Additive influences of soil and climate gradients drive tree community composition of Central African rain forests

Moses Bakonck Libalah1,2 | Vincent Droissart3 | Bonaventure Sonké1 | Nicolas Barbier3 | Gilles Dauby3 | Claire Fortune3 | Gyslene Kamdem1 | Narcisse Kamdem1 | Simon L Lewis4,5 | Gislain II Mofack1 | Stéphane Takoudjou Momo1 | Raphaël Pélissier3 | Pierre Ploton3 | Nicolas Texier6,7 | Donatien Zebazé1 | Pierre Couteron3

Abstract

Aim: Examining tree species–environment association can offer insight into the drivers of vegetation patterns and key information of practical relevance to forest management. Here, we aim to quantify the contribution of climate and soil gradients to variation in Central African tree species composition (abundance and occurrence).

Location: Tropical rain forests of southern and eastern Cameroon.

Methods: We established 82 1-ha permanent plots across seven localities and censused all trees ≥10 cm in diameter, representing a total of 37,733 trees and 455 species. In 60 of those plots, we measured 10 soil variables describing texture and nutrients levels and extracted 10 bioclimatic variables from global-gridded climate databases. We synthesized the main environmental gradients by conducting principal component analyses on climate and soil data, respectively. We performed unconstrained and constrained non-symmetric correspondence analyses to account for the individual and joint contributions of climate and soil on species abundance and occurrence.

Results: Climate and soil contributed similarly to variances of species abundance and occurrence (12–15% variance for climate vs 11–12% variance for soil). Climate influence mostly concerns some abundant species, while some of the less abundant species were mainly driven by soil. Fractions of species variances accounted for by climate and soil show strong correlation when assessed from species occurrence and abundance data.

Conclusion: Variation in occurrence and abundance of tropical forest trees can be partly shaped by both climate and soil gradients in Cameroon, which emphasizes the importance to jointly consider soil and climate in species distribution modeling. Less abundant species may express environmental influence differently than abundant species and convey complementary information about community assemblage. Though showing congruent patterns here, species abundance and occurrence reflect
different interacting community processes and both should be examined to better understand vegetation patterns.

KEYWORDS
Cameroon, climate gradient, soil gradient, species abundance, species occurrence, tropical rain forests

1 | INTRODUCTION

Species distribution along environmental gradients has the potential to inform on the dimensions of their realized niches (John et al., 2007; Toledo et al., 2012). For long-lived species such as trees, the presence and abundance of mature individuals can reflect their tolerance and adaptation to local abiotic conditions (Kraft et al., 2015). For most tropical tree species, a better understanding of the drivers of their distribution has strong fundamental implications in vegetation science and practical relevance in forest management and conservation (Swaine, 1996; Toledo et al., 2011; Toledo et al., 2012; Amissah et al., 2014).

From a fundamental perspective, species turnover along broad-scale gradients can provide insights on the strength of environmental filtering (Hardy and Sonké, 2004; Soininen et al., 2007). Such studies are still too scarce to allow grasping the variety of species–environment patterns especially in diverse parts of the paleotropics. From an applied perspective, determining the relative role of environmental factors such as climate or soil in species distribution can help to classify and map vegetation types and habitats and identify indicator species of a given environmental condition (Hall and Swaine, 1976; Diekmann, 2003). These outputs are important for conservation initiatives such as the sixth category of the High Conservation Value program dedicated to rare and threatened habitats, developed and used by the Forest Stewardship Council to support sustainable forest management. Yet, there have been too few studies on species–environment relationships at a regional scale in tropical forests, most of them located in the neotropics (Pyke et al., 2001; Engelbrecht et al., 2007; Toledo et al., 2012; Condit et al., 2013) and even scarcer in Africa (but see Réjou-Méchain et al., 2008; Amissah et al., 2014; Fayolle et al., 2014; Vleminckx et al., 2015) where most studies were at a local scale.

Most studies analyzing plot taxonomic data along broad gradients concluded that tropical tree species turnover is partly shaped by climate through rainfall, temperature and seasonality gradients (Swaine, 1996; Pyke et al., 2001; Engelbrecht et al., 2007; Parmentier et al., 2007; Toledo et al., 2011, 2012; Amissah et al., 2014). A limited number of studies also integrated information on soil, using either coarse geological proxies such as bedrock classes, bedrock-derived dominant texture (Van Rompaey, 1993; Réjou-Méchain et al., 2008; Fayolle et al., 2012; Guilet et al., 2015) or more accurate, continuous soil variables determined from local soil cores (Swaine, 1996; Toledo et al., 2011; Toledo et al., 2012; Condit et al., 2013; Vleminckx et al., 2015, 2017). The former group of studies concluded on substantial explanatory power of their substrate proxies, while the latter concluded on either strong (Condit et al., 2013) or moderate (Toledo et al., 2012) influences of soil variables. Another study described a confounding effect from correlated rainfall and soil fertility gradients (Swaine, 1996). Therefore, it remains unclear what is the relative contribution of climate and soil gradients to species turnover at regional scales in tropical rain forests.

