Multiple Stable Dominance States in the Congo Basin Forests

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Abstract: Understanding the dynamics of dominant tree species in tropical forests is important both for biodiversity and carbon-related issues. We focus on the Congo Basin (East of Kisangani) to investigate the respective roles of topographic/soil gradients and endogenous dynamics in shaping local variations in dominance. We used a dataset of 30 1-ha plots, in which all trees above 10 cm diameter at breast height (DBH) were censused. Soil samples were analyzed for standard pedologic variables and a digital elevation model permitted to infer topography and hydromorphy. We found that this forest is characterized by variations in the abundance of three dominant species: *Petersianthus macrocarpus* (P.Beauv.) Liben (PM), *Gilbertiodendron dewevrei* (De Wild.) J.Leonard (GD) and *Julbernardia seretii* (De Wild.) Troupin (JS). These variations occur independently of substratum or topography variations. At plot level, the local relative abundance never reached 50%, the threshold for monodominance proposed in the literature, but rather progressively increased to reach higher values for canopy trees (>60 cm DBH), where this threshold could be exceeded. We found no sign of shifting compositional dynamics, whereby the dominant species would switch between the canopy and the undergrowth. Our results, therefore, support the possibility of the existence of stable dominance states, induced by endogenous processes, such as biological positive feedbacks fostering monodominance. We also document a strong relation between monodominance level and alpha diversity, when giving more weight to abundant species which is expected ($R^2 = 0.79$) but also when giving more weight to rare species ($R^2 = 0.37$), showing that monodominance influences tree species richness patterns. Structural differences existed between groups, with the PM group having more (and on average smaller) stems and lighter wood on average, but paradoxically also higher biomass and basal area.

Keywords: DR Congo; forest dynamics; *Gilbertiodendron dewerei*; *Julbernadia seretii*; monodominance; soil; succession; *Petersianthus macrocarpus*

1. Introduction

The study of tree assemblages in tropical forests is gaining new impetus with the need to assess carbon emissions at high precision and resolution, while limiting the erosion of diversity and promoting sustainable forest management [1–3]. Heterogeneity in forest composition, diversity and structure is present at all spatial scales. Broad biogeographic variations can be linked to

speciation, extinction and migration events [4–6], climatic gradients, and the influence of specific geomorphological contexts inducing extreme edaphic conditions (e.g., hydromorphy or flooding, poor sandy soils, salinity, etc.) [7–11]. Identifying the drivers of forest heterogeneity at local (landscape) scales, over milder environmental gradients, requires careful analysis. The ecological literature is replete with possible mechanisms of deterministic or stochastic, endogenous or exogenous nature, leading to more or less stable variations in diversity and composition. Patches of contrasted composition could be induced by chance events leading to a random drift driven by stochastic mortality and recruitment [4], by deterministic processes such as biological feedbacks (e.g., density dependent dynamics) and interactions, or simply by the blueprint of soil and topographic variations acting as a filter on the adapted species. Time can also play a major role, via perturbations and succession, which can lead to a locally patchy, but overall homogeneous landscape [12]. These different mechanisms need not be happening independently of each other. For instance, biological feedback along successional gradients will alter both edaphic and (micro-) climatic conditions, leading in some cases to similar climax vegetation from different initial edaphic conditions [13]. Given this overwhelming complexity, how can we hope to glean the necessary pieces of understanding that could help in orienting management or conservation? Can a portion of the heterogeneity in lowland *terra firme* forests, outside blatantly extreme edaphic conditions, be considered as relatively stable and unambiguously driven either by exogenous (e.g., edaphic) or endogenous (e.g., biotic) processes, or is it all the result of chance dispersion or perturbation events and hence perpetually drifting [4]?

The case of monodominant tropical forests has been the focus of sustained research efforts over the past few decades, because they stand as a particularly prominent feature among otherwise very diverse forests. The quantitative definition of monodominance may be quite subjective: a 50% relative abundance threshold for trees > 10 cm diameter at 1.3 m breast height (DBH) has been proposed [14,15], but a recent meta-analysis in the Amazon region suggests this threshold might be too restrictive [16]. Dominance is obviously a continuous measure, but setting thresholds is useful for inter-comparisons and classification purposes. In any case, focusing on monodominant forests might help understanding crucial processes in more diverse forests. Questions indeed immediately arise regarding the different mechanisms listed earlier. Are these patches located in peculiar topographic/edaphic positions? Among the different types of monodominance described by [14], does the dominant species remain persistent for numerous tree generations (type I) or is the monodominant state an early successional category (Type II) or the result of mostly stochastic demographic and limited dispersion events? What biological feedback mechanisms might be at play? Mycorrhizae or allelopathy are often cited [17]. What about the apparent violation of the negative density-dependence [18,19]? Are monodominant patches expanding over surrounding forests, or is the mosaic stabilized by some feedback mechanisms?

A particularly studied case is that of widespread monodominance occurring across central African forests, with species like *Gilbertiodendron dewevrei* (De Wild.) J. Leonard or *Julbernardia seretii* (De Wild.) Troupin (Fabaceae-Caesalpinioideae) covering sometimes very extensive, although patchy extends across the Congo Basin and its surroundings [20,21]. According to [22] no less than two-thirds of the Northeastern part of the Congo Basin forest would in fact be covered by monodominant forests. Soil chemical fertility has not been found to be significantly different from surrounding forest types [23–25] apart from organic matter content [25], and geomorphological (catena) positions can also be considered to be similar [15,26,27]. Although [28] showed that some tree species were sensitive to edaphic gradients (from sandy to clayey soil) near Kisangani (DRC), these gradients did not seem to affect dominant species. In another study in Cameroon, ([29] *in review*) the authors also noticed that soil effects tend to influence relatively rare species, but not the most common ones. Therefore, the role of soil-related properties on monodominance seem little supported outside of extreme environments (swamps, white sands, etc.).

