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TRAINING IN GRADUATE
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HEALTH & ENVIRONMENTAL
SCIENCES

The Role of Environmental Drivers in Tree Community Structure of Central African Lowland Forests

Thesis submitted and publicly defended in fulfillment of the
requirements for the award of a Doctorat/Ph.D in Plant Biology

Par : **LIBALAH Moses BAKONCK**
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Sous la direction de
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Année Académique : 2018

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FACULTE DES SCIENCES
FACULTY OF SCIENCE

DEPARTEMENT DE BIOLOGIE ET PHYSIOLOGIE VEGETALES
DEPARTMENT OF PLANT BIOLOGY

ATTESTATION DE CORRECTION

****

Nous soussignés, membres du Jury de soutenance de la thèse de Doctorat/Ph.D en Biologie des Organismes Végétaux option Botanique-Ecologie de l'étudiant **LIBALAH Moses BAKONCK**, Matricule **13T2171**, soutenue publiquement le 19 Juin 2018 sur le sujet **«The role of environmental drivers in tree community structure of central African lowland forests»** attestons que les corrections conformément aux remarques et recommandations du jury lors de la soutenance de la dite thèse de Doctorat/Ph.D ont été effectuées par le candidat.

En foi de quoi, la présente attestation lui est délivrée pour servir et valoir ce que de droit./-

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10	NJILAH Isaac KONFOR	Maître de Conférences	En poste
11	NKOUMBOU Charles	Maître de Conférences	En poste
12	TEMDJIM Robert	Maître de Conférences	En poste
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30	NJOM Bernard de Lattre	Chargé de Cours	En poste
31	NYECK Bruno	Chargé de Cours	En poste
32	ONANA Vincent	Chargé de Cours	En poste

33	TCHAKOUNTE Jacqueline ép. NUMBEM	Chargé de cours	*CEA MINRESI*
34	TCHOUANKOUE Jean-Pierre	Chargé de Cours	En poste
35	ZO'O ZAME Philémon	Chargé de Cours	*S.G. MINTP*
36	TEMGA Jean Pierre	Chargé de Cours	*En poste*
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Répartition chiffrée des enseignants permanents par Département (Janvier 2017)

Département	**Nombre d'enseignants**				
	Pr	**MC**	**CC**	**ASS**	**Total**
BC	5 (1)	8 (3)	16 (9)	14 (6)	40 (19)
BPA	10 (0)	9 (1)	14 (6)	11 (4)	44 (11)
BPV	3 (0)	7 (1)	12 (3)	7 (6)	29 (10)
C.I.	6 (1)	8 (0)	14 (3)	7 (2)	35 (6)
C.O.	9 (0)	10 (3)	12 (3)	2 (0)	33 (6)
IN	3 (1)	2 (0)	7 (0)	18 (4)	30 (5)
MA	3 (0)	6 (0)	17 (1)	7 (0)	33 (1)
MB	1 (0)	4 (1)	6 (2)	2 (0)	13 (3)
PH	8 (0)	10 (1)	18 (2)	5 (2)	41 (4)
ST	3 (0)	10 (1)	20 (4)	10 (0)	44 (5)
Total	51 (3)	73 (11)	136 (33)	83 (24)	339 (70)

Soit un total de: 341 (70) dont

- Professeurs: 51 (3)
- Maîtres de Conférences : 73 (10)
- Chargés de Cours: 136 (33)
- Assistants: 83 (24)
- ( ) = Nombre de femmes.

DEDICATION

To

Mama Pauline BALAH MULONGO (of blessed memory)

Pa’a Jacob NDAKO NDAH (*alias* Pa’a 14)

Marie Claire VERANSO epse LIBALAH

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- LORD, TAKE THE GLORY.

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AGB: Aboveground Biomass

CAIV: Symetric Correspondence Analysis with Instrumental Variables

CALF: Central African Lowland Forests

FDP: Forest Dynamics Plot

H-D: Height-diameter relationship

LPC: Leaf Phosphorus Content

LNC: Leaf Nitrogen Content

NSCAIV: Non-Symetric Correspondence Analysis with Instrumental Variables

RMSE: Residual Mean Standard Error

ABSTRACT

Tree communities vary at different spatial scales and are influenced by environmental factors. To understand the role of environmental factors in tree communities requires a scale-wise analysis. The overall objective of this study was to analyse the influence of environmental drivers (soil and climate) on three aspects of tree community structure (floristic patterns, tree height–diameter relationship and leaf functional traits) at regional (>100 km^2) and local (0.5 km^2) spatial scales.

This study was conducted in Cameroon, Gabon and the Democratic Republic of the Congo, all belonging to the lowland (< 800 m) forests of Central Africa. For regional scale analyses, data from 183 plots of one ha (100 m × 100 m) were involved: 133 non-contiguous permanent plots of one ha separated by at least 500 m were established in mature forests and the 50 ha forest block in Korup, Cameroon which was split into into 50 single one ha plots. For local scale-analyses, only the data from the 50 ha forest block were used. For the entire study, each one ha plot was subdivided into 25 quadrats of 20 m × 20 m wherein all trees with diameter at breast height greater than or equal to 10 cm were measured, identired and mapped. Ten soil and ten climatic variables were collected and analysed for 78 plots drawn from all sites while five leaf functional traits (leaf area, specific leaf area, leaf phosphorus content, leaf nitrogen content and nitrogen: phosphorus ratio) were measured only in Korup. Principal component analyses permitted to determine soil and climate gradients, and correspondence analysis with instrumental variables enabled to decompose the respective influence of soil and climate on floristic patterns. The Second-order polynomial model permitted to model tree height-diameter relationship while linear regression and correlation were employed for trait-gradient analysis with the help of R statistical software.

At the regional scale, that is the case of the moist forests of eastern Cameroon, floristic patterns were characterised by few “abundant species” (> one individual ha^{-1} per site) and by many “scarce species” (≤ one individual ha^{-1} per site). The gradients in soil composition (soil texture, phosphorus and organic fertility) explained 15.42 % (76/493) mostly scarce tree species while the climatic gradients (rainfall, temperature and precipitation seasonality) explained 26.37 % (130/493) mostly abundant tree species. Still at the regional scale, that is, including all three countries, tree basal area and the climatic gradient improved the prediction of tree height with only 18.9 % model error as opposed to 20.2 % and 21.7 % model error from two existing pantropical height–diameter models (Chave and Feldpausch, respectively). The new height–diameter models also improved aboveground biomass prediction and revealed that the pantropical models consistently overestimated biomass by 25 and 55 Mg.ha^{-1}. At the local scale, that is, in Korup forest, soil fertility was the main gradient and significantly correlated with the leaf functional traits (leaf area, specific leaf area, leaf phosphorus and nitrogen contents). At this scale, up to 33 % of these traits were significantly either over-dispersed or under-dispersed (non-random distribution) confirming the influence of abiotic filtering by the soil fertility gradient.

