



Environmental filtering determines patterns of tree species composition in small mountains of Atlantic Central African forests

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ABSTRACT

The determinants of patterns of plant species composition on small mountains are poorly known, especially in Central Africa. We aimed here to identify variation in tree species composition throughout the Ngovayang Massif (southern Cameroon) and determine the relative contributions of environmental factors and spatial autocorrelation in shaping tree species composition. Vegetation surveys were conducted in fifteen 1-ha (100 m × 100 m) permanent plots established along a transect from lowland (200 m) to submontane forests (900 m) in which all trees with a diameter (dbh) ≥ 10 cm were inventoried. Data were investigated using ordination methods (Correspondence Analysis and Canonical Correspondence Analysis). At the local scale, the most important variable in determining tree species composition patterns was slope exposure, followed by distance from the ocean and altitude. Together, these environmental variables explained 28% of floristic variation among plots, and the spatial structure almost disappeared when the effects of these variables were removed. Spatial autocorrelation analysis showed that spatial variables (geographic coordinates of the plots) or geographic distance between plots explained only 1% of the total initial variance. Residual spatial variation not explained by the environmental variables probably reflects the history of vegetation and the effects of other climatic variables that were not included in this study. Floristic variation in the Ngovayang Massif is due to strong environmental heterogeneity. The sensitivity of floristic composition to environmental variables such as slope orientation and altitude suggests that tree species composition may shift with expected climate changes, such as changes in the movement of air masses, increase in mean annual temperatures or increasing severity of the dry season. Our study highlights the need for systematic on-the-ground measurements of climate variables in tropical montane areas in order to better understand the current climate regime and serve as a basis for modelling future changes.

1. Introduction

With an estimated deforestation rate of 1–2% per year, the disappearance of tropical forests, due to land use changes, comes at a time when our knowledge of their structure and functional dynamics remains inadequate (MacDicken, 2015). Tropical forests are among the most species-rich ecosystems on earth and provide many ecosystem services to humanity (Chazdon, 2008; Fisher and Turner, 2008; Slik et al., 2015). Knowledge of the spatial patterns of biodiversity of tropical forests is crucial to assess the consequences of their degradation and wider habitat loss caused by human activities, and to develop systematic strategies for their conservation and management, including

the ability to forecast future forest composition (Fjeldsø, 2007; Taylor et al., 2009). To understand the mechanisms underlying patterns of species distribution and floristic composition in a given area, it is necessary to gain knowledge about the factors determining these patterns (Chave, 2008). In tropical ecosystems, three main theories invoke processes that may shape, either singly or in interaction, the spatial structure of the floristic composition of ecological communities: niche theory (environmental filtering), neutral theory (dispersal limitation) and historical factors (Maley, 1996; Tilman et al., 1997; Hubbell, 2001). The relative importance of these factors is thought to vary according to the scale being considered (Huston, 1999; Ricklefs, 2004). However, evaluating their respective roles remains a challenge

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(Ricklefs, 2005).

Several studies in tropical montane forests have shown that altitude (Lovett et al., 2001; Kessler, 2002; Ashton, 2003; Schmitt et al., 2010; Mohandass et al., 2017), distance from the ocean, and rainfall (Foster, 2001; Tchouto, 2004; Senterre, 2005; Jarvis and Mulligan, 2010) are important factors shaping the distribution of species. The effect on species composition of slope exposure (which reflects the effect of wind exposure) was also found to be significant, but more frequent and marked in large tropical mountains (range of 3000–4000 m asl) than in smaller ones (range of 1000–1400 m asl; Cusset, 1989; Stadtmüller, 1987; Bruijnzeel, 2001; Svenning et al., 2009). Large gaps still remain in our knowledge of patterns of tree species composition and their determinants, especially within small altitudinal gradients, as these have been seldom studied in comparison with larger ones.

Within the coastal ranges of Central Africa, several areas of higher relief (range of 1000–1400 m asl) situated along the Atlantic coast have been reported to display high levels of biodiversity and endemism (e.g. Linder, 2001; Küper et al., 2004; Tchouto et al., 2009; Gonmadje et al., 2011, 2012; Parmentier et al., 2011). However, at present, floristic inventories and data on patterns of plant species composition and their determinants are far from complete in these areas. Studies of the environmental determinants of species composition in mountainous areas have mostly focused on the largest mountains of the Cameroon volcanic line (e.g. Portères, 1946; Proctor et al., 2007; Momo, 2009; Forbeseh et al., 2011); the smaller montane or hill ranges along the Atlantic coast still remain relatively poorly documented, including the Ngovayang Massif in southern Cameroon (but see some information in Tchouto, 2004; Senterre, 2005; Hardy and Senterre, 2007). While previous studies in these smaller hill ranges have examined the importance of some ecological factors (altitude, distance from the sea, rainfall) on species distribution, they have not addressed the relative importance of these ecological factors and geographic distance in shaping species composition patterns at the local level. In particular, they have not used multivariate partitioning methods to quantify the contribution of each variable.

Since the publication of Letouzey's phytogeographic maps of Cameroon (1985), largely based on qualitative field observations and extensive collection of botanical specimens, little work has been undertaken on the Ngovayang Massif, aside from the quantitative inventories reported on by Gonmadje (2012) and by Gonmadje et al. (2011, 2012, 2017). Letouzey (1985) included this upland area in the “District Atlantique Biafréen”, lowland forest characterized by a high number of species of gregarious caesalpinoid legume trees. He also identified submontane forests in this massif. The first quantitative studies in this small mountain area, carried out by Gonmadje et al. (2011), showed that this massif exhibits high levels of biological diversity and has a correspondingly high level of endemism. More recently, another study carried out by Gonmadje et al. (2017) aimed to understand how the above-ground biomass of old-growth forests of the Ngovayang Massif varies across a short altitudinal gradient, and whether changes in potential maximum tree height can explain this variation. The complex geo-topographical diversity of this massif thus provides a suitable context for exploring the relative importance of geographic distance (which would lead to spatial auto-correlation as a result of neutral processes; Condit et al., 2002) and environmental heterogeneity in shaping species composition patterns at local level.