To evaluate the contributions of climate and soil on species composition, data sets of high botanical accuracy covering large spatial and ecological breadths are valuable. Such sampling remains nevertheless challenging in tropical forests. Most regional-scale studies in tropical forests were limited to a subset of tree species (but see Condit et al., 2013), often focusing on the most reliably identified and abundant species in the field (Réjou-Méchain et al., 2008; Toledo et al., 2012) or those which are frequent enough for statistical analyses (Swaine, 1996; Amissah et al., 2014). Thus, studying a subset of the regional species pool may bias inferences drawn about climate and soil influences on tropical tree species. Expanding sampling to the whole species pool is worthwhile for arriving at valuable information on rare and potentially threatened species but also for additional insights on processes shaping regional-scale floristic patterns. For instance, less abundant species may respond differently to environmental gradients than more abundant species (Keddy, 1992). Accounting for less abundant and less frequent species is also interesting because species occurrence (i.e., presence–absence) and abundance data may inform on different assembly processes acting simultaneously (Toledo et al., 2012; Wilson, 2012). For example, the presence of a species in a local community from the regional pool may be the results of filtering processes permitting the species to establish and persist (Kraft et al., 2015). Conversely, the abundance of a species may reflect other processes such as demographic stochasticity, historical contingency and biotic interactions (Keddy, 1992; Cingolani et al., 2009; Raevel et al., 2012; Wilson, 2012). If abundant species also tend to be frequent, this would thus suggest...
pervasiveness of environmental filtering against other processes. Hence, comparing patterns of species occurrence and abundance can provide insights about the influence of environmental gradients on community assembly (Toledo et al., 2012).

Here, we analyze an unpublished data set of tropical trees sampled from 82 1-ha plots within a large tropical region across the southern and eastern Cameroonian plateau that simultaneously features broad climatic gradients and soil variables along with thorough botanical identification at the species level (91% of the trees). To our knowledge, this represents one of the most important data collection efforts to study variation in tree taxonomic composition with climate and soil along non-orographic gradients in the paleotropics. So far, there is scarce evaluation of environmental gradients driving species distribution within this region. We aim to quantify the effects of climate and soil in the variation of floristic composition in a region known to display both evergreen and semi-deciduous forests (Letouzey, 1985). More specifically, we address the following questions: (1) what are the main lines of floristic variation and the respective contributions of climate and soil; (2) to what extent is the distribution of abundant vs less abundant species informative on effects of climate and soil on the entire floristic composition; and (3) are species occurrence and abundance displaying congruent responses to climate and soil that would suggest strong environmental filtering?

2 | METHODS

2.1 | Study area

The study area spans about 110,000 km² in southern and eastern parts of Cameroon and encompasses dense lowland forests of different types along a gradient of climatic and edaphic conditions (Figure 1; Appendix S1). The vegetation has been referred to as the Cameroon-Congolese forest sector or dense moist Guineo-Congolese forest (Letouzey, 1985), which is interspersed with savannas, evergreen and semi-deciduous forests. This study area has been assigned to the Moist Central African floristic cluster by Fayolle et al. (2014), but likely encompasses other vegetation types that still require finer characterization. According to Letouzey (1985), for instance, the Mbam Djerem locality toward the north of the study area is occupied by a forest–savanna mosaic (Appendix S1), composed of tall trees (average canopy height of 10–20 m) such as Sterculia rhinopetala K. Schum., Celtis zenkeri Engl. and Croton sylvaticus Hochst. (Malvaceae ex Sterculiaceae–Canabaceae ex Ulmaceae forest type). The localities of Deng-Deng and Mindourou II are occupied by semi-deciduous forests and characterized by tall and large buttressed trees.

The climate is equatorial composed of a long dry season from November to March and a short dry season from June to July, and also a long wet season from August to October and a short wet season from April to May. The average number of wet months receiving precipitation >100 mm/month ranges from 6.6 months to 8.2 months per year, annual mean precipitation ranges from 1,300 mm to 1,900 mm and annual mean temperature ranges between 20°C and 25°C (CHELSA v1.2; http://chelsa-climate.org/). These low values compared to other lowland forest types of Central Africa are due to the moderately high elevation of the study area (between 500 and 800 m above sea level) which lessens temperatures and potential evapotranspiration.