At the regional scale, in the prospect of possible climate change, there may be a shift in species dominance for tree species in eastern Cameroon forests while the effects of soil on the scarce species pool may limit the risk of extinction. Still at this scale, this study thus presents an improved height-diameter model to predict the heights of Central African forest trees by integrating the effects of some easy-to-retrieve ecological predictors. At the local scale, leaf functional traits reveal the effect of soil gradient in the distribution of species and community assembly.

Keywords: Central Africa, community structure, floristic patterns, height–diameter relationship, leaf functional traits, lowland forests, Permanent Sampling Plot.

RÉSUMÉ

Les communautés d'arbres varient à différentes échelles spatiales et sont influencées par des facteurs environnementaux. Pour comprendre le rôle des facteurs environnementaux dans la structuration des communautés d'arbres, une analyse par échelles spatiales est nécessaire. L'objectif global de cette étude est d'analyser l'influence des facteurs environnementaux (sol et climat) sur trois aspects de la structure des communautés d'arbres, à savoir les patrons floristiques, les hauteurs des arbres et les traits fonctionnels foliaires, à échelle spatiale régionale (>100 km2) et locale (< 0,5 km2).

Le présent travail a été mené dans les forêts de basses altitudes (< 800 m) de trois pays d'Afrique centrale : le Cameroun, le Gabon et la République Démocratique du Congo. Pour les analyses à l'échelle régionale, les données de 183 parcelles d'un hectare (100 m × 100 m) ont été utilisées:133 parcelles permanentes d'un hectare, non contiguës et séparées d’au moins 500 m, ont été établies en forêt mature et le bloc forestier de 50 ha à Korup (Sud-ouest Cameroun), divisé en 50 parcelles d'un hectare. Pour les analyses à l’échelle locale, les données ont été obtenues dans un bloc forestier de 50 ha localisé dans le parc national de Korup (Sud-ouest Cameroun). Pour tous les inventaires, les parcelles ont été subdivisées en 25 quadrats de 20 m × 20 m et tous les arbres de diamètre à hauteur de poitrine au moins égal à 10 cm ont été identifiés, mesurés et cartographiés. Dix variables du sol et dix variables climatiques ont été recueillies et analysées pour 78 parcelles ; cinq traits fonctionnels foliaires (surface foliaire, surface foliaire spécifique, teneur en phosphore et en azote des feuilles, rapport azote/phosphore) ont été mesurés seulement pour le site de Korup. Les analyses en composantes principales ont été utilisées pour déterminer les gradients de sol et de climat, et l'analyse de correspondance avec des variables instrumentales a permis de décomposer leur influence sur les patrons floristiques. Le modèle polynomial de second degré a permis de modéliser la relation hauteur-diamètre de l'arbre, tandis que les analyses de régression linéaire et de corrélation ont été utilisées pour l'analyse de gradient-trait à l'aide du logiciel statistique R.

A l'échelle régionale, le cas des forêts humides de l'est du Cameroun, les patrons floristiques se caractérisent par quelques « espèces abondantes » (c’est à dire avec une moyenne par site > un individu ha-1) et par de nombreuses « espèces rares » (c’est à dire avec une moyenne par site ≤ 1 individus ha-1). Les gradients de fertilité (phosphore et matière organique) et de texture du sol expliquent la répartition de 15,42 % (76 / 493) des espèces, pour la plupart rares, alors que les gradients climatiques (température et la saisonnalité) expliquent la répartition de 26,37 % (130 / 493) des espèces, majoritairement qualifiées comme abondantes. Toujours à l'échelle régionale, c'est-à-dire, y compris les trois pays, l’intégration dans le modèle de la surface terrière des arbres et du gradient climatique améliore la prédiction de la hauteur des arbres avec une erreur associée de 18,9 %, contre 20,2 % et 21,7 % d'erreur associée pour les deux modèles pantropicaux préexistants. Le nouveau modèle hauteur-diamètre proposé améliore également la prédiction de la biomasse aérienne alors que les deux anciens modèles pantropicaux ont tendance à surestimer la biomasse de 25 et 55 Mg ha-1. A l'échelle locale (Korup), la fertilité du sol est le gradient principal qui explique la distribution des espèces ; il est significativement corrélée aux traits fonctionnels foliaires mesurés (surface foliaire, surface foliaire spécifique, teneur en phosphore et en azote des feuilles). Jusqu'à 33 % de la distribution des traits était soit sur-dispersée soit sous-dispersée (une distribution non aléatoire), confirmant l'influence de la filtration abiotique par le gradient de fertilité du sol.

Dans la perspective d'un éventuel changement climatique, ces résultats démontrent qu’à l’échelle régionale il pourrait y avoir un changement dans la dominance des espèces d’arbres tandis que l’influence marquée du sol sur la distribution d'espèces rares pourrait limiter le risque d'extinction de ces dernières. En outre, cette étude présente un modèle de hauteur-diamètre amélioré pour prédire les hauteurs et la biomasse des arbres d'Afrique centrale en intégrant certains prédicteurs écologiques faciles à obtenir. Enfin, il a été montré qu’à l’échelle locale l’étude des traits fonctionnels foliaires peuvent révéler des processus de filtration abiotique par le gradient de fertilité du sol.

Mots clés: Afrique centrale, communauté végétale, Forêts de basse altitude, parcelle permanente d'échantillonnage, patron floristiques, relation hauteur-diamètre, traits fonctionnels.

Chapter I

GENERAL INTRODUCTION

Chapter I: GENERAL INTRODUCTION

I.1. Context and justification

The structure of ecological communities is thought to respond to interrelated factors acting at different spatial scales (HilleRisLambers *et al.*, 2012; Hubbell, 2001; Ricklefs, 1987; Zobel, 1992). At regional scale, it is more likely to disentangle the effects of climate, historical and geological processes to determine community composition, whereas microclimate, edaphic conditions and species interactions play a major role in structuring communities and functional traits diversity at the local scale. Studies contributing to understand the structure of communities and underlying processes in tropical forests have scientific interests and practical goals. Particularly interesting are studies connecting explanatory factors acquired at regional scales (i.e. > 100 km^2) and local scales (i.e. < 100 km^2) with one or several components of forest structure (Fayolle *et al.,* 2014; Gourlet-Fleury *et al.,* 2011; Parmentier *et al.,* 2007; Réjou-Méchain *et al.,* 2014).