In this study we aimed to characterize variation in tree species composition in the Ngovayang Massif and to identify the underlying environmental determinants (wind exposure, altitude, rainfall, and distance from the ocean) of floristic variation. Based on the findings of the aforementioned studies, we hypothesized that environmental heterogeneity was the main factor structuring the composition of tree species in this massif, and we formulated and tested the following hypotheses:

- 1 The orientation of the Ngovayang Massif relative to the ocean, its

topography and its size result in a slope exposure effect despite the short altitudinal gradient. The slope facing the winds (windward) receives much more moisture and orogenic rainfall than the slope sheltered from the wind (leeward; Gemenen and Hazeu, 1999), thus inducing differences in species composition due to microclimatic differences between the two slopes of the mountain (Bruijnzeel, 2001; Foster, 2001; Jarvis and Mulligan, 2010);

- 2 Differences in altitude and in distance from the ocean lead to gradients in floristic composition, which varies from low and mid-altitude to sub-montane forests (Vázquez and Givnish, 1998; Givnish, 1999; Senterre, 2005), and from coastal to inland forests (Bruijnzeel, 2001; Foster, 2001; Tchouto, 2004; Jarvis and Mulligan, 2010);
- 3 In areas such as the Ngovayang Massif, with strong environmental heterogeneity (in topography, altitude and wind exposure), floristic variation is especially determined by environmental variables, and spatial autocorrelation (geographic distance) appears to be less important than in areas with little or very gradual variation of environmental factors (Condit et al., 2002; Réjou-Méchain et al., 2008).

2. Materials and methods

2.1. Study area

The Ngovayang Massif is a range of hills located in southern Cameroon, 80 km east of the Atlantic coast. The Massif covers an area of 102,000 ha and extends between 3°12' – 3°25' N and 10°30' – 10°45' E (Fig. 1). Altitude varies from 50 m above sea level in the western part to more than 1000 m in the eastern part, on the summits of the main hills. The area presents an oblique orientation to the coast, and it is characterized by highly dissected terrain, with alternating ridges and valley bottoms. The main ridge lines are parallel to the main axis of the massif and oriented north-east to south-west. The slope facing the Southeast has a steep topography while the northwestern slope is gentler and more exposed to solar radiation than the southeastern slope. Indeed, there is less cloud cover on the northwestern than on the southeastern slope (Gonmadje, 2012). The dominant soils in the Ngovayang Massif are ferralsols (IUSS Working Group WRB, 2006). The climate of the area is sub-equatorial. Average annual rainfall decreases eastward from the coast, from 2836 ± 393 mm at Kribi, west of the Ngovayang Massif, to 2096 ± 286 mm at Lolodorf (Olivry, 1986), to about 2000 mm annual rainfall in the area between Bipindi and Lolodorf at low altitude, i.e., 50 m asl (Waterloo et al., 1997). The mean annual temperature is 25 °C at low altitude, and decreases with increasing altitude, to below 18 °C at 1000 m (Olivry, 1986). Wind speeds are generally low throughout the year, with winds coming from the south-west or the west, especially during the rainy season (Olivry, 1986; Waterloo et al., 1997). The forests of the Ngovayang Massif are assigned to “wet Central African forests” (Swaine, 1996; Fayolle et al., 2014) and correspond to the “dense evergreen forest” classification of Letouzey (1985), with many caesalpinoid legumes in lowland areas (< 600 m asl). For more details see Gonmadje et al. (2011, 2017).

2.2. Forest inventory

Fifteen 1-ha (100 m × 100 m) permanent plots were established in old-growth terra firma forests (Fig. 1) at uniform intervals (of 200 m) along the altitudinal gradient and alternating on the southeastern and northwestern slopes, from 236 m to 1000 m. Floristic inventories were carried out from February 2008 to May 2010. Our design allowed testing of the influence of environmental factors on the floristic composition of the Ngovayang Massif. Within each plot, all trees with a diameter at breast height (dbh) ≥ 10 cm were identified. The diameter was measured with a diameter tape at 1.3 m above ground level, avoiding any protrusion on the trunk or lianas growing around it. All trees were permanently marked and labeled with numbered aluminum