The general question addressed here pertains to the possible endogenous nature of forest dominance patterns, the stability of the different states, and their consequences in terms of biomass (carbon stocks) and biodiversity. In the absence of long term sylvicultural experiments, only macroecological (correlative)

approaches can offer clues about processes driving monodominance in the Congo basin. The forests around Kisangani (DRC) present contrasted compositional and structural patterns hosting interlaced patches of mixed-species forest stands and monodominant stands of *G. dewevrei* and/or *J. seretii* [30]. The soils are also heterogeneous both at the landscape and at fine-scales [25,28]. We established 30 one-hectare tree plots with the aims to identify: (1) floristic groups characterized by dominant species, (2) local environmental drivers (soil, topography and forest stand attributes) potentially affecting floristic composition and (3) trends in composition across diameter size classes. We tested the hypothesis that variation in the local abundance of different dominant species is independent of environmental drivers (i.e., classical monodominance, sensu [17]) but possibly a signal of successional stages. Parallel to the question of drivers of local compositional dominance, we also document variations in forest stand attributes (stem density, basal area, above-ground biomass, the quadratic mean diameter and community wood density) and alpha diversity between the compositional groups in comparison with peculiarities noted by previous studies [31–33].

2. Material and Methods

2.1. Study Site

Data for this study were collected in a lowland moist dense tropical forest in the northeast of the Central Congo Basin, referred to as the Cuvette Centrale. Shown in Figure 1, the site is situated 79 km East of Kisangani between 0°25′34″–0°34′51″N; 25°46′25″–25°53′10″E, covering an area of 260 km². The forest is mostly semideciduous but evergreen monodominant stands of *Gilbertiodendron dewevrei* and *Julbernadia seretii* are common [30]. The climate is of the tropical rainforest type, *Af* in Köppen [34,35]. Two rainy seasons are distinguished with mean monthly precipitation above 100 mm and an annual average of 1772 mm and one dry season (December to February) with monthly precipitation lower than 100 mm [36,37]. Average daily temperature is 25.2 °C. Ferralitic soils dominate nonhydromorphic areas [25] and the topography is characterized by rocky outcrops (inselbergs) and sandy plateaus in the South. The local hydrographic network is led by the Selesele River which collects surrounding waters from the south and flows into the Tshopo River which is the largest in the study area. The latter cuts across the area in its northernmost part and is responsible for large alluvial or clay deposits.
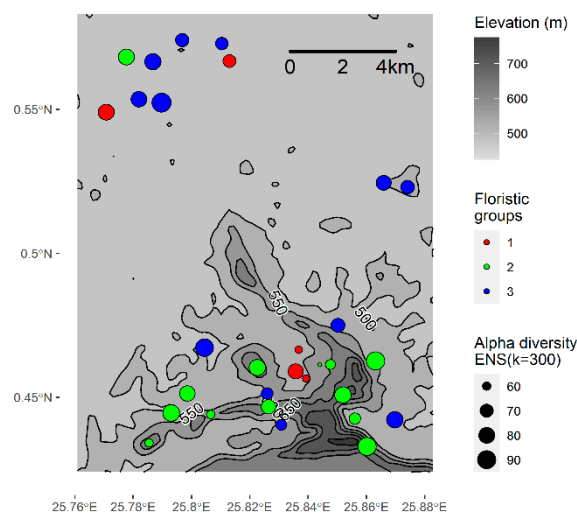

Figure 1. Distribution of one-hectare plots along an altitudinal gradient. Dots represent 1-ha plots; dot sizes are proportional to alpha diversity and colors represent plots within the same *k*-means derived groups.

2.2. Plot Establishment and Tree Census

We established thirty noncontiguous 100 m × 100 m (1-ha plot) distributed around the study area along altitudinal transects, as shown in Figure 1. To do this, we first surveyed a 100 m square area by placing stakes at the four corners of the intended area. Subsequently, we divided the 100 m square area into 25 quadrats of 20 m square each while avoiding destruction of all woody plants, using a Suunto® KB14 compass (Suunto ®, Vantaa, Finland) and measuring tapes. A consumer grade Garmin® 62 GNSS device (Garmin®, Olathe, KS, USA) was used to geolocate each 1-ha plot, by recording positions every 20 m around the plot contour to attenuate the effect of signal scattering in the vegetation [38]. We then censused all trees by the following methods: (i) the diameter of all woody stems (excluding lianas) ≥ 10 cm at 1.3 m breast height (DBH) or above buttresses and deformations was measured using a diameter tape. (ii) Maximum height of at least 40 trees within each 1-ha plot across the full DBH range was measured using a Trimble® LaserAce™ 1000 rangefinder (Trimble®, Westminster, CO, USA). The sine method was used to measure maximum tree height [39], which is done by standing at a given distance from the tree and open canopy, using the LaserAce™ 1000 rangefinder to measure the distance to the top and base of the tree and the angles from horizontal. (iii) We identified all trees to species level based on our field experience but also collected botanical samples for herbarium verification. All voucher specimens are stored at the University of Kisangani and the herbarium of the Université Libre de Bruxelles (BRLU). Nomenclature of plant families follows the Angiosperm Phylogeny Groups IV [40] and species names are according to the 2016 African Plants Database (version 3.4.0) [41].