Explanatory factors shaping ecological communities are many and can generally be grouped as deterministic or stochastic in nature. The relative role of these two groups of factors are widely debated in the literature (Condit *et al.,* 2002; Hubbell, 2001; Tuomisto *et al.,* 2010). The mainstream approach has been to partition the variance of a response ecological community between environmental and spatial explanatory factors and the unexplained fraction are interpreted as the consequence of stochastic factors (Legendre *et al.,* 2005). In its favour, environmental factors (environmental determinism) have received much attention in the last decades given the impact its variation may impose on ecological communities, especially on tropical forest communities.

Tropical forests host a remarkable biodiversity, containing over 50 % of known terrestrial biodiversity crowded in less than 10 % of the total land surface (Anonymous, 2011). The Central African forest is only comparable to the Amazonia in South America, covering 255 million ha of non-contiguous forests (de Wasseige *et al.,* 2014; Anonymous, 2011; Mayaux *et al.,* 2013). From geo-referenced records, these forests are estimated to host 15 387 plant species, of which 3013 are trees (Sosef *et al.,* 2017) and an average of 426±11 stems per one ha forest plot with diameter ≥ 10 cm (Lewis *et al.,* 2013). Despite the importance of the Central African forests for terrestrial biodiversity, the influence of environmental factors on its forest community structure remains poorly understood (Parmentier *et al.,* 2007).

At the regional scale, a major challenge to understand and disentangle the influence of environmental factors on tropical forest community structure is related to the floristic composition.

Indeed, the level of biodiversity in these forests is remarkable both locally (alpha diversity) and in terms of floristic turnover [beta diversity; e.g. (Duivenvoorden *et al.*, 2002; Kraft *et al.*, 2011)]. Ironically, the appealing high species diversity of tropical forests (Sosef *et al.*, 2017; Slik *et al.*, 2015), is an obtacle to disentangle environmental drivers of floristic composition. Particularly because data analysis is confronted with a dichotomy of many scarce (≤ 1 individual per one ha) and abundant species (> 1 individual per one ha) comprising tropical communities (Condit *et al.*, 2013). For instance, in a forest plot of one hectare and for trees ≥ 10 cm in diameter, tree diversity can reach 254 species (Condit *et al.*, 2005) with many of these species being scarce (Pitman *et al.*, 2013, 2001). Moreover, communities are dominated by few species that are common and widely distributed (Gaston, 1996; Gaston *et al.*, 2000). As such, one can observe a small set of ubiquitous common species which combine high frequency with high abundance to yield oligarchies (Arellano *et al.*, 2016; Pitman *et al.*, 1999, 2001; ter Steege *et al.*, 2013). Oligarchy in western Central Africa, has been documented by Kenfack *et al.* (2007) within a single 50 ha forest block while Chuyong *et al.* (2011) reported that most of the species were habitat specialists. Surprisingly, studies to disentangle the environmental drivers of scarce and abundant species are not common for tropical African forests.

Variation of environmental factors at regional scale may also play important roles in forest vertical structure and influence for example tree height (H) and aboveground biomass (AGB). Tree height is central in forest community structure; it scales allometrictically with tree trunk diameter (hereafter H–D relationship), improves estimation of aboveground biomass (Chave *et al.*, 2008; Feldpausch *et al.*, 2012; Lewis *et al.*, 2013) and have been employed recently to calibrate remotely sensed products for landscape forest monitoring (Asner and Mascaro, 2014; Saatchi *et al.*, 2011). However, measurement of H in tropical forests is difficult and its acquisition is usually by prediction from trunk diameter (D) by means of allometric models. As a result, several models have been developed to predict H from D [see details in the lmfor R package (Mehtatalo, 2017)] and the variation with environmental gradients (Moles *et al.*, 2009). Yet, empirical studies incorporating environmental factors in tree height prediction are not common albeit theoretical supports. Althought strongly criticised (Becker *et al.*, 2000), the hydraulic limitation theory accounts for the cessation of tree height with age. This theory hypothesised that resistance to water flow in plant vascular system limits height growth because when trees grow taller, the distance travelled by the sap increases and therefore more energy is required to propel sap over longer diatances (Ryan *et al.*, 2006; Ryan and Yoder, 1997). Therefore, maximum tree height is expected to be lower for trees of the same species on arid and resource-poor sites (Ryan *et al.*, 2006). However, H–D variation would not only depend on water transport through the xylem but also on the distribution and availability of resources (King, 1990; Muller-Landau *et al.*, 2006a). Also, the growth in tree trunk must mechanically sustain their own weight to avoid elastic buckling under their own weight when subjected to large externally applied mechanical forces (King, 1990; Mäkelä and Valentine, 2006; McMahon, 1973). It is likely, therefore, that external factors influence the spatial variation of H–D relationship between forest communities (Muller-Landau *et al.,* 2006b; Reich *et al.,* 2006). Notably, biotic drivers such as tree size, stem density and basal area (Coomes and Allen, 2007; Muller-Landau *et al.,* 2006b) and abiotic drivers including altitude, precipitation and temperature (Feldpausch *et al.,* 2011). Studies integrating both biotic and abiotic factors in predicting tree height are hard find in the literature.

At a local scales where floristic composition is known and H variability is weak, variation in community structure maybe mediated by functional traits that respond to the local environmental gradient such as topography and edaphic conditions (Díaz and Cabido, 1997; Keddy, 1992; Lavorel and Garnier, 2002; McGill *et al.,* 2006; Westoby *et al.,* 2002). Functional traits can therefore mediate and inform on intraspecific variation, species coexistence and prevailing environmental factors (Cornwell and Ackerly, 2009). From a global perspective, studies relating functional traits and environment factors have summarized a suite of traits that represent some general trade-offs or “economic spectra” (Reich, 2014; Shipley *et al.,* 2006). For example, in the leaf economic spectrum “slow-growing” plants with long-lived leaves, low values of specific leaf area (SLA), leaf phosphorus concentrations (LPC), leaf nitrogen content (LNC) and photosynthetic capacity are often associated with nutrient-poor soils (Ordoñez *et al.,* 2009; Wright *et al.,* 2001). In this case, traits may enhance resource-use efficiency by increasing photosynthetic carbon gain per unit of nutrient uptake. In contrast, “fast-growing” plants with the opposite sets of traits (short-lived leaves, high SLA, LPC, LNC and a high photosynthetic capacity) are rather associated with nutrient-rich soils (Wright *et al.,* 2004, 2001). Knowing that a suite of traits may maximize growth rate and enhance competitive advantage under certain soil nutrient conditions and be detrimental in others (Weiher and Keddy, 1995), an exploitation of this spectrum may enhance the understanding on community variation at local scale. Therefore, traits that capture species resource-use and competitive strategy maybe expected to be associated with a shift in soil nutrient conditions.