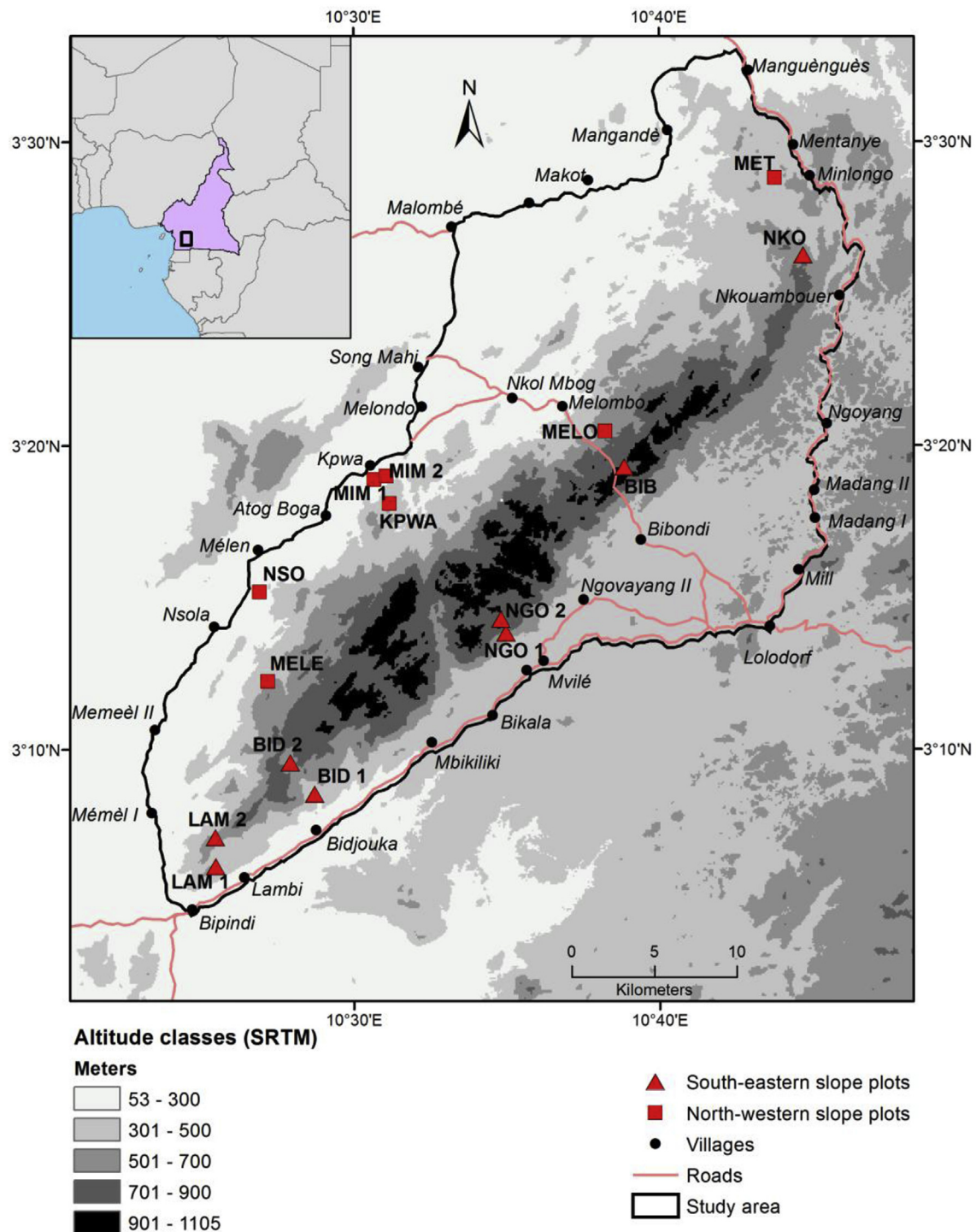


Fig. 1. Location of the 15 1-ha permanent study plots in the Ngovayang Massif.

tags. Details on protocols and measurement methods are described in Metcalfe et al. (2009).

Identification of the most common species was undertaken directly in the field whenever possible. Herbarium specimens of most species and morpho-species were collected, identified and preserved at the National Herbarium of Cameroon (YA). A total of 74% of morpho-species were subsequently identified to species level, 22% to genus level, 3% to family level and 1% remained undetermined. For the botanical nomenclature of families, we used the classification of the Angiosperm Phylogeny Group (APG IV; Byng et al., 2016). However, given the specificities of each of the subfamilies of Fabaceae sensu APG

III (Bremer et al., 2009; Caesalpinioideae, Mimosoideae, Faboideae), and the ecological importance of Caesalpinioideae in Central African forests (e.g. Letouzey, 1985; Doucet, 2003; Gonmadje, 2012), we considered each of the three subfamilies separately, which also enabled direct comparison with previous studies.

2.3. Environmental data

Each plot was characterized with a set of four environmental factors: altitude, slope exposure, distance from the ocean and mean annual rainfall.

Altitude (from 236 m to 1000 m) and geographic coordinates were recorded for each plot using a Garmin CSx 60 GPS (precision < 10 m), and distance from the ocean was calculated for each plot. The distance from the ocean varies from 50 km for the nearest plot to 95 km for the most distant plot. The slope exposure comprises two modalities: southeastern slope (n = 7 plots, 47% of the total number of plots) and northwestern slope (n = 8 plots, 53%). For the rainfall data, we used the literature (Olivry, 1986) and the WorldClim database (www.worldclim.org), which provides interpolated values of sparse data from climatic observations conducted between 1950 and 2000. This model shows a gradient of decreasing rainfall from the west (2400 mm) to the east (2050 mm) across the study area, which is congruent with the findings of Olivry (1986). The spatial variables were constituted by a third-order polynomial function of X and Y geographical coordinates of the plot centres (i.e. X, Y, XY, X², Y², X²Y, XY², X³ and Y³). Due to the relatively low heterogeneity of the geological substrate (mainly metamorphic rocks yielding acid soils), the combined effect of climate and substrate should have produced relatively uniform soils. Thus, plots were not differentiated according to soil type.

2.4. Data analysis

To describe the ecological importance of species and families within each plot as well as in the total flora, the Importance Value Index (IVI; Curtis and McIntosh, 1951) and the Family Importance Value index (FIV; Mori et al., 1983) were calculated.

IVI = relative density + relative frequency + relative dominance.

FIV = family relative diversity + relative density + relative dominance.

The main pattern of floristic composition was assessed with a Correspondence Analysis (CA; Hill, 1973) of the abundance matrix of 7967 trees belonging to 583 species in the 15 1-ha plots. We evaluated the relative importance of environmental variables in determining floristic composition patterns using Canonical Correspondence Analysis (CCA) and partial CCA (Legendre and Legendre, 2012). The environmental variables included quantitative variables (altitude, annual rainfall, and distance to the ocean) and a qualitative variable (slope exposure). To analyze the floristic patterns that were not explained by the environmental variables, we similarly performed a residual-CCA (i.e., a CCA of the residual table obtained once the effects of the explanatory variables have been removed). This enables examination of

whether the environmental variables selected really explain the main patterns emphasized by CA.

In order to investigate whether patterns in species composition were more related to geographic distance (spatial autocorrelation of environmental variables) or to environmental gradients, we conducted a partial CCA (Legendre and Legendre, 2012) by using the spatial variables as explanatory factors. To assess the statistical significance of each environmental/spatial variable before introducing them in the CCA ordination, Monte Carlo permutation tests were used (forward selection; Ter Braak and Smilauer, 2002).