The soils in the study area are generally “ferralitic soils” (Ségalen, 1967), i.e., Ferralsols (FAO-UNESCO, 1977) showing medium to high levels of weathering and desaturation. This area is also typical of Orthic, Xanthic, Rhodic and Plinthic Ferralsols with Dystric Gleysols predominating in low-lying areas (FAO-UNESCO, 1977). Though derived from different parent materials such as granites and schists, they share common characteristics, among which a strong dominance of clay content. The rocks which constitute the subsurface soil profile are essentially acidic crystalline rocks (various granites, embrechites, etc.), considered to originate from the lower Precambrian, though rocks of metamorphic origins have been attributed to the middle and upper Precambrian (Curis et al., 1955; Martin and Ségalen, 1966).

2.2 | Plot floristic inventory

We established a total of 82 non-contiguous 1-ha permanent sampling plots (PSPs) distributed in seven localities of the study area (Figure 1; Appendix S1): four in the Mbam Djerem National Park; 15 in the Deng-Deng National Park; 21 in Mindourou II; 17 in Mindourou I; 14 in Lomie; three in Ngoila and eight in Somalomo. We avoided seasonally waterlogged areas, monodominant stands (e.g., Gilbertiodendron dewevrei (De Wild.) J.Leonard), young secondary forests and areas dominated by short-lived pioneer species (notably Musanga cecropioides R.Br. ex Tedlie). To establish a 1-ha PSP, we subdivided a 100 m² area into 20 m × 20 m quadrats (Appendix S2). We set poles at each quadrat corner and at the plot corners (Appendix S2). A total of 25 GPS points were recorded along the plot contour using a high precision Trimble® Geo 7X (Trimble®, Westminster, CO, USA). Within each 1-ha PSP, we measured all trees with a diameter at breast height ≥10 cm. Large trees with buttresses or deformations were measured at 30 cm below or above the deformations. Taxonomic identifications were first conducted during tree measurement by observing leaves, flowers, trunk slash, habit and other diagnostic characters. A second identification was realized at the Plant Systematics and Ecology laboratory and the Herbarium of the Université Libre de Bruxelles (BRLU) where voucher specimens are deposited. In total, we collected 2,045 voucher specimens to ensure correct, verifiable and homogenous identification. Nomenclature for families and genera follows the APG IV (2016) classification while species names were corrected using the African Plant Database (African Plants Database, 2020).

2.3 | Soil variables for plots

Soil samples were analyzed for a subset of 60 1-ha plots following standard protocols. Samples from seven 1-ha plots in Somalomo and
Mbam Djere were analyzed as in Quesada et al. (2010) while the other 53 1-ha plots are described below.

We collected soil samples at four locations along the right-angle diagonal within each 1-ha PSP (Appendix S2). For each location, we dug four soil cores (excluding litter) at 10 cm intervals (0–10, 10–20, 20–30 and 30–40 cm) and air-dried separately. Equal proportions from each core were taken and pooled to form one sample for analysis. In total, four samples were analyzed per 1-ha plots. Each pooled soil sample was ground to pass through a 2-mm sieve. For nitrogen and carbon analyses, samples were further ground to pass through a 0.5-mm sieve using a motorized grinder (Retch RM200®). Soil pH in water was determined in a 1:2.5 (w/v) soil:water suspension. Total nitrogen (μg/g) was determined from a wet acid digest and analyzed by colorimetry (Baillie et al., 1990). Total phosphorus (μg/g) was determined from wet acid digest and also analyzed by colorimetry using the molybdate blue procedure described by Murphy and Riley (1962). Available phosphorus (μg/g) was extracted using Bray extractant and the resulting extract analyzed using the molybdate blue procedure. Moisture content (%) was determined by gravimetry using: 100 – (100*weight of sample oven-dried at 105°C divided by weight of air-dried sample). Organic carbon (%) was determined by chromic acid digestion and spectrophotometric analysis using a Genesys 10S UV/Vis spectrophotometer (Thermo Scientific™, Waltham, MA, USA). Particle sizes (% Sand, % Silt, and % Clay) were determined by Bouyoucos hydrometry (Bouyoucos, 1951; Day, 1953). Soil analyses were conducted at the Soil & Plant Laboratory of the International Institute of Tropical Agriculture (IITA)-Yaoundé.

In total, we measured 10 soil variables, which varied between localities (Appendix S3). These soil variables confirm the main common characteristics of the reddish ferrallitic soils (Ségalen, 1967) with the exception of Mbam Djere. Such soils are largely dominated by clay (40–60%), acidic pH (4–5), and low rates of organic carbon (1–2%) in spite of enduring forest cover. A Principal Component Analysis (PCA) was used to simplify the set of soil variables through new synthetic, uncorrelated variables and thereby keep a reasonable number of predictors compared to the number of plots (Harrel Jr., 2015, p.72). We used the Broken-stick model (Jackson, 1993) to retain three interpretable PCA axes and the plot scores were used as soil predictor variables.