2.3. Soil Data

Four soil samples were collected along the central diagonal of each plot. We focused soil collection on the upper 0–30 cm layer (excluding litter) to make comparisons with other local and regional studies ([29] *in review*). We collected 60 g from each point and 120 soil samples in total from the 30 1-ha plots. Each sample was numbered, separately air-dried and sieved with a 2 mm sieve prior to analyzing soil textural properties and a 0.5 mm sieve prior to analyzing chemical properties of the soil. The percentage proportion of clay (%, < 2 μm), silt (%, 2–50 μm) and sand (%, 50 μm–2 mm) were obtained by pipette sedimentation column. Soil pH was measured by 1:2.5 soil:deionized water ratio. Total organic carbon (C g/100) and total nitrogen (N g/100) were first analyzed by dry combustion and measured using a thermal conductive detector. Available phosphorus (P mg/kg) was extracted at pH 8.5 using 0.5 M ammonium fluoride and 0.5 M sodium bicarbonate via the spectrometric method. The concentration of calcium (Ca mg/kg), magnesium (Mg mg/kg) and potassium (K mg/kg) were extracted during saturation using 1M ammonium acetate and the residues were washed with ethyl alcohol. Soil analysis was conducted in the Laboratoire pédologique de l'Institut Facultaire des Sciences Agronomiques de Yangambi (IFA-Yangambi, DR Congo).

2.4. Topographic Data

We used the centroids of the 20 GPS coordinates of each 1-ha plot (see Section 2.2) to extract four variables proxies of local topography and hydromorphy, namely, the height above nearest drainage (HAND) index [42], topographic moisture index (TMI) [43], plot altitude, flow accumulation and slope. Data for these variables were at 1-arc second (30-m) resolution from Shuttle Radar Topography Mission (SRTM). This was obtainable at USGS-EarthExplorer (https://earthexplorer.usgs.gov/) by means of the routines implemented in RSAGA [44]. The same data were used to visualize the distribution of the plots.

2.5. Forest Stand Attributes

Five parameters describing forest attributes were calculated, including maximum tree height, basal area, stem density, wood density and quadratic diameter. We used the randomly selected trees heights measured from the 1-ha plots (40 to 191 trees measured per plot; Table S1) to predict the heights of unmeasured trees. To do this, we calibrated, for each plot, an allometric model of the Weibull form (Equation (1)) [45], using the *modelHD* function in the BIOMASS R-package [46]. We calculated the tree basal area (G, m^2, Equation (2)) as the sum of individual tree sections (diameter) at breast height in each plot. Stem density (N, counts), quadratic mean diameter (Dg, cm, Equation (3)), mean height (H, m) and mean wood density weighted basal area (WD, g cm^{-3}) were also derived. We employed Equation (4) of [47] to predict tree above-ground biomass (AGB, Mg ha^{-1}; Equation (4)) based on individual's DBH, tree height (H) and species mean wood density (WD) from the global repository (DRYAD; [48]).

$$H = a \times \left(1 - exp\left(-(DBH/b)^C\right)\right) \tag{1}$$

$$G = \sum_{i=1}^{N} \frac{\pi \times DBH}{4} \tag{2}$$

$$D_g = \sqrt{\frac{\sum DBH_i{}^2}{N}} \tag{3}$$

$$AGB = 0.0673 \times (WD \times H \times DBH)^{0.976} \tag{4}$$

where *a*, *b* and *c* are parameter estimates for Equation (1).

2.6. Multivariate Analysis

We identified the major floristic groups by means of a non-symmetric correspondence analysis (NSCA; [49–51]). This method is suitable here because it emphasizes abundant species from the plot profile via a 281 species by 30 1-ha plots contingency table. We focused only on fully and correctly identified species (98%) and excluded those with possible taxonomic issues or identified only at the genus level (<2% of all individuals). We extracted plots' and species' scores from the NSCA and grouped plots into three clusters based on a *k-means* clustering.

We determined correlates of the major floristic groups via the environmental vector fitting approach using the *envfit* function of the vegan R-package [52]. This non-constrained analysis simply displays the projection of linear correlations between variables of interest (potential drivers or forest structure variables) and floristic gradients in the chosen plane. The length and direction of the arrows of the multivariate environmental fitting are indicative of the strength and sign of the correlations, respectively. We then used a permutation test to determine the significance of each relationship. The latter analysis was conducted separately for the relationships between floristic gradients and forest attributes on the one side and floristic gradients and soil, topography-related variables on the other.

2.7. Characterization of Taxonomic Alpha Diversity

We compared taxonomic diversity at plot level (alpha diversity) across levels of monodominance (i.e., frequency of the most frequent species) and floristic groups. Taxonomic diversity within communities is influenced by the number of sampled individuals (N), the species richness (S), species relative abundance (evenness) and spatial aggregation [53]. Given these components of diversity change, it is necessary to use several diversity metrics [53,54]. Here, we were interested in changes in species abundance distribution which are influenced by both S and evenness. We used an individual-based rarefaction (IBR) framework transformed into equivalent number of species (ENS) [55]. IBR consists in calculating the expected number of species given k randomly sampled individuals (S_k). Increasing the parameter k proportionally increases the weight given to rare species. $S_{k=2}$ corresponds to the Gini–Simpson index which is an index of the diversity of abundant species while $S_{k=300}$ gives much more weight to rare species and can thus be considered as an index of species

richness unbiased by sample size [56]. The advantage to transform IBR into ENS (S_k converted into ENS_k) is that interpretation of diversity expressed as equivalent number of species values is more intuitive [55,57]. Finally, visualizing how ENS_k varies with k indicates the level of evenness of species distribution within the community: if all species are equally frequent, ENS_k remains constant across k values, whereas in a community dominated by one species while all other species are rare, will have ENS_k increasing steeply with k. We computed ENS_k in the R environment using functions developed by [55] and available in github (github.com/gdauby/hurlbert_ens).