I.1.1. General and specific objectives

I.1.2. General objective

The general objective of this research was to analyse the influence of regional and local environmental drivers on community structure of Central African lowland forests.

I.1.3. Specific objectives

The four specific objectives of this study were:

- to evaluate the variation of species diversity between sites in the Central African lowland forests;
- to determine the role of soil and climate gradients on floristic patterns at regional scale;
- to evaluate the contribution of some ecological factors in improving tree height prediction for Central African forest trees;
- to study how topography and soil composition influence the distribution of functional traits at local scale.

I.1.4. Research questions

The four research questions for this study are formulated and summarised viz.

Are forest types and sites significant different between each other in terms of species diversity? A regional scale analysis on floristic data collected from the three countries was necessary to:

- identify the main forest types found in sites for all three countries where data were collected;
- determine species diversity via diversity indices;
- conduct multiple comparison test for statistical significance between forest types and sites.

To what extent could gradients in environmental factors explain regional patterns in floristic composition and distribution within lowland moist forest communities? To answer this second question, a regional scale analysis was conducted to determine:

- the main floristic patterns in terms of scarce and abundance tree species;
- the main gradients in soil composition and bioclimatic variables and
- the respective proportions of scarce and abundance species variances explained by the soil and/or bioclimatic gradients.

Could the integration of ecological factors in height–diameter relationship improve tree height prediction for Central African forest trees? Data for this question was collected from three countries of the central African lowland forest region (regional scale analysis) in order to:

- identify which factors including gradients in soil composition and bioclimatic variables, topography and forest structural properties, are likely to influence tree height–diameter allometric relationship;
- analyse how integration of these factors in height–diameter allometric model reduce error and bias in tree height prediction compared to existing height–diameter allometric models;
- evaluate whether accounting for ecological factors in height prediction improve AGB estimates by reducing error propagation.

How do leaf functional traits associate with gradients in soil composition to mediate community assembly? This question examined, at a local scale in Korup forests (South-western Cameroon) how soil composition gradients and topography influence the distribution of leaf functional traits in community assembly.

- Four leaf functional traits were measured on trees present in 20 m × 20 m quadrats;
- the main gradient in soil composition was identified;
- Shifts in quadrat-level weighted mean trait and functional divergence were associated with the main soil gradients;
- the trends of intraspecific trait variation along the main soil gradients were determined.

I.2. Literature review

The study of floristic and functional trait distribution along environmental gradients in Central African lowland forests requires:

- An appreciation of the biophysical environment where the forests are located and characterization of the geological features and climatic conditions. Here, a review of the literature was conducted for the entire range of the study or regional scale [i.e., three countries belonging to the Congo Basin forests zone: Cameroon; Gabon and Democratic Republic of Congo (Congo DR)] and a local scale case study in the Korup forest, south-western Cameroon;
- an understanding of community assembly particularly processes underlying floristic patterns. Knowledge of the approach introduced by functional traits in community ecology.

I.2.1. Biophysical environment

I.2.1.1. Location and choice of the study sites

The study areas hereafter referred to as the Central African lowland forests (CALF) is distributed around 5° – 30° E and -5° – 10° N of the equator. The selected sites are found in the centre, eastern and south-western Cameroon, north-eastern Democratic Republic of Congo (DR Congo) and west-central Gabon (Fig. 1). The total area of CALF has been estimated at 178 million hectares (de Wasseige *et al.*, 2014; Mayaux *et al.*, 2013) with an estimated 44 % extensive forest cover in six countries (Vegetation

The vegetation of the CALF has been recognised as part of the Guineo-Congolian phytogeographic region (White, 1983); comprising both Lower Guinea and Congolia subregions. The floristic identity of these subregions is capitalised in the majority of endemic species belonging to certain plant families such as Annonaceae, Fabaceae, Euphorbiaceae, Malvaceae and Combretaceae (White, 1979) [family notation follows The Angiosperm Phylogeny Group (APG

IV, 2016)]. Nevertheless, evidence of forest zones have also been capitalised by using large plant families such as Euphorbiaceae (Leonard, 1965) and Rubiaceae (Robbrecht, 1996). Indeed, the floristic identity of tropical Africa have encouraged a variant of vegetation delimitations for well over many centuries (Chapin, 1923; White, 1979) but are still in many instances similar to the phytogeographic regions delimited by pioneer studies. For instance, a recent delimitation by Linder *et al.* (2005) was based on a combination of ordination (cluster) analysis and species distribution data identified six regions (Upper Guinean, Congolian, Congolian transition from the Lake Victoria area around the south of the Congo basin, and three Zambesian phytochoria).
Table I). However, the area covered by lowland forests in Cameroon, Gabon and DR Congo collectively accounts for about 75 % of CALF while the other countries account for less than 15 % (Malhi *et al.*, 2013).