All statistical analyses were performed with R software (R Development Core Team, 2015) using the ade4 (Thioulouse et al., 1997) and diversity (Pélissier and Couteron, 2007; <http://pelissier.free.fr/Diversity.html>) packages.

3. Results

3.1. Inventory data

The 15 plots contained a total of 7967 stems with dbh ≥ 10 cm, belonging to 583 species, 259 genera and 76 (sub-) families in the study area. The three most important family-level taxa in terms of number of species were Fabaceae-Caesalpinioideae (49 species), Annonaceae (43 species) and Malvaceae (32 species). The most important ones in terms of FIV were the Fabaceae-Caesalpinioideae (FIV = 41) and Myristicaceae (FIV = 20), due in large part to the abundance and basal area of *Tetraberlinia bifoliolata* (Caesalpinioideae) and *Coelocaryon preussii* (Myristicaceae), the species with the most important IVI values, respectively 12 and 9. The four most abundant species were *Treculia obovoidea* (Moraceae, 4% of all individuals), *Tetraberlinia bifoliolata* (3.5%), *Coelocaryon preussii* (3.4%) and *Dacryodes klaineana* (Burseraceae, 2.6%). These four species represented 14% of all individuals.

3.2. Variation in tree species composition

The Correspondence Analysis (CA) of the species abundance matrix showed clear differences in tree species composition within the Ngovayang Massif (Fig. 2). Eigenvalues showed an irregularly decreasing pattern, indicating the presence of a strong structure in the floristic table, with the first two prominent axes accounting for 22.2%

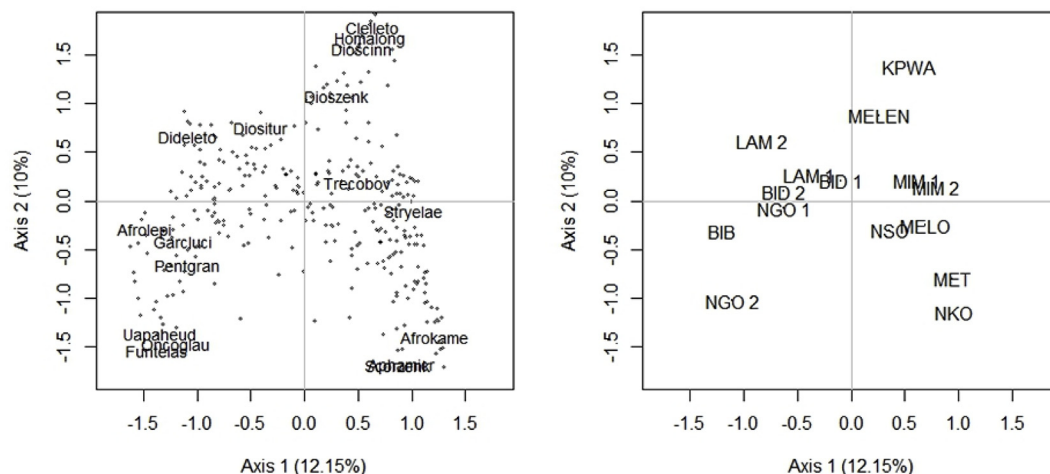


Fig. 2. Factorial plane defined by the first two axes of the Correspondence Analysis (CA) performed on the abundance matrix of 583 tree species in 15 1-ha sampling plots. The biplot shows the projection of species and plots respectively.

of the total inertia.

Axis 1 (12.2% of explained variation) of the CA reflected slope exposure. Plots from the southeastern slope, with negative values, were clearly separated from those of the northwestern slope, which had positive values (Fig. 2). Height species contributed strongly to Axis 1: *Pentadesma grandifolia*, *Garcinia lucida*, *Funtumia elastica*, *Didelotia letouzeyi* and *Afrostryax lepidophyllus*, with negative values, and *Treculia obovoidea*, *Strychnos elaeocarpa* and *Greenwayodendron suaveolens*, with positive values.

Axis 2 (10% of the explained variation) was most closely related to the variable “distance from the ocean”, but was also related to “altitude”. There was a separation between plots that were more distant from the ocean (≥ 70 km) with positive values, and plots that were nearest the ocean (distance < 70 km) with negative values. Within each slope exposure, the plots were clustered according to altitude. The lowland and mid-altitude forest plots (200 m - 700 m) were separated from submontane forest (high altitude) plots (top right and left; 800 m - 1000 m).

This second axis was mainly determined by *Afrostryax kamerunensis*, *Oncoba glauca* and *Hymenostegia afzelii*, species found further from the ocean and at higher altitude with positive values, and by *Cleistanthus letouzeyi*, *Diospyros zenkeri* and *Homalium longistylum*, species closer to the ocean and at low altitude with negative values. Rare species, which often unduly influence results of CA, had little influence on these first two axes.

Afroame: *Afrostryax kamerunensis*, Afrolepi: *Afrostryax lepidophyllus*, Cleileto: *Cleistanthus letouzeyi*, Dideleto: *Didelotia letouzeyi*, Dioscinn: *Diospyros cinnabarina*, Diositur: *Diospyros iturensis*, Dioszenk: *Diospyros zenkeri*, Funtelas: *Funtumia elastica*, Garcluci: *Garcinia lucida*, Homalong: *Homalium longistylum*, Oncoglau: *Oncoba glauca*, Pentgran: *Pentadesma grandifolia*, Stryelae: *Strychnos elaeocarpa*, Trecobov: *Treculia obovoidea*, Uapaheud: *Uapaca heudelotii*.

Ocean: distance from the ocean; Slope NW: northwestern slope; Slope SE: southeastern slope.

3.3. Environmental and spatial factors affecting plant species composition

After forward selection (Monte Carlo permutation test, see Appendix A), three variables (slope exposure, distance from the ocean and altitude) were found to be significantly related to floristic variation and together explained 28% of the total inertia (variability) of the abundance matrix (Table 1). The first two axes accounted for 72.5% of this explained variance and 20% of the total variance (Table 1). The eigenvalues of the two first canonical axes were relatively high for species (>0.4), indicating considerable beta diversity along the gradients.