2.4 Climate variables for plots

We used the GPS (Garmin®, Olathe, KS, USA) coordinates (i.e., plot centroids) of each 1-ha plot to select 10 variables from an initial set of 21 after a preliminary screening and discarded strongly correlated variables. The latter was to identify only variables contributing to the main climatic patterns. Variables were obtained at 30 arc-second (ca. 900 m) ground resolution from Climatologies at High Resolution for the Earth’s Land Surface Areas (CHELSA v1.2; http://chelsa-climate.org/), based on a quasi-mechanistic statistical downscaling of the climatic reanalysis interim global circulation model (Karger et al., 2017). Mean cloud frequency’s yearly standard deviation was retrieved from Wilson and Jetz’ EarthEnv data set (Wilson and Jetz, 2016) to account for variation in the radiative budget.

We performed a regional-level PCA based on the above set of climate variables but over the broader zone covered by broadleaved evergreen and semi-deciduous forest for tropical Africa [zone determined in the Global Land Cover Map for 2009; (Arino et al., 2012)]. Plot scores along the first three principal components were taken as climate predictors which permitted a reasonable comparison to the number of plots (Harrel Jr., 2015, p.72). These three principal components were retained following the Broken-stick model (Jackson, 1993).

2.5 Statistical analyses

2.5.1 Species abundance and occurrence

For each species, we defined: (1) regional abundance as the total number of individuals over the plots; (2) local abundance as the average number of individuals over the plots where the species was present; and (3) occurrence as the number of plots in which the species was present.

2.5.2 Variance partitioning

We used a variance partitioning approach based on individual species variance (Appendix S4) that was independently applied to both species abundance and species occurrence data tables (Couteron and Pélissier, 2004). We used Non-Symmetric Correspondence Analysis (NSCA) to ordinate plots and species along common gradients. NSCA only differs from popular Correspondence Analysis (CA) by applying the “species profile transformation” sensu Legendre and Gallagher (2001) instead of chi-square metric (Pélissier et al., 2003). Otherwise both rely on the same partitioning of individual species variance which is close to the use of the Hellinger transformation (Legendre and Gallagher, 2001). The NSCA was used on our floristic tables (82 1-ha plots, 455 tropical tree species) to analyze variations of species abundance and occurrence across forest communities (plots). We presented results only for NSCA because it was similar to that for CA on species abundance. We repeated the NSCA on a reduced floristic table (60 1-ha plots, 416 species) corresponding to plots with both soil and climate data. Preliminary analyses revealed no substantial changes in the main clines of floristic variation when switching the floristic tables (see Appendix S5 and Figure 2 for results with 82 and 60 plots, respectively).

To directly ordinate species along soil and climate gradients, we employed constrained analyses, namely NSCA with Instrumental Variables (NSCA IV; sensu Couteron et al., 2003). To assess the individual and joint influence of soil and climate on species abundance and occurrence, we apportioned inter-plots variation with respect to soil gradients (S∇), climate gradients (C∇), and their joint contributions (S∇ + C∇). The variance apportioning calculates the
shares of individual species variances explained by climate, soil and both. We also calculated the proportion of variance accounted for by climate when the effects of soil were factored out ($C_{IV} - S_{IV}$), i.e., corresponding to a partial ordination and the proportion of variance accounted for by soil when the effects of climate were factored out ($S_{IV} - C_{IV}$). Finally, we tested the statistical significance of the variance portions obtained at both individual and multi-species scales using Monte-Carlo permutation tests (i.e., by randomizing the rows of the floristic table irrespective of the values of the environmental gradients). This classical randomization procedure breaks the relationship between floristic composition and environmental variables and yields a distribution of projected variance values under the null hypothesis against which the observed value can be compared.

All statistical analyses were performed with the R statistical software version 3.5.2 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria), using routine R functions and the diversity.R package (Péligier, Diversity analysis package (v.1.5-13)) and also with the varpart() function with transfo = “total” of the vegan package.
package in the R software (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

3  |  RESULTS

3.1  |  Floristic diversity

The 82 1-ha plots comprised 37,733 trees belonging to 455 species and 257 genera, grouped in 61 families. The subset of 60 1-ha plots for which both soil and climate were available contained 26,726 trees belonging to 416 species and 234 genera, grouped in 60 families. The 60 1-ha plot data excluded 798 (2.7%) unidentified individuals and 1,741 (5.9%) individuals identified at genus level only. We deposited the data used in this study in the official repository dedicated to the trees and plots network for Central Africa (https://github.com/umr-amap/centrafrivplots).