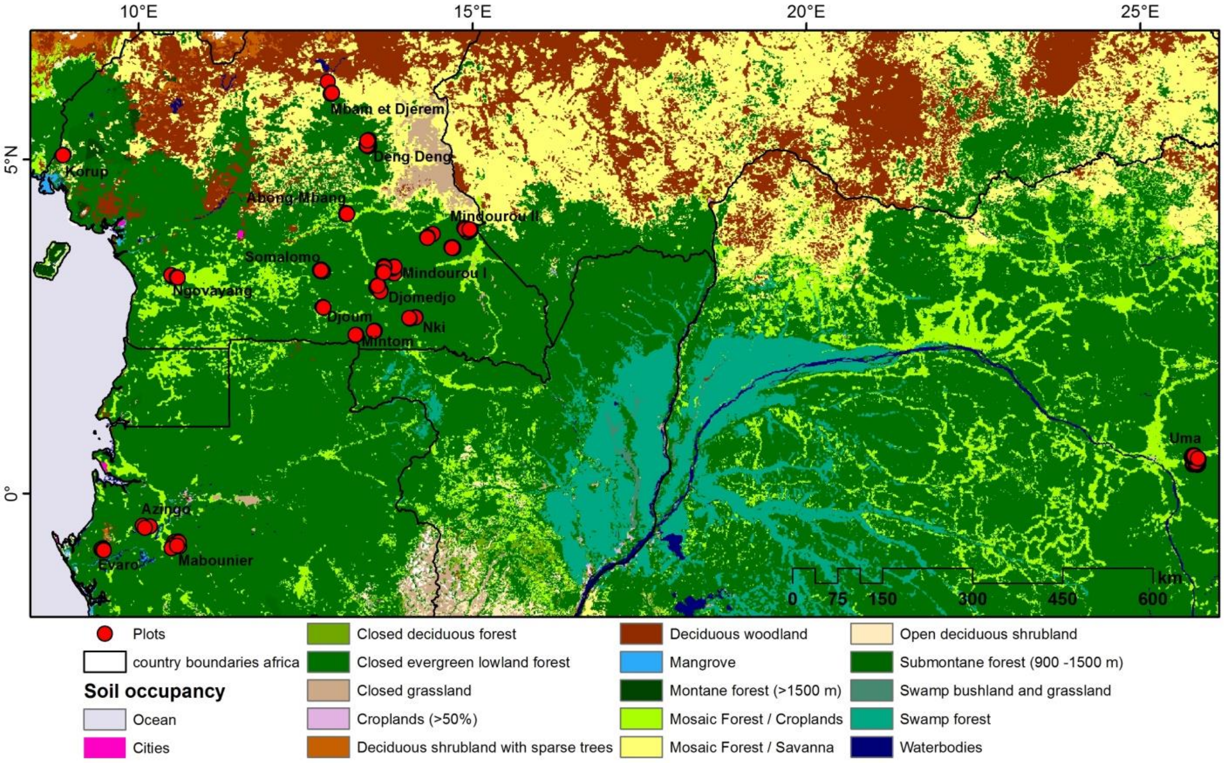


Fig. 1. Geographical location of permananent sampling plots and forest types in Central Africa (adopted from Mayaux *et al*, (2013)).

The choice of the three countries was motivated by the fact that they account for an important proportion in the sheer size of lowland humid forest in Africa hence any conclusions drawn from the present study could be applied to the entire lowland humid forest zone. These forests have a diversity of forest types and strong climatic and edaphic gradients thereby making it particularly suitable to study the influence of environmental factors on floristic patterns and aboveground biomass estimation. The existence of a wealth of floristic inventory data from permanent forest plots and ambition to study tropical forest dynamics also motivated the selection of these sites.

I.2.1.2. Vegetation

The vegetation of the CALF has been recognised as part of the Guineo-Congolian phytogeographic region (White, 1983); comprising both Lower Guinea and Congolia subregions. The floristic identity of these subregions is capitalised in the majority of endemic species belonging to certain plant families such as Annonaceae, Fabaceae, Euphorbiaceae, Malvaceae and Combretaceae (White, 1979) [family notation follows The Angiosperm Phylogeny Group (APG IV, 2016)]. Nevertheless, evidence of forest zones have also been capitalised by using large plant families such as Euphorbiaceae (Leonard, 1965) and Rubiaceae (Robbrecht, 1996). Indeed, the floristic identity of tropical Africa have encouraged a variant of vegetation delimitations for well over many centuries (Chapin, 1923; White, 1979) but are still in many instances similar to the phytogeographic regions delimited by pioneer studies. For instance, a recent delimitation by Linder *et al.* (2005) was based on a combination of ordination (cluster) analysis and species distribution data identified six regions (Upper Guinean, Congolian, Congolian transition from the Lake Victoria area around the south of the Congo basin, and three Zambesian phytochoria).

Table I. Proportion of lowland forest in Central Africa
(Mayaux *et al.*, 2013; Malhi *et al.*, 2013).

	Central Africa lowland forests		Lowland and swamp forests
Country	(x1000 ha)	(% cover in Country)	(% cover in Africa)
Cameroon	20.037	42	10.0
DR Congo	107.181	46	53.6
Gabon	22.416	84	11.2
Congo	20.932	61	10.4
Central African Republic	5.833	9	n.a.
Equatorial Guinea	2.163	77	n.a.
Total	178.562	44	n.a.

Also, using a similar approach but with plant and animal data Linder *et al.* (2012) partitioned seven biogeographical regions; Congolian, Zambezian, Southern African, Sudanian, Somalian, Ethiopian and Saharan. However, the later partition did not assign East Africa, the West African coast, and the transitions between the Congolian, Sudanian and Zambezian regions. Therefore a more recent classification of tropical African forests based on a combination of bioclimatic factors, historical factors and tree species composition, described six floristic clusters; Coastal and Upland for East Africa, Dry and Wet-Moist for West Africa, and Moist and Wet for Central Africa (Fayolle *et al.*, 2014). Considering the parameters used in the later studies (Fayolle *et al.*, 2014; Linder *et al.*, 2012, 2005; White, 1983), the vegetation of this study area have been re-grouped by considering additional parameters such as leaf phenology (semi-deciduous versus evergreen forest types) and can occur terre firme or hydromorphic soils (Letouzey, 1985; Viennois *et al.*, 2013). Nonetheless, gallery forests have been identified in regional flora (Table II).