The first axis of the CCA analysis was mainly determined by the slope exposure variable. The distance to the ocean and altitude were correlated with axis 2 (Fig. 3). CCA results confirmed those of CA. Indeed, almost all the species that significantly contributed to the first

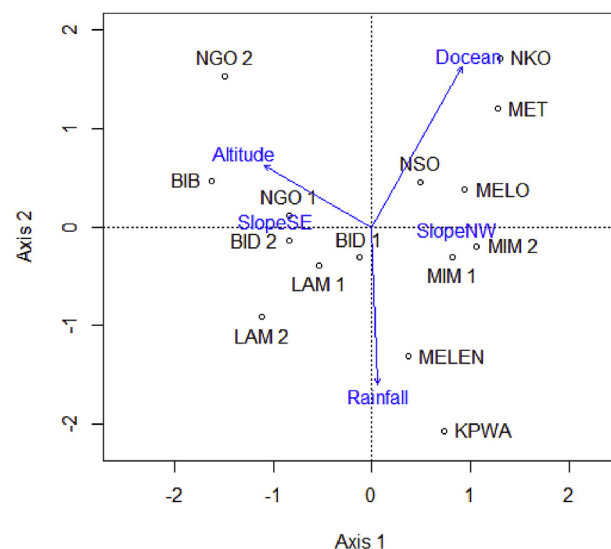


Fig. 3. A canonical correspondence analysis biplot of vegetation plots and environmental variables.

factorial CA plane also contributed to the first factorial CCA plane. The Redundancy Analysis (RDA) also revealed the same main gradients of floristic composition (Appendix B) as those from the CCA. This means that the dataset is sufficiently structured that the method used does not influence the main conclusions.

By using a partial CCA (Table 2), we observed that the slope exposure alone had greater explanatory power (11.3%) than the variables distance from the ocean (9.2%) and altitude (8.6%). The proportion of the variance explained by the set of these three parameters (28%) was similar to the sum of variances of different parameters taken separately (29.1%).

Furthermore, the proportion of the variance of the floristic table explained by the slope exposure, after the effects of distance from the ocean and altitude respectively were eliminated, remained high, representing about 31 and 32% of the total variance jointly explained by the two sets of variables (Table 2). Similar results were obtained for all other combinations of these three variables. This means that slope exposure, distance from the ocean and altitude were non-redundant for predicting floristic composition. For example, patterns for some species were well explained either by the slope exposure (e.g., *Pentadesma grandifolia*, *Plagiostyles africana*, *Strychnos elaeocarpa*), the distance from the ocean (e.g., *Diospyros zenkeri*) or altitude (e.g., *Afrostryax kamerunensis*, *Garcinia lucida*), while patterns for very few species (*Drypetes simulans* and *Albizia zygia*) were well explained by both axes (three variables).

3.4. Residual spatial patterns

In order to analyze whether the environmental variables really explain the main floristic patterns emphasized by the CA, we analyzed the unexplained part of the floristic table in a residual CCA.

The first two axes of the residual CCA (1–2) lost a great part of the initial structure represented by the CA (Fig. 4). There was no longer a slope exposure gradient for axis 1, nor gradients in distance from the ocean and altitude for axis 2. However, the first two axes of the residual CCA still contained a small proportion of the initial structure and thus had some similarities with the first two axes of the CA (Fig. 2). Indeed, the first axis of the residual CCA is still characterized by species with

Table 1

Summary results of Canonical Correspondence Analysis (CCA) related to floristic variance and environmental factors.

	Axis 1	Axis 2	Axis 3	Total variance
Eigenvalues	0.516	0.402	0.348	4.526
Percentage of explained variance	11.4	8.88	7.69	
Cumulative percentage of explained variance	11.4	20.28	27.97	
Variance explained				1.266
Unexplained variance				3.260

Table 2
Percentage of total variability of the floristic table explained by the ecological variables.

	Islope	Iocean	Ialt	Islope/ocean	Islope/alt	Iocean/slope	Iocean/alt	Ialt/slope	Ialt/ocean
CA	11.3	9.2	8.6	9.4	9.0	7.5	8.3	6.7	7.8

I_{slope} , I_{ocean} , I_{alt} , correspond to the variances explained by slope exposure, distance from the ocean and altitude, respectively. Values where two variables are separated by a slash (Islope/ocean, etc.) correspond to the variance explained by slope exposure once the effect of the distance from the ocean has been eliminated, etc.

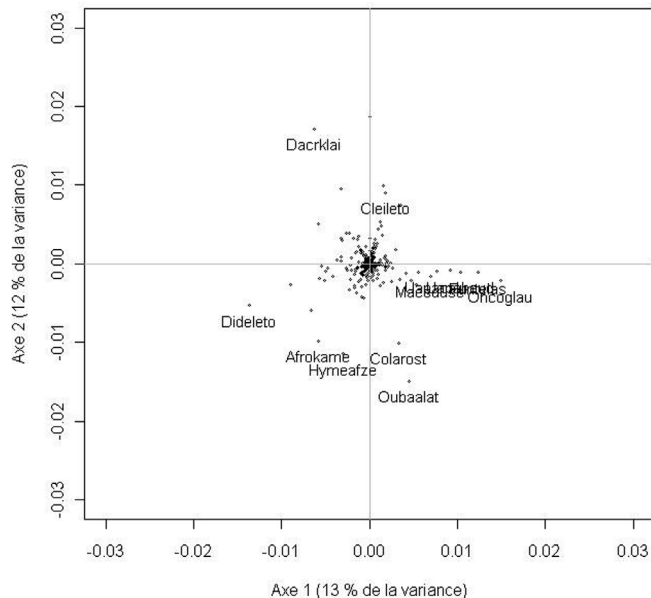


Fig. 4. Factorial plane defined by the first two axes of the residual Canonical Correspondence Analysis once the effects of the explanatory variables have been removed.

high contributions such as *Funtumia elastica* and *Didelotia letouzeyi*. So, the distribution of these species is poorly explained by the slope exposure variable. Similarly, axis 2 of the residual CCA is still characterized by species such as *Cleistanthus letouzeyi* and *Afrotyrax kamerunensis*; the distribution of these species is not related to distance from the sea and altitude variables. None of these species showed a clear distribution gradient. So, their distribution might be explained by variables other than the ones that were measured here. However, although the variance explained by the environmental variables measured was somewhat less than 30%, these variables contributed greatly to the main floristic patterns observed in CA.