We expect to observe a very good correlation between $ENS_{k=2}$ and level of monodominance because high monodominance level means low diversity of dominant species. For higher k values, a strong correlation is expected only if strong monodominance also implies low diversity of rare species.

2.8. Insight into the Forest Dynamics of the Study Area

We used a synchronous approach to investigate possible compositional shifts or trends in the forest floristic composition. Trees of each species were split into two size categories based on a cut-off at 60 cm DBH (i.e., 10–60 cm and >60 cm). This allowed to distinguish the 'mature' canopy while keeping sufficient sample sizes, i.e., around 25 trees (range: 17–36) in the canopy [58].

3. Results

3.1. Species Compositional Gradients and Stand Attributes

A total of 13 433 trees (≥10 cm at 1.3 m diameter breast height (DBH)) were recorded across the 30 one-ha plots belonging to 281 species, 179 genera and 44 families. The frequency and relative abundance in the plots were dominated by a few prominent species such as *Julbernardia seretii* (De Wild.) Troupin, *Gilbertiodendron dewevrei* (De Wild.) J.Leonard (both Leguminosae), *Petersianthus macrocarpus* (P.Beauv.) Liben (Lecythidaceae), *Greenwayodendron suaveolens* (Engl. & Diels) Verdc. and *Anonidium mannii* (Oliv.) Engl. & Diels (both Annonaceae), as shown in Figure 2. The first two species (*J. seretii* and *G. dewevrei*) were present in about half of the plots scoring relatively high mean abundance (5.6% and 7.6% respectively; Figure 2A) but *G. dewevrei* scored the highest maximum abundance of 39.1%, as shown in Figure 2B. Other species, namely *P. macrocarpus, G. suaveolens* and *A. mannii* were more frequent, i.e., present in all or nearly all plots and also abundant. Each of these species scored mean percentage abundance of 5.8, 4.6 and 4.9%, respectively, as displayed in Figure 2A, and up to 23.9% maximum local relative abundance for *A. mannii*, as displayed in Figure 2B.

Four species (*J. seretii*, *G. dewevrei*, *P. macrocarpus* and *A. mannii*) characterized three major floristic groups as depicted by the *k-means* clustering and non-symmetric correspondence analysis (NSCA), as shown in Figure 3A. The first two compositional axes of the NSCA together constituted 48.25% of the total floristic variance. The first axis (negative side) was clearly pulled by *G. dewevrei* while the second axis opposed plots dominated by *P. macrocarpus* (positive side) and *J. seretii* and *A. mannii* on the negative side.

Changes in forest stand attributes were substantial with wide range values recorded for each of the 30 1-ha plots; number of stems (332–557; mean: 447.8 count), quadratic mean diameter (27.2–35.5; mean: 30.2 cm), basal area (22.7–39.5; mean: 31.9 m^2) and above-ground biomass (331.9–590.6 mean: 447.8 Mg.ha^{-1}). The average maximum tree height per plot ranges between 16.9 m and 28.4 m, shown in Table S1.
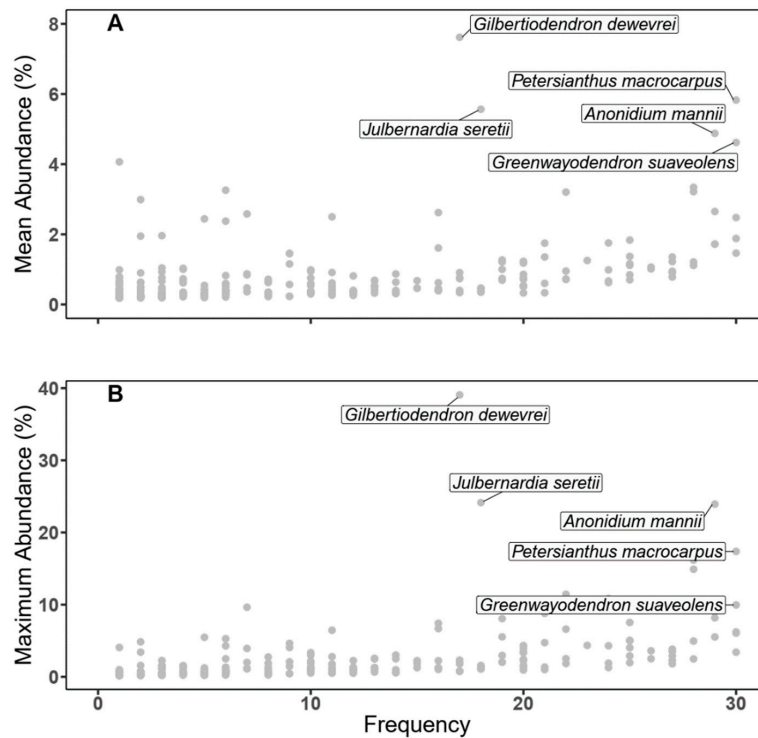
Figure 2. Mean and maximum local relative abundance against species frequency of occurrence in the 30 1-ha plots. (**A**) Mean local relative abundance (only accounting for plots where the species is present) and (**B**) maximum local relative abundance. Only species frequencies > 18, mean abundance > 4.5 and max abundance > 10 are shown for legibility.
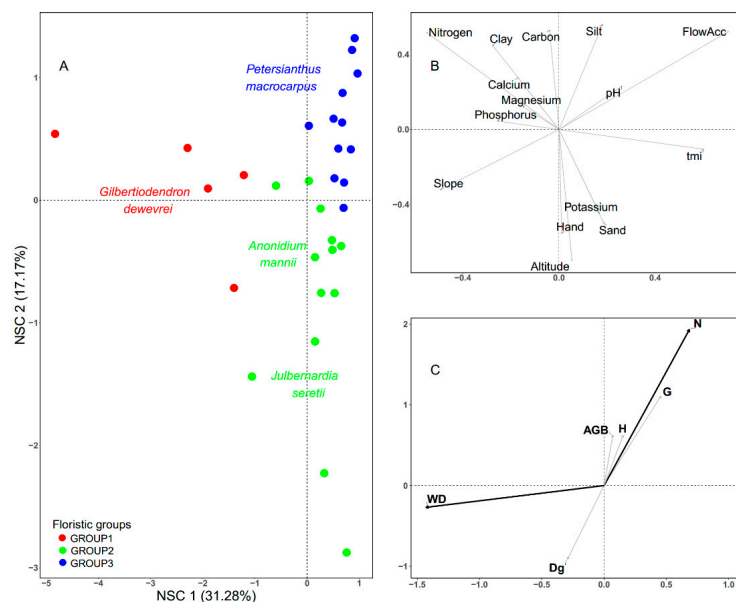

