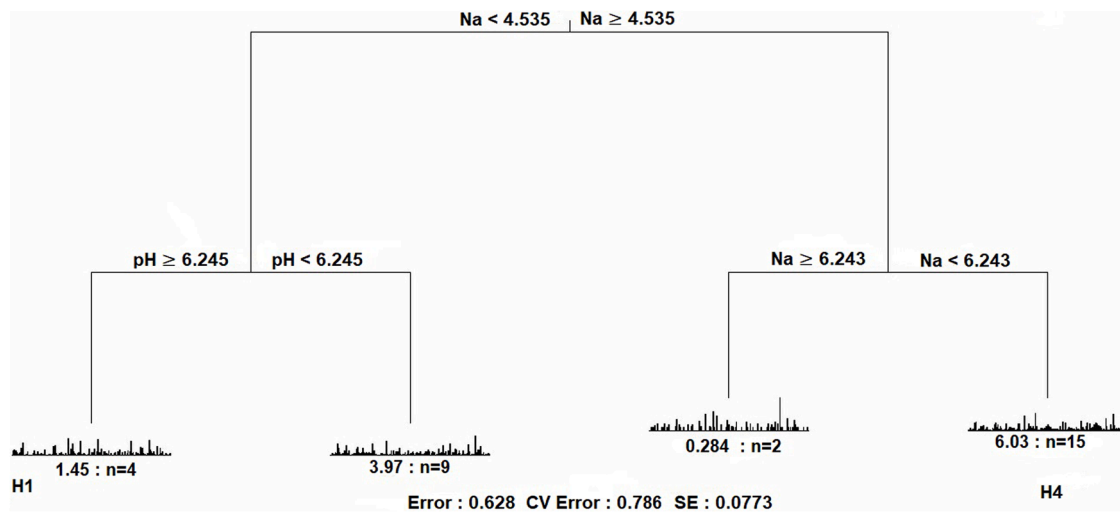
Further, some strong or moderate indicator species within the large trees class changed to either non-indicator or intermediate indicator species in the understorey trees class. Two species of the genus *Anthonotha* (*A. macrophylla* and *A. lamprophylla*) and *Mallotus subulatus* Müll. Arg. (Euphorbiaceae) are among the best species indicators that strongly characterize the first habitat within the understorey trees group. Within the second habitat of the understorey's trees class, only *Annickia chlorantha* (Oliv.) Setten & Maas appear to be the strongest species ($p < 0.001$) despite their moderate index value of 0.57 (Table 7). For the fourth habitat, *Celtis philippensis* is the best and the strongest species indicator. In contrast, for the third habitat, *Berlinia* sp., *Mansonia altissima* and *Grossera macrantha* with at least 0.80 index values each appear to be among the best species indicators.

3.4. Abundance and species richness variation among habitats

Despite the imbalance between the numbers of plots constituting each habitat within the different trees size classes, no variation in the number of species was found. In contrast, for trees species abundance, a



(a)



(b)

Fig. 4. Community habitat associations of: (a) the large trees size class (b) and understorey trees size class. H1-H4 represents the four habitats given by the Multivariate regression tree; SE = standard error; CV Error = Error coefficient of variation; the bar graphs show the species abundance in each habitat; n = number of plots belonging to that habitat.

slight difference was found. Within the large and understorey trees class, habitat 1 ($pH \leq 6.245$; $Na < 4.535$) and habitat 4 ($Na \geq 6.243$) have high average abundance stem values per hectare than the other habitats. Among the small stems class, the two habitats types with the highest trees abundances were the high CEC and influence of Aspect habitat three and habitat 4 with approximately 6560 and 6380 stems ha^{-1} , respectively (Table 1).