3.2  |  Correlations between species regional abundance and occurrence

We found a strong correlation between species regional abundance and occurrence across the 60 1-ha plots ($r = 0.71; df = 414; t = 20.46$), but a weak correlation between species local abundance and occurrence ($r = 0.23; df = 414; t = 4.91$). The results were similar for the 82 1-ha plots, that is, strong correlation for regional abundance and occurrence ($r = 0.72; df = 453; t = 22.38$) and weak correlation for local abundance and occurrence ($r = 0.21; df = 453; t = 4.46$). Frequent species (i.e., present in more than 80% of plots) such as *Tabernaemontana crassa* Benth., *Anonidiummannii* Oliv., & *Diels* and *Greenwayodendron suaveolens* (Engl. & Diels) Verdc. were also highly abundant at regional scale (i.e., recorded from more than 1,000 individuals each; Appendices S6a and S7). Other species (e.g., *Plagiostyles africana* (Müll.Arg.) Prain, *Baphia leptobotrys* Harms, *Parkia biglobosa* (Jacq.) R.Br. ex G.Don) were less frequent and, when present, showed high local abundance (Appendix S6b).

3.3  |  Patterns of floristic composition

Both occurrence and abundance data sets reveal congruent patterns of regionally frequent or abundant species, respectively (Figure 2). NSCA on the species occurrence matrix for 60 1-ha plots revealed a first axis (8.65% variance) mostly determined by regionally abundant species such as *Albizia adianthifolia* (Schum.) W.Wight, *Celtis adolfi-friderici* Engl. and *Mansoniaaltissima* (A.Chev.) A.Chev. and *Pandaoleosa* Pierre, *Carapa procera* DC. and *Cylcodiscus gabunensis* Harms (Figure 2a). This first axis opposed plots from the drier localities (Mbam Djerem, Deng-Deng and Mindourou II) to plots from wetter localities (Lomié, Mindourou I and Somalomo) (Figure 2b). The second axis (7.14% variances) was characterized by species such as *Celtiszenkeri* Engl. and species such as *Drypetesleonensis* Pax and *Phyllocosmusafricanus* (Hook.f.) Klotzsch (Figure 2a). This axis opposed plots from the Mbam Djerem against those of Lomie localities (Figure 2b).

Non-Symmetric Correspondence Analysis on species abundance matrix for 60 1-ha plots revealed a first axis (12.17% of total variance) driven by regionally abundant species (Figure 2c) such as *Anonidiummannii* (1,253 individuals), *Greenwayodendron suaveolens* (1,098 individuals), *Funtumia africana* (Benth.) Staf (495 individuals), *Plagiostyles africana* (459 individuals), *Uapaca guineensis* Müll. Arg. (452 individuals), *Heisteriaparvifolia* Sm. (346 individuals) and *Strombosis grandifolia* Hook.f. (651 individuals). This first axis represented a dry to wet gradient of localities including Lomie, Somalomo and Deng-Deng. The second axis (9.95% of total variance) featured species of young dry forests (e.g., *Markhamialutea* (Benth.) K.Schum. and *Parkia biglobosa*) in the Mbam Djerem locality and a blurring effect of the pioneer *Musanga cercocephala* (417 individuals) in one plot of the Mindourou I locality (Figure 2d).

3.4  |  Gradients of soil and climate

The main gradients in soil variables were summarized by the first three axes of the PCA that together explained 64.5% of variance. The first axis (27.6% variance) corresponds to a texture gradient, the second axis (22.3% variance) to a fertility gradient and the third axis (14.7% variance) to an organic content gradient (Figure 3a,b).

Principal Component Analysis on climate variables was less interpretable in terms of single climatic factors because of the patterns of covariation between climate variables. The climate variables from the first three axes were reduced to a three-dimensional space and this together explained 84.9% of total variance (Figure 3c,d) while entailing: (1) seasonality (in temperature, precipitation and cloud frequency); (2) mean annual temperature (with a weak link to seasonality); and (3) precipitation (with a loose correlation between total, wet- and dry-season precipitations).

3.5  |  Variance partitioning of species local abundance and occurrence with respect to climate and soil

Comparable levels of explained variances emanated from species abundance and occurrence with soil and climate gradients (Table 1). Climate alone explained 15.2% species variance for abundance and 12.4% for occurrence. Soil alone explained almost equal fractions of variance of abundance and occurrence (11.6% and 11.2%, respectively). The joint effect of soil and climate accounted for 25.8% of variance for species abundance and 23.0% variance for species occurrence (Table 1).

The proportion of unexplained variance once either soil or climate effects were factored out revealed that soil and climate gradients appeared fairly additive (i.e., small fractions of shared explained
FIGURE 3 Correlation circles of Principal Component Analysis on soil composition and bioclimatic variables. Variables of first three axes for soil (a, b); moisture = soil moisture content; Org$_C$ = organic carbon; total$_N$ = total nitrogen; total$_P$ = total phosphorus; Bray$_P$ = assimilable phosphorus; C$_N$ = carbon/nitrogen ratio; pH; Clay, Sand and Silt contents and for climate (c, d); amT = annual mean temperature; Tar = temperature annual range; aP = annual precipitation; Psea = precipitation seasonality; $mTwq$ & $mTcq$ = mean temperature of warmest and coldest quarters; $Pwtq$ & $Pdq$ = precipitation of wettest and driest quarters. Modscf$_{sd}$ = standard deviation of cloud frequency. A quarter is a period of three successive months, i.e., 1/4 of the year.