Figure 3. Linking floristic gradients to environmental variables. (**A**) Biplot of first two axes of floristic composition depicted from nonsymmetrical correspondence analysis (NSCA); dots represent 1-ha plots and dot colors represent groups from *k*-means clustering. (**B**) Projected correlation with soil and topographic variables. (**C**) Projected correlation with forest attributes. Grey arrows represent nonsignificant correlations and bold arrows represent significant correlations after permutation test. All variables are defined in Table 1.

3.2. Relationships with Environmental Variables and Forest Attributes

The relationships were generally weak between the main floristic axes (NSCA 1 and NSCA 2) and topographic, soil variables shown in Figure 3B and forest attributes shown in Figure 3C. The correlations between soil and topography variables and floristic gradients were not significant according to the permutation tests, as presented in Table 1. Nevertheless, 12 out of 13 plots of *J. seretii* occupied sites on higher altitude and height above drainage (HAND), as shown by a post hoc test (multiple comparison test with Bonferonni adjusted thresholds, Table 2) and the map of the floristic groups to altitudinal gradient (Figure 1), possibly with poorer sandy soils, as displayed in Figure 3B. *G. dewevrei* stands were apparently (but not significantly) correlated with slopes and showed no preference for lower topographic or hydromorphic positions. *P. macrocarpus* stands seemingly favored richer, lowland fine textured soils. Two forest stand attributes significantly correlated with the floristic composition axes according to the permutation test, as shown in Figure 3C and Table 1. Plot level wood density (WD) was negatively correlated with the first NSCA axis, due to the relatively high wood density of *G. dewevrei* (0.707 g cm^{-3}). Plot level stand density (N) was strongly positively correlated with the second NSCA axis, indicating high stem numbers in *P. macrocarpus* forests, as shown in Table S1. Basal area (G), quadratic mean diameter (Dg) and above-ground biomass (AGB) were not significantly correlated with the second NSCA axis, suggesting higher biomass in *P. macrocarpus* forests, despite larger trees on average (Dg) in the two other forest types (Table S1).

Table 1. Correlation between the first two non-symmetric correspondence analysis (NSCA) axes of species composition and soil, topographic variables and stand structure variables. Significance (*P*-value) provided by a permutation test (999 permutations) and bold-faced characters indicate statistically significant correlation at *P* < 0.05. HAND: height above nearest drainage; TMI: topographic moisture index; FlowAcc: flow accumulation; G: tree basal area; N: stem density; Dg: quadratic mean diameter; H: mean tree height; AGB: tree above-ground biomass; WD: species mean wood density.

	Range	Axis1	Axis2	*P*-Value	R^2
Soil					
Sand	33–90	0.349	−0.937	0.534	0.046
Clay	6–52	−0.524	0.852	0.530	0.045
Silt	4–15	0.307	0.952	0.495	0.056
Nitrogen	5.39–16.73	−0.728	0.686	0.259	0.092
Carbon	6.388–7.063	−0.074	0.997	0.536	0.045
pH	3.9–4.162	0.747	0.664	0.765	0.020
Phosphorus	0.035–0.415	−0.985	0.172	0.816	0.011
Magnesium	0.22–0.35	−0.775	0.632	0.926	0.006
Calcium	0.083–0.145	−0.525	0.851	0.806	0.017
Potassium	1.7–3.825	0.351	−0.936	0.611	0.037
Topography					
Altitude	461–687	0.076	−0.997	0.322	0.079
Slope	2.64–12.63	−0.837	−0.547	0.432	0.056
HAND	−451–247	0.020	−1.000	0.500	0.049
TMI	−3.35–2.9	0.985	−0.172	0.473	0.059
FlowAcc	−6–1.185	0.803	0.596	0.181	0.124
Stand structure					
G	24.22–39.58	0.381	0.925	0.103	0.159
N	**322–557**	**0.334**	**0.942**	**0.001**	**0.466**
Dg	27.26–35.51	−0.307	−0.952	0.233	0.102
H	18.25–32.37	0.186	0.983	0.496	0.048
AGB	333.43–590.69	0.112	0.994	0.568	0.044
WD	**0.56–0.68**	**−0.983**	**−0.186**	**0.018**	**0.235**