4. Discussion

In a forest ecosystem characterized by its vertical components (i.e., forest strata) and horizontal components (i.e., light levels, groundwater, soil properties, etc.), tree species' co-existence can be promoted by the spatial heterogeneity of the environment. Topo-edaphic gradients in DCF play a fundamental role in shaping plant species distributions as found in other forests elsewhere (Webb and Peart, 2000, Baldeck et al., 2013a). Using MRT, the 30 1-ha plots in the DCF were found to be structured into four habitats types primarily by edaphic variables, and

that habitat types change with tree size classes, contrary to the results of other tropical (Punchi-Manage et al., 2013) and subtropical forests (Wang et al., 2017). Among edaphic variables, soil pH and Na concentrations were the two most important factors related to local species composition within the whole tree community and tree size classes, except for small stems where CEC concentration, soil moisture content (MC), and aspect were the most critical topo-edaphic variables. Applying the similar methods, the long-term tropical forest dynamics plots of the Center for Tropical Forest Science (CTFS) network were divided into five habitats (Baldeck et al., 2013a). Contrary to our results, these authors found topography as the most important abiotic factor causing spatial variation in the tropical forest structure since it is commonly correlated with other critical environmental variables, notably the groundwater regime and the soils physical and chemical properties. The low topographical gradients across DCF plots may explain these differences.

The species assemblage variance explained by topo-edaphic variables in the DCF plot (37.23 %) was higher than that in Sinharaja (22.73

Table 4
Variance explained by species per splits, nodes and the tree of large trees class

Species	Species variance (%) explained by tree splits and the total tree						
	pH ≤ 6.245	pH > 6.245	Species node 2	Na ≥ 6.243	Na < 6.243	Species node 3	Total tree
<i>Annickia chlorantha</i>	0.03	0.15	3.51	0.00	0.00		0.18
<i>Anthocleista schweinfurthii</i>	0.16	0.00	5.92	0.00	0.00		0.16
<i>Berlinia</i> sp.	0.00	0.00		0.13	0.01	4.47	0.14
<i>Drypetes</i> sp.	0.00	0.00		0.20	0.08	4.31	0.28
<i>Ficus exasperata</i>	0.12	0.00	3.54	0.00	0.00		0.12
<i>Ficus mucoso</i>	0.15	0.01	4.51	0.00	0.00		0.16
<i>Grossera macrantha</i>	0.00	0.00		0.36	0.08	25.20	0.44
<i>Mallotus subulatus</i>	0.14	0.00	4.22	0.00	0.00		0.14
<i>Margaritaria discoidea</i>	0.19	0.01	7.13	0.00	0.00		0.20
<i>Pycnanthus angolensis</i>	0.25	0.17	1.69	0.00	0.00		0.42
<i>Streblus usambarensis</i>	0.00	0.00		0.28	0.05	16.52	0.33
<i>Terminalia superba</i>	0.19	0.08	3.16	0.00	0.00		0.27
<i>Trichilia dregeana</i>	0.12	0.23	3.27	0.12	0.23	3.86	0.70
<i>Upaca guineensis</i>	0.07	0.21	4.85	0.00	0.00		0.28
Other species	9.43		58.20			45.64	13.61
Total species variance	11.71		100	4.18			17.43
				5.72			

Table 5
Variance explained by species per splits, nodes and the total tree of understorey trees class