TABLE 1 Variance proportions of species abundance (i.e., relating to Simpson beta-diversity) and occurrence apportioned with respect to soil and/or climate gradients

<table>
<thead>
<tr>
<th></th>
<th>Total beta-diversity</th>
<th>Constrained ordination</th>
<th>Partial ordination</th>
<th>Residual ordination</th>
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<tbody>
<tr>
<td></td>
<td></td>
<td>$S_{IV}$</td>
<td>$C_{IV}$</td>
<td>$S_{IV} + C_{IV}$</td>
</tr>
<tr>
<td>Variance for species abundance</td>
<td>0.02989</td>
<td>0.00345$^{**}$</td>
<td>0.00452$^{**}$</td>
<td>0.00769$^{**}$</td>
</tr>
<tr>
<td>Variance for species occurrence</td>
<td>0.00607</td>
<td>0.00068$^{**}$</td>
<td>0.00076$^{**}$</td>
<td>0.00139$^{**}$</td>
</tr>
<tr>
<td>Fractions for species abundance (%)</td>
<td>100</td>
<td>11.561</td>
<td>15.179</td>
<td>25.799</td>
</tr>
<tr>
<td>Fractions for species occurrence (%)</td>
<td>100</td>
<td>11.195</td>
<td>12.443</td>
<td>22.988</td>
</tr>
</tbody>
</table>

Note: Environmental descriptors (Instrumental variables [IV]) i.e., first three PCA axes for soil ($S_{IV}$) and climate ($C_{IV}$) are used to explain multi-species diversity (from species abundance and occurrence) determined via non-symmetric correspondence analysis (NSCA). Entries denote values or fractions of Simpson–Gini diversity and species variance explained by soil ($S_{IV}$), climate ($C_{IV}$), soil and climate ($S_{IV} + C_{IV}$), climate without soil ($C_{IV} - S_{IV}$), soil without climate ($S_{IV} - C_{IV}$) and the residuals [total − ($S_{IV} + C_{IV}$)]. Monte-Carlo permutation test of significance (1,000 repetitions) for each operation is denoted by an asterisk.

*p < 0.05
**p < 0.01.

Species showed affinity to the climate or soil gradients (Figure 4). For some species, the variance in their abundance was well explained by climate but not soil (e.g., Strombosia tetrandra Engl., Desbordesia insignis Pierre ex Tiegh.). For other species, the variance in abundance was well explained by soil but not climate (e.g., Dialium angolense Welw. ex Oliv., Pentaclethra eetveldeana De

variances) for species abundance and occurrence (Table 1). Factoring out the effects of soil, climate explained 10.2–11.3% variance and factoring out the effects of climate, soil explained 8.2%–9.1% variance of species distribution. Interaction between soil and climate based on pairwise multiplicative effects of explanatory variables ($C_{IV} \times S_{IV}$) was very low (i.e., <2% variance).
**FIGURE 4** Fractions of species variances explained by climate and soil gradients. Variance fraction is projected variance divided by observed variance. Circles represent species and sizes are proportional to species abundance (i.e., total number of individuals sampled). Only the best explained of the 416 species are labeled to improve legibility.

**FIGURE 5** Relationships of explained variances between species abundance and species occurrence. Climate-explained variance (a: regression slope = 0.53) and Soil-explained variance (b: regression slope = 0.58). To improve legibility, only species (12 out of 416) departing from the main regression trend are labeled on both graphs and circles are proportionate to abundance.
Wild. & T.Durand, Monodora myristica (Gaertn.) Dunal. The former group of species tends to be regionally abundant (fairly large circles in Figure 4), while the latter encompasses less abundant species (Figure 4). Few species (located along plot diagonal in Figure 4) simultaneously displayed high levels of explained variances for both factors and were mostly not abundant (e.g., Khaya ivorenensis A.Chev., Markhamia lutea, and Vitex doniana Sweet).

We found positive relationships between explained variance in species abundance and occurrence: $R^2 = 0.58$ for soil gradient (Figure 5b) and $R^2 = 0.53$ for climate gradient (Figure 5a). Despite these strong relationships, several species deviated from the regression trends. For example, for Greenwayodendron suavolens, one of the most abundant and frequent species of our data set (Appendix S6), soil well explained variance in its occurrence, but not its abundance. Parkia biglobosa, an infrequent species that tends to be locally abundant within dry forests (Appendix S6B), exhibits the same pattern. For Funtumia africana, one of the regionally abundant and frequent species (Appendix S6A), climate well explained its abundance but not its occurrence. For Panda oleosa, also regionally abundant (Appendix S7), climate well explained its occurrence but not its abundance.