Table 2. Relationship between floristic groups and structural and topo-soil-related variables. Significant differences at $P < 0.05$ for each variable between the floristic groups, obtained from multiple comparison tests with Bonferroni adjustment, are shown between brackets. For a given variable, groups with the same bracketed letters are not significantly different.

Variables	GROUP1 ($n = 5$)	GROUP2 ($n = 13$)	GROUP3 ($n = 12$)
Soil			
Clay	23.2 ± 17.31*(a)*	21.92 ± 15.1*(a)*	32.75 ± 11.67*(a)*
Sand	69.6 ± 20.13*(a)*	69.62 ± 18.9(a)	58.25 ± 11.44*(a)*
Silt	7.2 ± 3.11*(a)*	8.46 ± 4.25*(a)*	9 ± 3.72*(a)*
Nitrogen	8.24 ± 2.16*(a)*	9.82 ± 2.97*(a)*	8.67 ± 1.62*(a)*
Carbon	6.77 ± 0.15*(a)*	6.75 ± 0.17*(a)*	6.66 ± 0.16*(a)*
pH	4 ± 0.08*(ab)*	3.97 ± 0.06*(b)*	4.06 ± 0.06*(a)*
Phosphorus	0.08 ± 0.02*(a)*	0.12 ± 0.11*(a)*	0.1 ± 0.05*(a)*
Magnesium	0.29 ± 0.02*(a)*	0.3 ± 0.03*(a)*	0.28 ± 0.03*(a)*
Calcium	0.11 ± 0.003*(a)*	0.12 ± 0.01*(a)*	0.11 ± 0.02*(a)*
Potassium	2.21 ± 0.36*(a)*	2.71 ± 0.66*(a)*	2.41 ± 0.46*(a)*
Topography			
Altitude	**513.2 ± 27.24*(b)***	**585.85 ± 58.94*(a)***	**505.58 ± 30.8*(b)***
Slope	5.32 ± 1.24*(a)*	5.92 ± 2.95*(a)*	5.19 ± 1.97*(a)*
HAND	−415.2±21.91*(b)*	−347.38 ± 53.18*(a)*	−415.33 ± 22.69*(b)*
TMI	−1.96 ± 2.16*(a)*	−1.89 ± 2.15*(a)*	0.14 ± 2.31*(a)*
FlowAcc	−3.5 ± 3.42*(a)*	−4.37 ± 3.12*(a)*	−3.8 ± 3.28*(a)*
Stand structure			
G	31 ± 2.33*(a)*	30.73 ± 5.11*(a)*	33.77 ± 3.99*(a)*
N	418 ± 40*(b)*	417 ± 58*(b)*	493 ± 56*(a)*
Dg	30.79 ± 1.95*(a)*	30.66 ± 2.5*(a)*	29.56 ± 1.55*(a)*
AGB	453.17 ± 58.83*(a)*	442.23 ± 79.33*(a)*	461.29 ± 60.06*(a)*
H	25.64 ± 5.69*(a)*	27.21 ± 4.41*(a)*	26.82 ± 2.9*(a)*
WD	0.67 ± 0.01*(a)*	0.63 ± 0.03*(b)*	0.63 ± 0.01*(b)*

3.3. Alpha Diversity across Monodominance Levels and Floristic Groups

As expected, we observed a strong relationship between the level of monodominance and alpha diversity expressed as $ENS_{k=2}$ which essentially estimates the diversity of abundant species (R^2 of the linear regression reached 0.79). This correlation was still present, although weaker, when giving more weight to rare species (R^2 of the linear regression between level of monodominance and $ENS_{k=300} = 0.37$), as shown in Figure 4. Alpha diversity appeared to vary independently of floristic group regardless of the metric used, as displayed in Figure 4.