Species	Species variance (%) explained by a tree, splits, species nodes and the total tree						
	pH ≤ 6.245	pH > 6.245	Species node 2	Na ≥ 6.243	Na < 6.243	Species node 3	Total tree
<i>Annickia chlorantha</i>	0.02	0.18	5.85	0.00	0.12	2.42	0.32
<i>Annona</i> sp.	0.01	0.07	1.82	0.00	0.08	1.28	0.16
<i>Anthocleista schweinfurthii</i>	0.10	0.00	2.56	0.00	0.00	0.00	0.10
<i>Anthonotha macrophylla</i>	0.19	0.01	7.82	0.00	0.00	0.00	0.20
<i>Aptandra zenkeri</i>	0.05	0.14	2.16	0.00	0.00	0.00	0.19
<i>Celtis mildbraedii</i>	0.02	0.12	2.47	0.16	0.08	1.19	0.38
<i>Celtis philippensis</i>	0.00	0.00	0.00	0.00	0.12	2.52	0.12
<i>Ficus exasperata</i>	0.09	0.00	2.08	0.00	0.00	0.00	0.09
<i>Funtumia elastica</i>	0.17	0.06	2.90	0.00	0.00	0.00	0.23
<i>Grossera macrantha</i>	0.00	0.00	0.00	0.13	0.04	11.39	0.17
<i>Hylodendron gabunense</i>	0.22	0.10	3.03	0.00	0.00	0.00	0.32
<i>Mallotus subulatus</i>	0.24	0.02	10.52	0.00	0.00	0.00	0.26
<i>Margaritaria discoidea</i>	0.09	0.00	2.05	0.00	0.00	0.00	0.09
<i>Monodora tenuifolia</i>	0.00	0.00	0.00	0.00	0.13	3.06	0.13
<i>Myrianthus arboreus</i>	0.00	0.00	0.00	0.00	0.12	2.43	0.12
<i>Polyalthia suaveolens</i>	0.02	0.14	3.51	0.00	0.15	3.97	0.31
<i>Pycnanthus angolensis</i>	0.00	0.00	0.00	0.00	0.11	2.23	0.11
<i>Staudtia kamerunensis</i>	0.00	0.00	0.00	0.00	0.11	2.23	0.11
<i>Streblus usambarensis</i>	0.11	0.00	2.75	0.50	0.08	31.43	0.69
<i>Trichilia dregeana</i>	0.14	0.29	5.41	0.16	0.25	1.54	0.84
Other species	4.89		45.07			34.31	8.81
Total species variance	7.49		100	3.92		100	13.75
				6.26			

Table 6
Variance explained by species per splits, nodes, and the total tree of small stems. MC: soil moisture content; A: aspect of the terrain

Species	Species variance (%) explained by a tree, splits, species nodes, and the total tree						
	MC > 33.64	MC ≤ 33.64	Species node 2	A < -0.8175	A ≥ 0.8175	Species node 3	Total tree
<i>Memecylon</i> sp.	0.12	0.00	2.11	0.00	0.12	3.94	0.24
<i>Microdesmis puberula</i>	0.76	0.37	22.81	0.63	0.51	3.44	2.27
<i>Ochna</i> sp.	0.00	0.00	0.00	0.09	0.26	8.38	0.35
<i>Rinorea</i> sp.	0.10	0.72	58.67	0.53	0.23	24.34	1.58
<i>Sorindeia grandifolia</i>	0.19	0.37	4.76	0.21	0.10	3.12	0.87
<i>Strychnos</i> sp.	0.00	0.00	0.00	0.04	0.16	3.52	0.20
<i>Thomandersia hensii</i>	0.00	0.00	0.00	0.00	0.43	49.02	0.43
Other species	5.97		11.65			4.24	7.81
Total species variance	8.60		100	5.03		100	13.75
				8.34			

Table 7

Results of indicators species analysis for the whole tree community and trees size class. * $p < 0.05$; ** $p < 0.01$ *** $p < 0.001$.