I.2.1.2.1. Semi-deciduous forest types

Semi-deciduous or semi-evergreen is a botanical term that refers to seasonal leaf loss due to unfavourable growth conditions, especially water stress. Therefore semi-deciduous forest refers to those forest types with about 70 % of the species losing their leaves during such periods (Reich, 1995). These forest types occur in areas where yearly dry periods exceed three months. Tall canopy species are prominent in this forest type such as; *Staudtia kamerunensis* Warb., *Pausinystalia macroceras* (K.Schum.) Pierre ex Beille, *Celtis* spp., *Chrysophyllum* spp., *Terminalia superba* Engl. & Diels and *Antiaris toxicaria* (Engl.) C.C.Berg. etc. while species with large trunks and undulating canopies (e.g. *Entandrophragma* spp., *Triplochiton scleroxylon* K.Schum., *Milicia excelsa* (Welw.) C.C.Berg) characterized this forest type (Letouzey, 1985)

In the study areas (Fig. 1), semi-deciduous forests occur on terra firme, hence terra firme semi-deciduous forests where the forest under storey is dominated by *Anonidium mannii* (Oliv.) Engl. & Diels, *Baphia* spp., *Strombosiopsis tetrandra* Engl., *Aidia* spp. etc (Letouzey, 1985, 1968). This is the predominant forest type in most sites in Centre and eastern Cameroon (Table II). Semi-deciduous forests also occur on hydrophormic soils, hence hydrophormic semi-deciduous forests. Here the forest is flooded, at least, for a period of the year with forest floor void of shrub and grasses. Species of Arecaceae (Raphias such as *Raphia hookeri* etc, Rattans such as *Laccosperma* spp., *Eremospatha* spp. and others) can be spotted in some areas of eastern Cameroon (Table II).

Also identified in the semi-deciduous forest is a forest-savanna mosaic that defines an abrupt habitat discontinuity between the extensive Guineo-Congolian forests and Sudanian/Sahelian grasslands (Letouzey, 1985; Mayaux *et al.*, 1999). The forest-savanna mosaic is part of a continuum that extends from the Cameroon Highlands in the west, across central Cameroon and the southern Central African Republic through south-western South Sudan, north-eastern DR Congo and north-western Uganda (Dexter *et al.*, 2015; Fayolle *et al.*, 2014; Mayaux *et al.*, 1999; White, 1983). This forest type is a major vegetation in the Deng-Deng site in Cameroon (Letouzey, 1968).

I.2.1.2.2. Evergreen forest types

Evergreen forests are geographically located in areas where the dry period last no longer than two months. Plants in these forests keep their leaves all-year-round. Generally, the forest canopy is shorter compared to semi-deciduous forest; the upper storey is between 35 – 45 m and is dominated by few species such as *Brachystegia laurentii* (De Wild.) Hoyle, *Berlinia* spp. and other species of the Fabaceae (Leguminosae) (Leal, 2004; Letouzey, 1985). Trees develop large interlocked canopies that block light penetration and limit the growth in height of shrubs, grass and epiphytes at the lower canopy and forest floor. The evergreen forests of the study sites stretch along the coast of south-western Cameroon to about 200 km inland of Gabon (Leal, 2004; White, 1979) (Fig. 1).

Specific to some evergreen forests are conspicuous stands dominated by a single species (monodominant forests). Monodominant forests refer to forests blocks whose floristic 2/3 or 60 % is dominated by a single species. Within the study sites, this forest type is composed of *Gilbertiodendron dewevrei* (De Wild.) J.Leonard and *Julbernardia seretii* (De Wild.) Troupin in Uma, DR Congo (Lebrun and Gilbert, 1954) and *G. dewevrei* in Cameroon (Letouzey, 1968). In Gabon, monodominant forests are composed of *Aucoumea klaineana* Pierre (Hart *et al.*, 1989). The *Gilbertiodendron dewevrei* and *Julbernardia seretii* stands in Uma and the *Aucoumea klaineana* forests in Gabon are characterised by well-drained soils with high soil-water retention capacity (Hart *et al.*, 1989; Lebrun and Gilbert, 1954).

Table II. Eleven main sites and different forest types sampled in this study

Country	Sites	No. plots	Forest type	Reference
Cameroon	Mindourou I	17	terra firme evergreen forests & hydromorphic semi-deciduous forests	Letouzey 1985
	Mindourou II	21	terra firme semi-deciduous forests & hydromorphic semi-deciduous forests	
	Deng-Deng	15	Forest-savanna mosaic & terra firme semi-deciduous	Letouzey 1985; Mayaux *et al.*, 1999
	Mbam Djerem	4	Forest-savanna mosaic & terra firme semi-deciduous	Letouzey 1985; Mayaux *et al.*, 1999
	Somalomo	8	terra firme evergreen forests, terra firme semi-deciduous forests & hydromorphic semi-deciduous forests	Letouzey 1985
	Ngoila	3		
	Lomie	14	terra firme evergreenforests	
	Korup	52	terra firme evergreen forests	White1983; Letouzey 1985; Leal 2004
Gabon	Mabounie	5	terra firme evergreen forests	
	Azingo	3	terra firme evergreen forests	
DR Congo	Uma	26	terra firme evergreen forests, Gilbertiodendron-Julbernardia monodominant forests	Lebrun & Gilbert 1954