3.4. Shift in Species Dominance

Overall, the relative abundance of all dominant species in the canopy (≥ 60 cm DBH) was strongly correlated to their own abundance in the lower strata (10–60 cm DBH), and not to the abundance of any other dominant species, as shown in Figure 5. Hence, analyzing differential relative abundance of the three dominant species in the lower strata and in the canopy shown in Figure 6 did not provide evidence of shifts in dominance, in which a species would obviously tend to replace another through time in any of the three floristic groups. We noticed however, that in six plots dominated by *J. seretii*, the order of dominance in the lower strata was different from that in the canopy, to the benefit of either or both the other dominant species. For the three dominant species, the relative abundance was always lower in the lower strata than in the canopy, as shown in Figure 6. If we focus on cases with plot level dominance exceeding 10%, relative density differences between the canopy and the lower strata were on average 11.3% for *G. dewevrei*, 45.6% for *J. seretii* and 14.1% for *P. macrocarpus.* Many species with a relatively high abundance in the lower strata rarely reach the canopy, and hence have a negative density difference, such as *A. mannii* (a typical lower strata tree), with −21%.
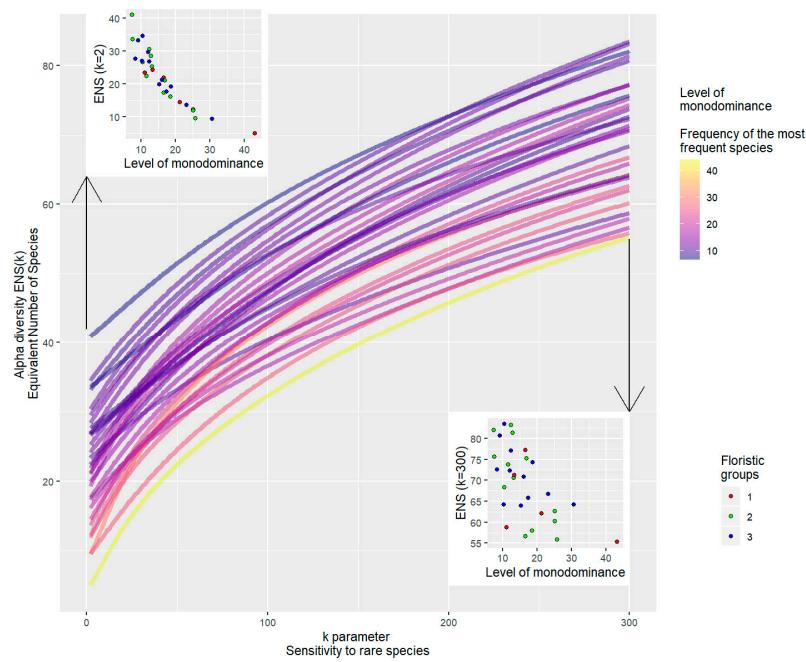
Figure 4. Individual-based rarefaction curves for the 30 plots expressed as equivalent number of species of the expected number of species in k randomly sampled individuals $ENS_{k=2}$. Colors of the curves reflect the level of monodominance expressed as the frequency of the most frequent species. Increase in the k parameter (x-axis) increases the sensitivity to rare species. The insert on the top left corner shows the relation between alpha diversity and the level of monodominance for $ENS_{k=2}$ thus being insensitive to rare species while the insert on the bottom right corner shows the relation between alpha diversity and the level of monodominance for $ENS_{k=300}$, thus being strongly sensitive to rare species. Colors of the dots in inserts correspond to the three floristic groups identified.

Figure 5. Correlation matrix for size classes (cutoff at 60 cm diameter at breast height (DBH)) of the main dominant species. Cutoffs for diameter class are either <60 cm (species name only) or >60 cm (species name_60; where tree size exists).
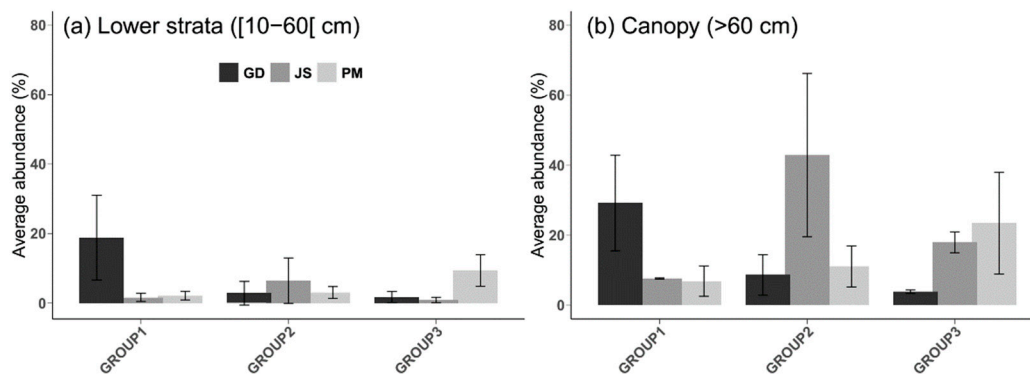
Figure 6. Mean relative abundance of the three main dominant species among floristic groups. Groups are defined from *k*-means clustering on nonsymmetric correspondence analysis scores. (**a**) In the lower strata (≤60 cm DBH); (**b**) in the canopy (>60 cm DBH). GD is *Gilbertiodendron dewevrei*; JS is *Julbernadia seretii*; PM is *Petersianthus macrocarpus*.

4. Discussion

Using a sampling of 30 1-ha plots sampled across a 260 km^2 area, we evidenced strong variations in the abundance of dominant species characterized by *Gilbertiodendron dewevrei*, *Julbernadia seretii*, *Petersianthus macrocarpus* and *Anonidium mannii*, as shown in Figure 3A. The variation in dominance of these species seems to occur nearly independently of substratum variations, as shown in Figure 2B, despite marginally significant differences for the group dominated by *J. seretii*. This result corroborates previous studies refuting soil characteristics [23–25,59,60] and topography [26] as potential drivers of monodominance in tropical forests. Two forest stand attributes (wood and stem densities) correlated with the floristic gradients, as shown in Figure 3C. Wood density was on average higher in the floristic groups dominated by *G. dewevrei*. On the contrary, stem density was significantly higher in the *P. macrocarpus* floristic group. These results taken together could suggest a higher maturity of a late successional stage for the Fabaceae groupings (i.e., *G. dewevrei* and *J. seretii*). Contrary to [31], basal area and above-ground biomass (AGB) were not correlated to the dominance by *G. dewevrei*. Instead, *P. macrocarpus* stands, despite lighter woods, had a higher basal area and AGB owing to the abundance of both taller and more numerous trees. This counterintuitive result can be related to other studies in Central Africa. For instance, taller trees in denser stands tend to have higher biomass in semideciduous forests compared to evergreen forests [61] or in wet forests compared to moist forests [62,63]. Interestingly, the AGB range in *G. dewevrei* forests in our study area (379 to 533 Mg ha^{-1}, 453 Mg ha^{-1} average, 5 plots) appeared to be slightly lower that the AGB obtained in a similar study in closed canopy forests in Cameroon (514 Mg ha^{-1} average, 23 plots of *G. dewevrei* forests) [31,32]. This result may suggest that *G. dewevrei* plots in the study area are still stocking above ground biomass.