Species	Whole tree community		Large trees		Understory trees	
	Habitat index	Index value	Habitat index	Index value	Habitat index	Index value
<i>Albizia adianthifolia</i>	1	0.72**	1	0.72**	1	0.75**
<i>Albizia glaberrima</i>			1	0.46*		
<i>Albizia zygia</i>	1	0.59*	1	0.60*	1	0.42*
<i>Annickia chlorantha</i>	2	0.38*	2	0.38**	2	0.57***
<i>Annona</i> sp.	4	0.49*	4	0.49*		
<i>Anthocleista schweinfurthii</i>	1	0.99***	1	0.98***	1	0.50*
<i>Anthonotha lamprophylla</i>	3	0.52*	3	0.52*	1	0.87***
<i>Anthonotha macrophylla</i>	1	0.68***	1	0.68***	1	0.87***
<i>Antidesma membranaceum</i>	3	0.47*				
<i>Aptandra zenkeri</i>	2	0.77*	2	0.76*	2	0.67*
<i>Barteria fistulosa</i>	2	0.58***	2	0.58**		
<i>Berlinia</i> sp.	3	0.91***	3	0.91***	3	0.89***
<i>Bridelia micrantha</i>	1	0.88***	1	0.88***		
<i>Caloncoba glauca</i>					1	0.38*
<i>Ceiba pentandra</i>					1	0.50*
<i>Celtis philippensis</i>	4	0.61***	4	0.61***	4	0.93***
<i>Celtis zenkeri</i>	3	0.5**	3	0.50**		
<i>Chrysophyllum boukokoense</i>	4	0.48**	4	0.49**		
<i>Chrysophyllum lacourtianum</i>	2	0.42*	2	0.42*		
<i>Chrysophyllum perpulchrum</i>	3	0.89**	3	0.89**		
<i>Cola pachycarpa</i>	2	0.44*	2	0.44*		
<i>Detarium macrocarpum</i>	3	0.57*	3	0.57*		
<i>Diospyros suaveolens</i>	4	0.52*	4	0.52*		
<i>Dracaena arborea</i>	2	0.50*	2	0.50*		
<i>Drypetes</i> sp.	3	0.62**	3	0.70***	3	0.58**
<i>Duboscia macrocarpa</i>	4	0.36*	4	0.36*		
<i>Duguetia staudtii</i>	4	0.45*	4	0.45*		
<i>Elaeis guineensis</i>	1	0.69**				
<i>Ficus exasperata</i>	1	0.76**	1	0.76**	1	0.75**
<i>Ficus mucoso</i>	1	0.71**	1	0.72**		
<i>Funtumia elastica</i>					1	0.44*
<i>Gossweilerodendron balsamiferum</i>	3	0.62**	3	0.62**		
<i>Grossera macrantha</i>	3	0.82***	3	0.82***	3	0.88***
<i>Homalium</i> sp.	4	0.40*	4	0.40*	4	0.47**
<i>Hylodendron gabunense</i>					1	0.57**
<i>Irvingia gabonensis</i>					3	0.68*
<i>Khaya anthotheca</i>	3	0.75**	3	0.75**		
<i>Khaya grandifoliola</i>	4	0.8***	4	0.80***		
<i>Klainedoxa gabonensis</i>	4	0.39**	4	0.39**		
<i>Lasiodiscus marmoratus</i>	3	0.43*	3	0.42*		
<i>Leplaea cedrata</i>	3	0.46*	3	0.46*		
<i>Leplaea thompsonii</i>	4	0.35*	4	0.35*		
<i>Macaranga hurifolia</i>	1	0.49*	1	0.50*		
<i>Mallothus subulatus</i>	1	0.88***	1	0.88***	1	0.86**
<i>Mansonia altissima</i>	3	0.46*	3	0.45**	3	0.83**
<i>Margaritaria discoidea</i>	1	0.87***	1	0.87***	1	0.66*
<i>Millicia excelsa</i>	1	0.59*	1	0.59*		
<i>Millettia mannii</i>	1	0.60*	1	0.61*		
<i>Monodora tenuifolia</i>	4	0.45*	4	0.45*	4	0.54*
<i>Morinda lucida</i>	1	0.72**	1	0.73***		
<i>Myrianthus arboreus</i>					4	0.54**
<i>Ochthocosmus</i> sp.	4	0.6*				
<i>Pachylobus trimerus</i>	2	0.39*	2	0.38*		
<i>Persea americana</i>	1	0.75**	1	0.75**		
<i>Phyllocosmus africanus</i>	2	0.56**	2	0.56**		
<i>Polyalthia suaveolens</i>	4	0.35*	4	0.35*	4	0.45*
<i>Polyscias fulva</i>	1	0.57*	1	0.58*		
<i>Pterygota macrocarpa</i>					3	0.62*
<i>Pycnanthus angolensis</i>	1	0.39*	1	0.40*	1	0.44*
<i>Rauvolfia caffra</i>	1	0.53*				
<i>Rauvolfia vomitoria</i>	3	0.49*	3	0.49*		
<i>Rhizophora racemosa</i>	3	0.90**	3	0.90***		
<i>Sorindeia grandifolia</i>	4	0.36*	4	0.36*		
<i>Staudtia kamerunensis</i>	4	0.44**	4	0.44**	4	0.67***
<i>Streblus usambarensis</i>	3	0.71**	3	0.70*	3	0.73*
<i>Strombosia pustulata</i>	3	0.48*	3	0.48*		
<i>Strombosia scheffleri</i>			2	0.48*		
<i>Synsepalum dulcificum</i>	4	0.55*				
<i>Terminalia superba</i>	1	0.45**	1	0.46**		
<i>Theobroma cacao</i>	1	0.5*	1	0.50*		
<i>Thomandersia hensii</i>	1	0.49*			4	0.73**
<i>Trichilia dregeana</i>	2	0.33*	2	0.33*	2	0.34*
<i>Uapaca guineensis</i>	2	0.58**	2	0.57***		