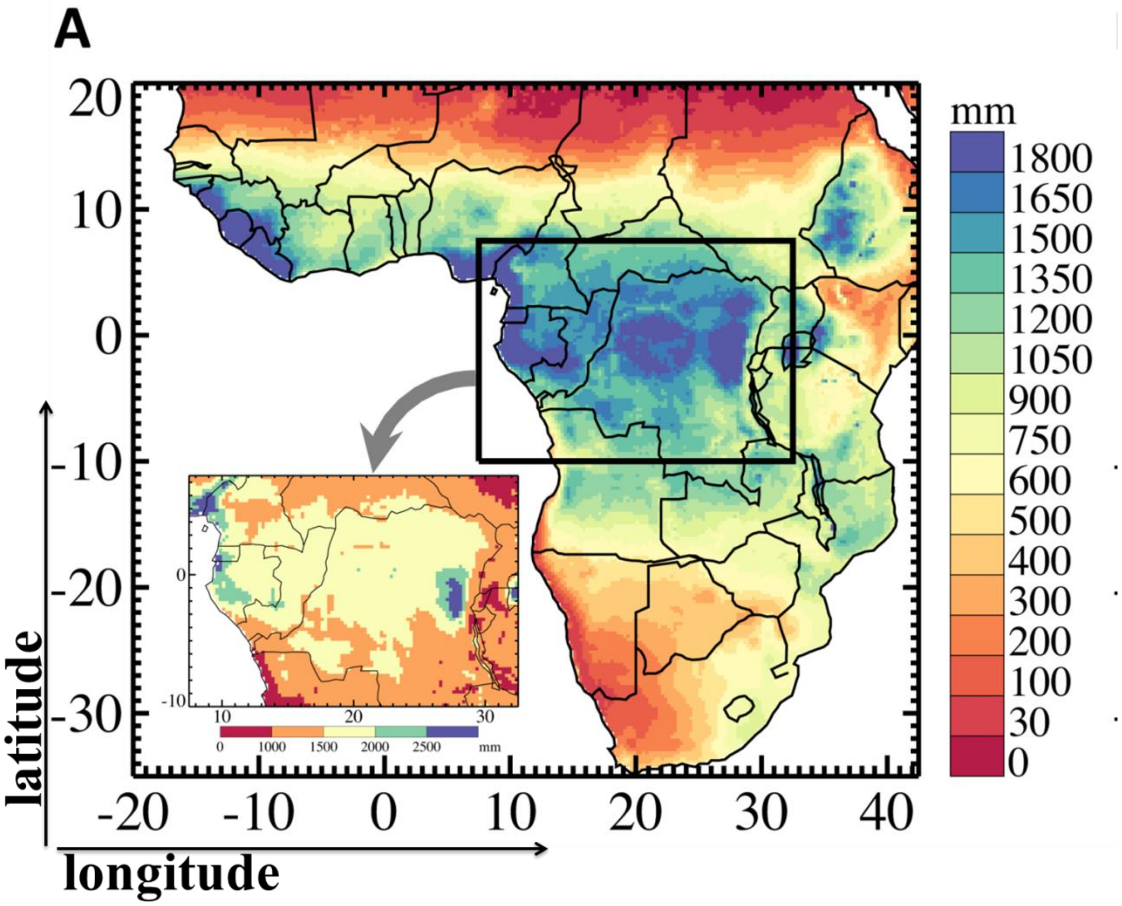
I.2.1.3. Climate

Overall, the climate across the CALF is the tropical humid climate but is also referred to as the equatorial fully humid climate according to the Köppen Climate Classification (Köppen, 1900; http://hanschen.org/koppen). This classification is broadly determined by critical temperature and the seasonality of precipitation. The process controlling seasonality in the study area is complex. However, it has been reported that rainfall seasonality is driven by the inter-tropical convergence zone where the northern and southern air masses converge and crosses the study area twice a year during equinoxes, typically producing low atmospheric pressure (Gond *et al.*, 2013). Precise climatology data are scarce and data that are readily accessible are often generated from satellite-climate models (Deblauwe *et al.*, 2016; Schietti *et al.*, 2013; Washington *et al.*, 2013). Variation in rainfall is considerable with unpredictable seasonal changes hence the region, receives the highest amount of precipitation in the continent (Dezfuli, 2017). The rainfall gradient is influenced by local features such as proximity to rivers, mountains and forest cover. Annual precipitation ranges from 1500 mm to 3300 mm (Dezfuli, 2017; Hijmans *et al.*, 2005) but exceeds 3300 mm towards the coast, i.e., from Libreville to the foot of Mount Cameroon where the annual average rainfall varies between 3000 mm to about 11000 mm (Anonymous 1, 2006) and the number of dry months per year rarely exceeds three (Anonymous 1, 2006). The equatorial climate is marked by bi-seasonality; a rainy season (> 200 mm average monthly rainfall) and a dry season (< 200 mm average monthly rainfall) that is difficult to differentiate in the course of the year in some areas (Fig. 2A). For instance, some sites of the study area observed two periods of rainy and dry seasons yearly. The rainy season is observed thus: April–May & September–December (eastern Cameroon); March–November (south-western Cameroon and west-central Gabon) and March–June & August–December (north-eastern DR Congo). Within these sites, the average minimum monthly rainfall of the rainy seasons is 622 mm and the average minimum monthly rainfall of dry season is 133 mm (Fig. 3; Hijmans *et al.*, 2005).

The temperature of the Central African lowland forest shows little variation with a mean annual range between 20–26 °C and an average of 25 °C (Fig. 2B). The low temperature variation may probably be due to persistent cloud cover. The thermal amplitudes rarely exceed 3 °C. According to the Köppen Climate Classification, the average yearly minimum temperatures occur in July and the average maximum temperatures occur between February and March every year (http://hanschen.org/koppen).

I.2.1.4. Geology

Many descriptions of the geological features of Central Africa points that it is almost entirely underlain by Precambrian crystalline basement with an extensive cover of Phanerozoic rocks, recent sediments laterites and vegetation (De Wit and Linol, 2015; Milesi *et al.*, 2006). Geochronological studies suggest that the entire Congo Basin witnessed a complex evolution starting in the Precambrian era governed by the interplay of tectonic and climatic factors (Milesi *et al.*, 2006). This era include the Archean cratonic blocks (formed about 4.6 billion to 541 million years ago) and numerous Paleoproterozoic to Mesoproterozoic mobile belts forming six Archean cratonic blocks around the Congo Basin (Fig. 4). The blocks formed by Ntem in Cameroon, Gabon and the DR Congo (West-Nilian) has been grouped as the West Central Africa craton composed of various granite–gneiss complexes (De Wit and Linol, 2015).