Finally, after the Monte Carlo permutation test on the spatial variables (X, Y, XY, X^2 , Y^2 , X^2Y , XY^2 , X^3 and Y^3), significant geographic coordinates (X, Y) introduced in the CCA explained 18.9% of the total initial variance of the floristic table. For the same analysis conducted on the residual environmental table, i.e., once the effects of slope exposure, altitude and distance to the ocean were removed, the spatial variables explained only 1% of the total initial variance. This means that 17.9% of the total variation was explained by the environmental variables. This result further demonstrates that the environmental variables - slope exposure, altitude and distance to the ocean - have a significant effect on the multi-species spatial patterns in this forest. Hence, most of the multi-species spatial structure was closely related to environmental variation.

Afrokame: *Afrotyrax kamerunensis*, Colarost: *Cola rostrata*, Dideleto:

Didelotia letouzeyi, Cleileto: *Cleistanthus letouzeyi*, Dacrkilai: *Dacryodes klaineana*, Oncoglau: *Oncoba glauca*, Hymeafze: *Hymenostegia afzelii*, Oubaalat: *Oubanguia alata*.

4. Discussion

We have shown here that, even on a small mountain barely exceeding 1000 m asl, the Ngovayang Massif, the slope exposure, distance from the ocean and altitude all explained a significant part of the variation in species composition across short spatial gradients. These environmental factors were non-redundant and all contributed significantly to explaining floristic variation in the Ngovayang Massif, in decreasing order: slope exposure (11.3%) > distance from the sea (9.2%) > altitude (8.6%). The results support our prediction that strong environmental heterogeneity is the primary factor determining species composition at the local scale.

4.1. Slope exposure

Slope exposure, which potentially reflects wind exposure and humidity (Jarvis and Mulligan, 2010), had greater explanatory power for species composition than distance from the ocean or altitude. This slope exposure effect was not noted in earlier studies carried out in other massifs along the Atlantic coast of Central Africa (Achoundong, 1995; Tchouto, 2004; Senterre, 2005). These studies showed that it was mainly the distance from the ocean, rainfall gradients, altitude or human disturbances that structured plant communities. This is certainly due to the fact that the sites subject to these studies were mostly isolated hills, while the Ngovayang Massif is a single larger massif.

On the other hand, similar results have been shown for other large hills in Atlantic Central Africa, mainly in the Congo Republic (Cusset, 1989; Doumenge, 1992), and elsewhere in the tropics (Jarvis and Mulligan, 2010). Indeed, in the absence of geological and soil differences, the importance of slope exposure may be due in large part to the very marked relief of the Ngovayang Massif, which presents ridge lines that are very well delimited and high enough to influence the local climate. The orientation of the Ngovayang Massif relative to the coast and the prevailing winds, its topography and size result in a slope effect despite the short altitudinal gradient. The explanation of this effect is not evident at first glance, as the main axis of the Ngovayang Massif is NE-SW, parallel to the main winds coming from the SW, but which can vary in direction from SSW to W (Olivry, 1986; Waterloo et al., 1997). The data available on precipitation (i.e. WorldClim) tend to show that the southwestern parts of both slopes are wetter than the northeastern ones, and they do not show obvious precipitation differences between slopes. However, these data are coarse.

Nevertheless, there are some indications showing that the south-eastern slope is more humid compared to the northwestern slope of the mountain. Firstly, although data on wind directions are available only from a few meteorological stations (e.g., Kribi) and not at all for sites within or near the Ngovayang Massif, global circulation models tend to show that winds coming from the ocean are hitting first the south-eastern slope (but see Djoufack Manetsa, 2011). Furthermore, data on

the length of the raining season and on the frequency of clouds with cold top (sources of precipitations) shows decreasing gradients from the Southeast to the Northwest in this region (Tsalefac and Dagnone, 1990). This is in favor of a more humid and cloudier southeastern slope. The southeastern side of the mountain is characterized by steeper slopes, which may induce more active vertical air movements, mists and low clouds that bathe the forest, leading to higher local precipitations through cloud stripping, higher relative humidity, lower evapotranspiration and lower air temperatures compared to the northwestern side (Bruijnzeel, 2001; Jarvis and Mulligan, 2010).

Secondly, all of these local climatic differences have an impact on the vegetation (Hamilton et al., 1995). The forests of the southeastern slope are characterized by a greater abundance of mosses and epiphytes than the northwestern slope (Gonmadje et al., 2011; Gonmadje, 2012), which is a sign of a more humid climate (Letouzey, 1985; Senterre, 2005). These microclimatic differences between the two slopes can thus explain the gradients in species composition (Bussmann, 2001). More humidity on the southeastern slope and a foehn effect on the other one could explain, at least partially, the differences in floristic composition between slope exposure that were observed here (Bruijnzeel and Proctor, 1995; Bruijnzeel, 2001).