Strong correlations were observed between the dominance of a given species in the canopy (≥60 cm diameter at 1.3 m breast height (DBH)) and its abundance in the lower strata (10–60 cm DBH). This suggests that in this study area the states of dominance in the vegetation are stable across generations, that successional dynamics are very slow or that they are localized to peculiar locations (e.g., forest edges). Dominant species were however less dominant in the lower strata than in the canopy, as shown in Figure 5. Under the hypothesis of stable dynamics, the latter could be explained by biological feedbacks operating after recruitment. The case of *P. macrocarpus*, considered as a light-demanding nonpioneer species shows that succession to oneself does not necessarily imply shade tolerance. The canopy heterogeneity within one hectare is indeed considerable, leading to a mosaic of patches of contrasted microenvironments [12]. These findings suggest that monodominant forest patches could constitute stable states maintained by endogenous feedbacks [64], such as biological interactions between individuals or species, either positive (mycorrhiza associations, root anastomosis) [31,65,66] or negative (competition for light or nutrients, allelopathy) [14,66,67], short range seed dispersal and

enhanced resistance to pathogens and herbivores leading to mild negative density dependence ([18,19] Hypothesis). An unknown combination of the above mechanisms could lead to stabilizing patches dominated by one or a few species. We cannot, however, discard the hypothesis that widespread historical human disturbance may have been at the origin of state change from one forest type to another, as hypothesized by [68], or that the temporal scale necessary for compositional changes are not properly captured by our synchronic observations. Another possible explanation, involving random drift in the community composition (neutral theory [4]) would imply, at least intuitively, that dominance should be achieved by radically different species across locations, and not repeatedly by the same few species across the landscape or even the continent [29].

Although some of the sampled forests correspond to typical examples of monodominant forests, the 50% abundance threshold was never reached at plot level. We suggest that the conclusion of recent studies based on this threshold and making inferences about the rarity of monodominant forests (e.g., in the Amazon, [16] and in the Congo Basin, [15]) should be reconsidered. At a 20% abundance threshold, the same authors reported 18% of monodominant plots. Indeed, at the 20% abundance threshold in our study site, 13.3% of the plots could be considered monodominant, and up to 30% of the plots had a 15% dominance level. Moreover, this only considers the dominant species one by one. What perhaps matters more is that the plot composition often tends to become uneven and that most plots are distributed along a gradient of dominance by one or a handful of species.

Unsurprisingly, the level of monodominance strongly influences the diversity of abundant species. This effect is not only the result of stronger unevenness in relative species distribution. Indeed, if monodominance only resulted in changes in evenness, all rarefaction curves in Figure 4 would tend to converge when increasing k values [53]. Monodominance was also, to a lesser extent, correlated to diversity estimated by $ENS_{k=300}$ and thus associated with low richness of both rare and abundant species.

Monodominance is common among species of the Fabaceae [17] and two dominant species (*G. dewevrei* and *J. seretii*) in our study site are known to be gregarious and belong to the Fabaceae (*Detarioideae*). Much has been written on possible mechanisms driving local dominance in this family, such as competitive advantages provided by ectomycorrhizae, shade tolerance or heavy litter accumulation [65,66]. However, this focus largely occults the fact that species from other families (in our case Lecytidaceae e.g., *P. macrocarpus* and Annonaceae e.g., *A. mannii*) are both more frequent and nearly as locally dominant. Species from other families such as Apocynaceae, Burseraceae and Moraceae [17] have also been reported elsewhere.

Given the importance and prevalence of dominance patterns observed in our site but also elsewhere in the Congo Basin ([29] in review) or in the neotropics [16], and the implications in terms of plant diversity, evolution (e.g., the role of density dependence), forest functioning and structure, we advocate more in-depth studies of the mechanisms leading to the emergence and maintenance of multiple stable states in tropical forests.

5. Conclusions

This paper provides new results from tree communities at the heart of the Congo Basin forests documenting the respective roles of environmental gradients and endogenous dynamics in shaping local variations in dominance. We show that a few species compete to dominate tree communities, mostly independently of abiotic (edaphic, topographic) constraints. Moreover, succession seems to be stalling, with the locally dominant species tending to dominate the understory as well. This is evocative of either emergent patterning or multiple stable states induced by biological feedbacks [64]. Although we are not at this stage able to provide a fully documented mechanistic explanation, we think this contribution should help initiate fruitful future interdisciplinary studies involving both experimental biology and mathematical modelling.

We show that the level of monodominance has a significant impact on tree diversity patterns and is thus an important feature to document and understand for efficient biodiversity conservation. Finally,

dominance by one or another species also has implications in terms of forest structure and biomass. The different states are therefore not equivalent regarding carbon stocking or other ecosystem services.

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