4 | DISCUSSION

This study contributes to the ongoing debate about the impact of local edaphic factors (Clark et al., 1999; Prada et al., 2017) and/or climate (Swaine, 1996; Toledo et al., 2012; Condit et al., 2013) on plant compositional turnover, which has not been sufficiently addressed in the tropics (but see Swaine, 1996; Toledo et al., 2012; Condit et al., 2013) and within the African rain forests in particular. We show that patterns from species abundances and occurrences are overall congruent and that climate and soil do not have the same influence on abundant and less abundant species. This result might reflect divergent but interacting processes shaping plant community composition and thus increasing beta diversity at the landscape scale (Tuomisto et al., 2010; Morera-Beita et al., 2019).

4.1 | Relative importance of climate and soil gradients

Climate and soil explained similar proportions of variances of species abundance and species occurrence, with low shared explained variances (1–3%), suggesting that climate and soil were non-redundant in explaining species distribution. This result is in line with Condit et al. (2013) who reported that rainfall and soil phosphorus shape the tree community of the Panamanian forest. The relative importance of soil and climate on biomass and forest structure has also been highlighted for other African (Lewis et al., 2013) and Amazonian (Quesada et al., 2012) forests. We are aware that climate and soil variables used in this study likely display different ranges of spatial autocorrelation. But we believe it is inherent to the context of the region, which is mostly a plateau, devoid of any short-distance change in elevation, and part of old, highly weathered surfaces of the African craton. Conversely, soil variation is expected to be moderate (we did not sample extreme topographic situations) and occur over short distances, along gentle catenas. Indeed, the existing soil map show the same type of soil mosaic over most of the area (Ségalen, 1967, p. 148). Thus, spatial autocorrelation is not expected to influence the measured effects of the two factors in the same way, but it is intrinsically linked to the ecological context and the research question.

Studies that emphasized stronger importance of climate over soil were done in drought-sensitive regions, where water availability is a limiting factor (Toledo et al., 2011; Toledo et al., 2012). Conversely, soil (or geology) can trump climate in areas of extreme soil conditions (e.g., sandstone, alluvium) (Réjou-Méchain et al., 2008; Fayolle et al., 2012). Extreme soil conditions may develop distinct textural (e.g., very sandy or clayey), chemical and structural properties (e.g., ferruginous nodules and duricrust as in some forests: Gourlet-Fleury et al. (2011)), and consequently have different levels of nutrients and water availability. Soil conditions can also be a stronger driver of species distribution in regions of weak climatic heterogeneity (Clark et al., 1999).

Climate and soil left 74–77% variance unexplained in our data set and other unaccounted factors certainly affect species abundance and occurrence. However, large shares of unexplained variance are common-place in species-rich tropical forests (e.g., Couteron et al. (2003); Réjou-Méchain et al. (2008)). In addition to community diversity itself, unexplained variances can result from unmeasured factors (e.g., human and natural disturbances and biotic interactions) and neutral processes (e.g., dispersal limitation and demographic stochasticity, Munoz et al., 2008). Bearing this in mind, we concluded on rather high fractions of explained variances for a tropical forest data set that did not sample extreme conditions, and this pleads for considerable influences of climate and soil on forest composition.

Unexplained variances could originate from forest gaps which are legacies of past natural or human disturbances. Forest gaps are rapidly colonized by light-demanding and short-lived pioneer species (Gourlet-Fleury et al., 2013). Even though our sampling avoided recently disturbed forests, pioneers such as Musanga ceccropioides (Figure 2c) and light-demanders like Sterculia rhinopetala and Desbordesia insignis (Figure 2c) were noticeable. Hence, different degrees of disturbance across the sampled forest are likely to be an influential factor we did not take into account. Accounting for such an effect may not be possible without historical records or observation of the forest dynamics. It is also likely that variation in forest composition reflects to some extent historical events on long time scales such as anthropogenic disturbances during the last centuries. For instance, the upper strata of a large part of forests in Cameroon are indeed dominated by long-lived, light-demanding species without...
apparent regeneration, suggesting past large-scale disturbances (Vlemmix et al., 2014; Morin-Rivat et al., 2017).

Another source of unexplained variance could be geographic distance. Inter-site variation is a sound basis for assessing neutral-like migration limitation (sensu Munoz et al. (2007); Munoz et al. (2008)) but it also underlies climate variation and both are difficult to disentangle. However, Hardy and Sonké (2004) found that species distribution could be better explained by limited dispersal (measured as the probability of finding two non-conspecific individuals according to the distance) than habitat heterogeneity in the Dja Biosphere Forest Reserve (a section of Somalomo locality, Figure 1, Appendix S1). Studies detailing population genetics and dispersal ability of species could also help reveal the role of neutral-like processes in these tropical forests and disentangle it from influence of present climate.