Certain taxa were more frequent on the southeastern slope than on the northwestern slope. These were mostly species characteristic either of submontane forests (e.g. *Garcinia lucida*, *Pentadesma grandifolia*) or of forests having a particular ecology characterized by high atmospheric or edaphic humidity (Letouzey, 1985; Stadtmüller, 1987; Senterre, 2005), such as forest on hydromorphic soil, swamp forest or valley forest (e.g. *Dacryodes klaineana*, *Oubanguia alata*, *Uapaca heudelotii*). Their presence on this slope can be explained by the phenomenon of ecological compensation due to atmospheric humidity (Budowski, 1965; Senterre, 2005). In addition, plots located at comparable altitudes on the two slopes and at almost equal distance from the ocean differed by the physiognomy of their vegetation (e.g. in the abundance of mosses and epiphytes; Gonmadje, 2012) and their floristic composition, confirming the predominance of the slope exposure effect relative to those of the other variables studied.

4.2. Distance from the ocean

Increasing distance from the ocean reflects the continuous decline of marine influence on the climate (Senterre, 2005; Jarvis and Mulligan, 2010). In the Ngovayang Massif, available climatic data show a relatively marked rainfall gradient between its extremities closest to and farthest from the ocean, respectively 2400 mm and 2000 mm. Although rainfall was not a significant predictor in this study - perhaps due to limited resolution of WorldClim data - it was negatively correlated with distance from the ocean (Table 1). Indeed, with increasing distance from the ocean, the air progressively discharges its humidity (Bruijnzeel, 2001; Senterre, 2005; Jarvis and Mulligan, 2010). Therefore, the mean annual rainfall in this part of Cameroon, as elsewhere in the world, generally decreases with increasing distance from the ocean (Olivry, 1986).

As a result, the floristic composition changes progressively from the coast to the interior. The area closest to the coast was characterized by the abundance of indicator species of hyper-wet and coastal forests, tolerant of high levels of rainfall, such as *Oubanguia alata*, *Sacoglottis gabonensis* and *Diospyros* spp. (*D. iturenensis* and *D. zenkeri*). The part of the massif furthest from the coast was characterized by the abundance of species such as *Scorodophloeus zenkeri* and *Afrostryax kamerunensis*, which are indicators of mixed and semi-deciduous forests, and therefore typical of less humid areas (White, 1979; Letouzey, 1985; Senterre, 2005). Similar results related to the effect of distance from the ocean on

floristic variation have also been demonstrated in other forests in Central Africa (Tchouto, 2004; Senterre, 2005; Kouob, 2009) and in Amazonia (Torres et al., 1997; Oliveira-Filho and Fontes, 2000), but usually over a much greater range of distances.

4.3. Altitude

Although the altitudinal gradient was short (800 m), it played an important role in tree species distribution and floristic variation of the Ngovayang Massif, confirming similar results found in the few other African tropical forests with a short altitudinal gradient, of less than 1000 m, which have been studied (Achoundong, 1995; Doucet, 2003; Eilu et al., 2004; Tchouto, 2004; Senterre, 2005). It is well known that increasing altitude is accompanied by a decrease in temperature, combined (in tropical forests) with an increase in atmospheric humidity, exerting therefore a strong influence on forest structure and composition (Takyu et al., 2005; Sesnie et al., 2009; Toledo et al., 2011; Sevegani et al., 2016).

The floristic patterns we found at different taxonomic levels with increasing altitude coincide with those cited by other authors for Central African forests (White, 1983; Letouzey, 1985; Maley, 1987; Senterre, 2005; Forbeseh et al., 2011). For example, some families, such as Burseraceae, Clusiaceae and Apocynaceae, became more abundant and diverse with increasing altitude, while Fabaceae-Caesalpinioideae, particularly the gregarious species, decreased with altitude (Gonmadje et al., 2017), confirming these previous findings. Similarly, some species rare in the lowlands were abundant at high altitudes (800–1000 m). These include *Hymenostegia afzelii* (an exception among caesalpinioideae legumes), *Garcinia lucida*, *Afrostryax lepidophyllus* and *Pentadesma grandifolia*. These species are known as indicators of submontane forest in other sites in Central Africa (Letouzey, 1985; Achoundong, 1995; Doucet, 2003; Tchouto, 2004; Senterre, 2005).

In addition to these ecological differences, there are physiognomic and structural differences between lowland and submontane forests (Gonmadje et al., 2017). Whereas the lowland forests in Ngovayang are characterized by a high canopy (up to 45 m) and the abundance of emergent trees, submontane forests possess a lower canopy (20–35 m), a greater representation of individuals of small diameter and fewer emergent trees (Gonmadje, 2012; Gonmadje et al., 2017). A major physiognomic trait of submontane forests is also the proliferation of mosses and epiphytes on trees. The presence of epiphytes is linked to frequent and persistent mist and to the lower temperatures and greater cloud cover and atmospheric humidity than in lowland forests (Achoundong, 1995; Doucet, 2003; Tchouto, 2004; Senterre, 2005). In the Ngovayang Massif, submontane forests begin to appear at around 600 m, their presence at this low altitude being strongly related to the proximity of the ocean, where clouds form at lower altitudes than further inland, and to the cloud stripping phenomenon mentioned above, as shown by previous studies in various tropical regions (Bruijnzeel and Hamilton, 2000; Gillet et al., 2003; Sosef et al., 2004; Senterre et al., 2009; Jarvis and Mulligan, 2010).

4.4. Residuals: exploring the potential causes of unexplained variance

The analysis of residual, unexplained variance in tree community composition allowed evaluation of whether the environmental variables measured were really responsible for the major trends that were observed (Couteron et al., 2003). Indeed, if the initial structure of the CA is no longer apparent in the residual table of CCA when the effects of environmental variables are removed, this means that these variables had a significant effect on the distribution of species. On the contrary, if the patterns of the initial floristic table (CA) were still strongly present

in the residual table, this would mean that the environmental variables measured poorly explained this pattern, regardless of the percentage of unexplained variance (Couteron et al., 2003).