%), and BCI (20.8 %) plots obtained by [Punchi-Manage et al., \(2013\)](#). Several reasons may explain these differences. First, the sample size may reduce unexplained variance, and that has been demonstrated by several findings ([Punchi-Manage et al., 2013](#), [Wang et al., 2017](#)). Second, the higher explanatory power of topo-edaphic habitats in the DCF plot may suggest more substantial soil properties' driving forces for tree communities assembly than in these forests. Hence, these results agree with findings in tropical forest dynamics plots of the CTFS, highlighting that adding soil characteristics in topographic variables increases species variance composition ([Baldeck et al., 2013a](#)). However, the species variance obtained in the present study is similar to the value of 34 % obtained in a subtropical forest in China ([Wang et al., 2017](#)), suggesting that the topography gradient may play a significant role.

There is still essential unmeasured environmental variation (i.e., light, drainage) that contributes to the species assemblages in these forests. Indeed, variables such as drainage, which exhibit spatial variation over larger spatial scales (hundreds of meters), may contribute to the spatially structured variation yet unexplained by our environmental variables set. Hence, the unexplained proportion of spatially structured variance and remains unaccounted by either soil or topographic variables suggests an essential role for dispersal-assembly alongside habitat niche processes in community structure in this forest. Also, this study highlights the importance of soil properties on the tree assemblages, as mentioned in previous research ([John et al., 2007](#), [Baldeck et al., 2013b](#)).

The distribution and growth of plant species are conditioned mainly by soil chemical properties ([Dubuis et al., 2013](#)). Effectively, across the whole tree community and the tree size classes, except for the small stems class, two edaphic factors were found responsible for habitat structuring at the DCF plot: the cations Na^+ and the pH.

Firstly, the concentrations of Na^+ are the ones that contributed significantly to the formation of the tree, giving the fourth habitat, and it is also the one influencing the scission of nodes giving habitats 3 and 4 for all size classes except for small stems class. The plant community analysis of the four habitats showed that habitats 3 and 4 have high species richness, tree densities, and many species indicators for the whole tree community, the large and understorey trees classes (see [Table 1](#)). In nature, plant communities are exposed to a substrate with a wide range of saline statut. However, Na is unusual as a mineral nutrient for plant life, although it may be a beneficial element at low concentrations or essential for certain plants ([Kronzucker et al., 2013](#), [Adams and Shin, 2014](#)), where it plays a role in the regulation of turgor pressure and cell expansion ([Haro et al., 2013](#)). In many cases, excessive Na concentrations in plant tissues affect plant fitness, especially in plants highly sensitive to salt stress ([Islam et al., 2019](#)). Hence, the observed increased abundance value of plants with increased soil Na content suppose the range of Na concentrations in the studied area (DCF) is well below the threshold of Na toxicity for common plants, where the Na beneficial effects are still effective.

Although nonessential for most plants, Na is an essential element for animals and decomposers ([Kaspari, 2020](#), [Welti and Kaspari, 2021](#)). With this in mind, we cannot rule out the possibility the higher species abundance in habitats rich in soil Na could be associated with a higher activity of decomposers (macro- and microorganisms), leading to a more efficient turnover of soil organic matter, thus a better provision of mineral nutrients and humus for plant growth in those habitats (H3 and H4). Validation of this assertion is warranted in further investigations in an attempt to explore the unexplained variance detected in this study.