Other processes could also have contributed to the observed pattern of regionally abundant plant species such as interactions between trees and animal seed dispersers (Chanthorn et al., 2019) and differences in range size could also blur the pattern of environmental filtering by climate and soil.

4.2 | Insights from abundant and less abundant species

It has been frequently observed that diverse tropical forests are dominated by a small suite of species showing very high abundance, while the majority of other species are less abundant or rare (Gaston et al., 2000; Pitman et al., 2001; ter Steege et al., 2013). Drivers of this abundance pattern include habitat (ter Steege et al., 2013), demographic stochasticity (Hubbell, 2001), intra-specific competition, herbivory and other density-dependent mortality (Janzen, 1970; Comita et al., 2010). Abundance patterns and proportions of climate- or soil-explained species variance (Figure 4, Appendix S7) in our study area suggested climate fitness for the abundant species and soil fitness for the less abundant species. This result is similar to habitat–species associations reported in Korup, Cameroon (Chuyong et al., 2011), Ecuador (Valencia et al., 2004) and Bolivia (Toledo et al., 2012).

4.3 | Information of species occurrence versus local abundance

We showed tight relationships between explained variances of species abundance and occurrence in relation to climate and soil. Species presence in a community may reflect its ability to pass through the environmental conditions (Kraft et al., 2015). Species abundance on the other hand can reflect multiple processes operating simultaneously at the community level. Hence, similar relationships with environmental gradients for species abundance and occurrence, as observed here, could indicate that the effect of environmental gradients is the main process driving community assembly. This result has not been previously reported for rain forest tree communities. Despite overall strong relationships, some species deviate from this relationship, i.e., apparent influence of environment (climate/soil) on abundance but poor influence on occurrences, or the reverse (Figure 5).

Practical information of positive species occurrence–abundance relationships has been reviewed with major emphasis on cost-effectiveness of sampling effort in favor of presence/absence (Gaston et al., 2000; Wilson, 2012). In practice it is, however, difficult to conduct such a sampling scheme in tropical forests given the high stem and species densities. In addition, abundance data are also crucial for the evaluation of conservation status and for studying forest dynamics and assess biomass and carbon stock.

5 | CONCLUSION

Based on a large data set collected at regional scale in tropical rain forests of the Congo Basin, we found that climate and soil explain notable variance shares in tree species composition (abundance and occurrence). We showed that climate explains only a slightly higher fraction (~2.5%) of variance on species composition compared to soil, which challenges the notion of strong climate hierarchy over soil for tropical rain forests in Cameroon. Climate and soil jointly explain a very small proportion of variance in species composition, indicating that they have complementary and additive effects on species composition. We equally noticed that climate-explained variance mainly concerns species of high abundance while soil-explained variance mainly concerns species of less abundance. Finally, we found that species abundance and occurrence show congruent patterns across the soil and climate gradients although some species depart from the overall trend. Beyond the fundamental implication of unraveling environmental processes that underlie tree species abundance and occurrence, our results highlight that considering both climate and soil in modeling species distribution can improve mapping species range and distribution for tropical rain forests.

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AUTHOR CONTRIBUTIONS

MBL, VD, BS, NB, PP, RP, SL and PC designed the study; MBL, VD, BS, NB, PP, GK, NK, GM, STM, NT, SL and DZ collected field data; VD
and NB produced the maps; MBL, GD and PC performed statistical analyses; MBL wrote the paper with assistance from CF, GD and PC. All authors discussed the results and commented on the manuscript.

**ORCID**
Moses Bakanck Libalah  [ID](https://orcid.org/0000-0001-8848-8001)
Vincent Droissart  [ID](https://orcid.org/0000-0001-9798-5616)
Bonaventure Sonké  [ID](https://orcid.org/0000-0002-4310-3603)
Nicolas Barbier  [ID](https://orcid.org/0000-0002-5323-3866)
Gilles Dauby  [ID](https://orcid.org/0000-0002-9498-413X)
Claire Fortunel  [ID](https://orcid.org/0000-0002-8367-1605)
Gislain II Mofack  [ID](https://orcid.org/0000-0003-2261-1378)
Stéphane Takoudjou Momo  [ID](https://orcid.org/0000-0002-1226-4826)
Pierre Couteron  [ID](https://orcid.org/0000-0002-9498-413X)
Raphaël Pélissier  [ID](https://orcid.org/0000-0002-4045-992X)
Nicolas Texier  [ID](https://orcid.org/0000-0002-5323-3866)

**REFERENCES**


Appendix S5. Regional distribution of species abundance and species occurrence for 82 1-ha plots
Appendix S6. Relationship between species abundance and frequency at two spatial scales
Appendix S7. Species variance partitioning with respect to climate and soil gradients