In our study, analysis of residuals showed that there was no clear structure once the effects of environmental variables were removed. Therefore, the slope exposure, distance from the sea and altitude were able to account for a large part of the variation in floristic structure of this massif. However, some species whose contributions were already apparent in the initial structure were still represented in the residual table. Thus, the distribution of these species was poorly explained by the measured variables. It is noteworthy that each of these species was present and abundant in only one or two plots. At least some of them, e.g., *Cleistanthus letouzeyi* and *Didelotia letouzeyi*, have very low dispersal capacities, which could explain their presence in only one or two plots. In contrast, species with high dispersal potential such as *Afrostyrax kamerunensis* and *Funtumia elastica* (Doucet, 2003; Senterre, 2005), do not contribute to any clearly interpretable structure in the residual table. Furthermore, when the statistically significant geographic coordinates (X,Y) were taken into account in the partial CCA, the spatial variables explained only 1% of the total initial variance once the effects of environmental variables were removed. This result confirmed once again the effects of the environmental variables on floristic patterns of these forests, despite an eventual spatial autocorrelation of the environmental variables.

In tropical forests, most environmental variables explain only a limited proportion of the floristic variation (Couteron et al., 2003), because factors related to stochasticity always generate a part of unexplained variance (Chave, 2004; Tilman, 2004). However, the fact that slope exposure was an important factor in explaining tree species composition suggests that other climatic variables that could not be measured directly in this study could also influence species distribution. These other variables include in particular wind speed, atmospheric humidity, clouds and horizontal precipitation (through cloud stripping), local rainfall and temperature at each station, intensity and duration of solar radiation and evapotranspiration (Ter Steege et al., 2000; Slik et al., 2003). These variables may have contributed partially to the unexplained variance.

5. Conclusion

This study has shown that floristic variation in a rather small mountainous massif is primarily explained by strong environmental heterogeneity. Indeed, we show that, over a short altitudinal gradient (800 m), slope exposure, distance from the ocean and altitude are important drivers of floristic variation. The fact that these variables are related to climate is indicative that species distribution is primarily determined by climatic differences along the massif (cloudiness, temperature, humidity, rainfall, wind speed, evapotranspiration and solar radiation). Although stochastic processes always generate some of this unexplained variance, it is necessary to carry out further investigation on these other climatic variables that were not considered in this study,

as well as multiple biotic interactions. In Central Africa, the poor network of meteorological stations (Bigot et al., 2016) and, especially, the lack of climatic data in mountainous environments, are particularly serious with respect to climate change. There is a great need to consolidate these climatic data in order to validate satellite estimates and better understand climate-vegetation relationship. This is especially important because any prediction of the effects of climate change on tropical forest requires reliable data on the present climate and the interaction between bioclimatic factors and species.

Furthermore, quantifying the historical causes of the current distributions of species remains a goal for future research in these small mountains, which are suspected to have harbored forest refugia during past climatic fluctuations (Maley, 1996). As climate change scenarios for tropical forests predict increased temperatures and stronger dry seasons (IPCC, 2007), tree species composition may shift with climate change. Although prediction on changes due to global changes (climate and land use changes) impacts are generally measured at a broad scale, projections tend to indicate a smaller increase in mean temperature and more stable precipitations close to the Atlantic coast than further inland, and especially compared to the central Congo basin (see de Wasseige et al., 2015). Nevertheless, submontane species adapted to a cooler and more humid climate will be most affected, and will be at risk of disappearance from smaller mountains. Taking these factors into account in planning decisions and in the management of these forests will ensure more successful conservation outcomes.

Author contributions

Christelle Gonmadje and Charles Doumenge conceived and designed the experiments. Christelle Gonmadje conducted fieldwork and analyzed the data. Christelle Gonmadje, Terry Sunderland, Doyle McKey and Charles Doumenge wrote the manuscript.

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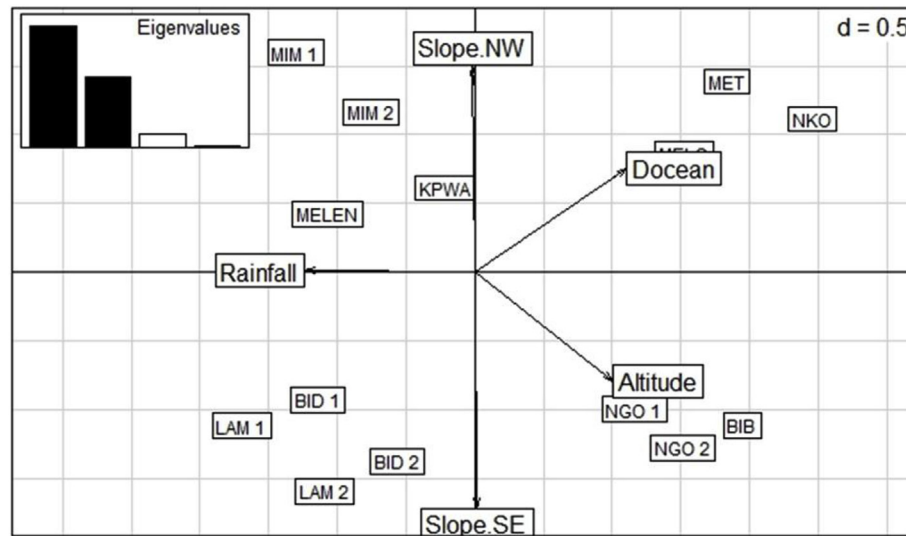
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Appendix A. Results of Monte Carlo permutation tests showing the statistical significance of each environmental variable. Environmental variables with $p < 0.05$ were considered significant.

Variables	AIC	F	Number of permutations	p
Slope exposure	118.90	1.6587	199	0.005 **
Distance from the ocean	119.26	1.3122	199	0.035 *
Altitude	119.36	1.2248	199	0.045 ·
Rainfall	119.46	1.1263	99	0.190

Signif. codes: ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘.’ 0.1 ‘ ’ 1.

Appendix B. A Redundancy Analysis (RDA) biplot of vegetation plots and environmental variables.



Docean: distance from the ocean; Slope NW: northwestern slope; Slope SE: southeastern slope.

Appendix C. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2018.04.001>.

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