Overall, results show that the habitats conditioned by the intermediate and higher concentrations in Na may be well suited for low-growing canopies tree species such as *Celtis philippensis*, *Drypetes* sp., *Homalium* sp., *Mansonia altissima*, *Monodora tenuifolia*, *Staudtia kamerunensis* and *Streblus usambarensis*, which reach high understorey and large trees densities in these habitats.

Besides Na content, the second soil edaphic parameter structuring habitat species association was the pH. While plants may survive in a

wide range of soil pH, it is well established that the pH values ranging from 5.5 to 6.5 are optimal for plant growth, as the availability of nutrients is optimal. Moreover, regarding their growth rate within this pH range, plants are more likely to produce more root exudates, which serve as a carbon source necessary for the survival and soil microorganisms. Correspondingly, this pH range (5.5–6.5) is also optimal for soil microorganism activity ([Msimbira and Smith, 2020](#)).

In contrast to large trees and understorey stems classes, CEC was the primary determinant variable accounting for community structure response for the small stems class. Basically, the influence of CEC value on plant growth is two folds. Firstly, in soil sciences, CEC is considered mostly for its impacts on nutrients retention in the soil matrix. A lower soil CEC predisposes the habitat to lost nutrients following soil organic matter minerals, which results in an insufficient stock of mineral nutrients. Moreover, a low CEC is commonly associated with a higher potential for soil acidification, rendering mineral nutrients less available for plant nutrition ([Clark et al., 2007](#)). This clearly explains the observation of higher species abundance values in habitats H3 and H4 ([Table 1](#)), where higher CEC (>6.48) are recorded ([Fig. 3](#)).

This study showed that habitats' variance increased during the transition from small stems and understorey to large trees classes, and the CVRE decreased. Also, it has been shown that small stems density increases following canopy opening, gaps are often even sites of high species diversity ([Denslow, 1995](#)). However, the explained differences in variance and CVRE were tiny, indicating that during the transition from small stems to understorey trees and from understorey trees to large trees, stochastic effects outweighed the effects of filtering and competition from the habitat or filtering and habitat competition processes counterbalanced each impact. This result was also found in the tropical forest of CTFS, and they attribute that to neutral mortality rather than habitat filtering ([Baldeck et al., 2013b](#)).

Across different tree size classes, except for small stems, topographic and edaphic habitats types were relatively stable. This constancy in habitat types may be because species suffer substantial seed dispersal limitations that cause understorey trees to locate large trees nearby ([Webb and Peart, 2000](#)). In DCF, almost all indicator species for the large trees habitats were also indicators for understorey tree habitats.

5. Conclusion

Here, we aimed to understand better how low environmental gradient shaped community structure in a tropical forest. Four distinct species-habitat associations for the whole tree community and the tree size groups of the 30 1-ha plots were found in this study. Surprisingly, these species-habitat associations were shaped by soil parameters (i.e., Na and pH) for the whole tree community, the large and understorey tree's size, and CEC for the small stems size class. Furthermore, this study found species variances range from 25% to 37%, suggesting the existence of essential unmeasured environmental variations that contribute to the assemblages of species in this forest. The intriguing influence of Na on shaping community structure at the whole tree community and tree size groups found in this study suggests some general functional strategies that might correspond to diversification events which may account for the unexplained variance in the formation of species-habitat associations in the Doume communal forest. Hence, it is suspected that environmental factors and/or processes under the influence of soil Na content might be determinants in dictating the structure of the plant community in the semi-deciduous tropical rainforest, which needs to be validated.

CRedit authorship contribution statement

Jules Christian Zekeng: Conceptualization, Methodology, Data curation, Writing – original draft. **Jean Louis Fobane:** Data curation, Writing – review & editing. **Maginot Ngangyo Heya:** Data curation, Writing – review & editing. **Rozane Wandji Sakou:** Data curation,

Writing – review & editing. **Theodore Mulembo Mwamba:** Writing – review & editing. **Wanda N. Mphinyane:** Supervision, Writing – review & editing. **Reuben Sebego:** Supervision, Writing – review & editing. **Marguerite Marie Mbolu:** Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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