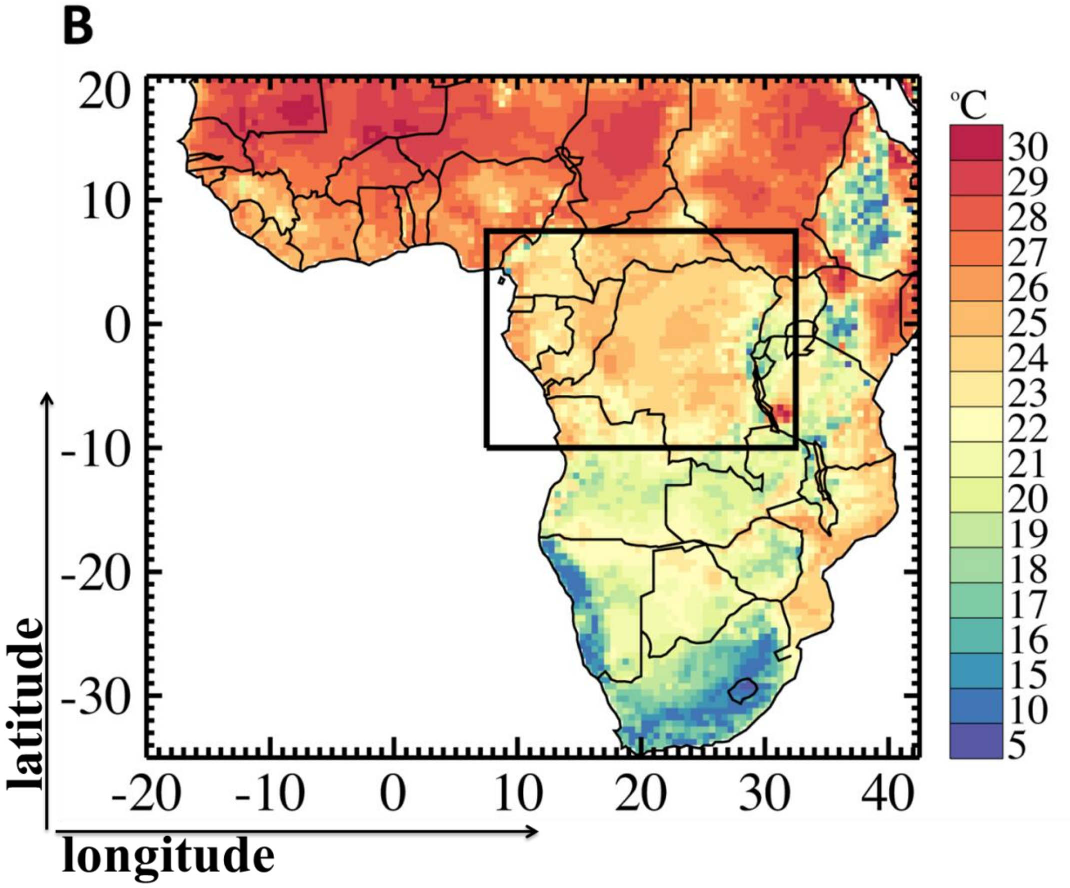


Fig. 2. Annual rainfall and air temperature across Central African forests region and environs Black box = location of Central African lowland forests and environs (Dezfuli, 2017).

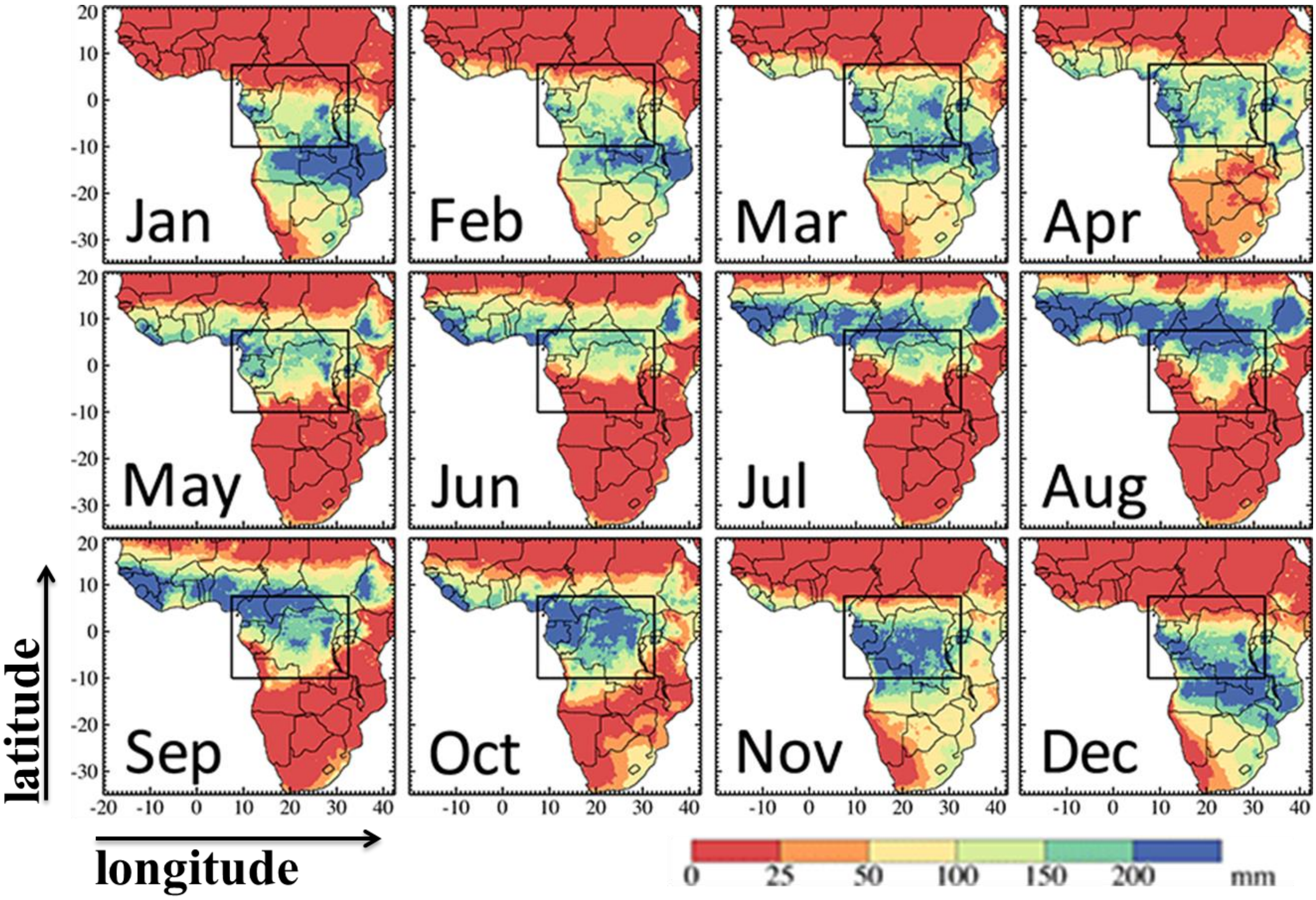


Fig. 3. Monthly mean precipitation patterns based on multisatellite precipitation analysis data. Black box: location of Central African lowland forests and environs (Dezfuli, 2017).

I.2.1.5. Soils

A considerable diversity of soils types occurs in the CALF (

Table III), influenced by major differences in moisture but also by other factors such as lithology and age, the degree of weathering of parent materials, relief, and altitude (Van Wambeke, 1989). The ferralsols and Acrisols are the most predominant soil groups (Fig. 5). These are a group of Oxisols characterised by low Base Exchange Capacity, low clay activity and low minerals content (Anonymous, 2013; Anonymous 1, 2006). Ferralsols and Acrisols are common in well-drained positions and with Plinthosols and Gleysols where drainage is poorer. The soils of upland forests are highly weathered, often deep and generally infertile. Most nutrients that are essential for plant growth (e.g. potassium, phosphorus) occur in low concentrations due to high rainfall. The soils are red or yellow in colour and may be several meters deep (Fig. 6) (Anonymous, 2013).

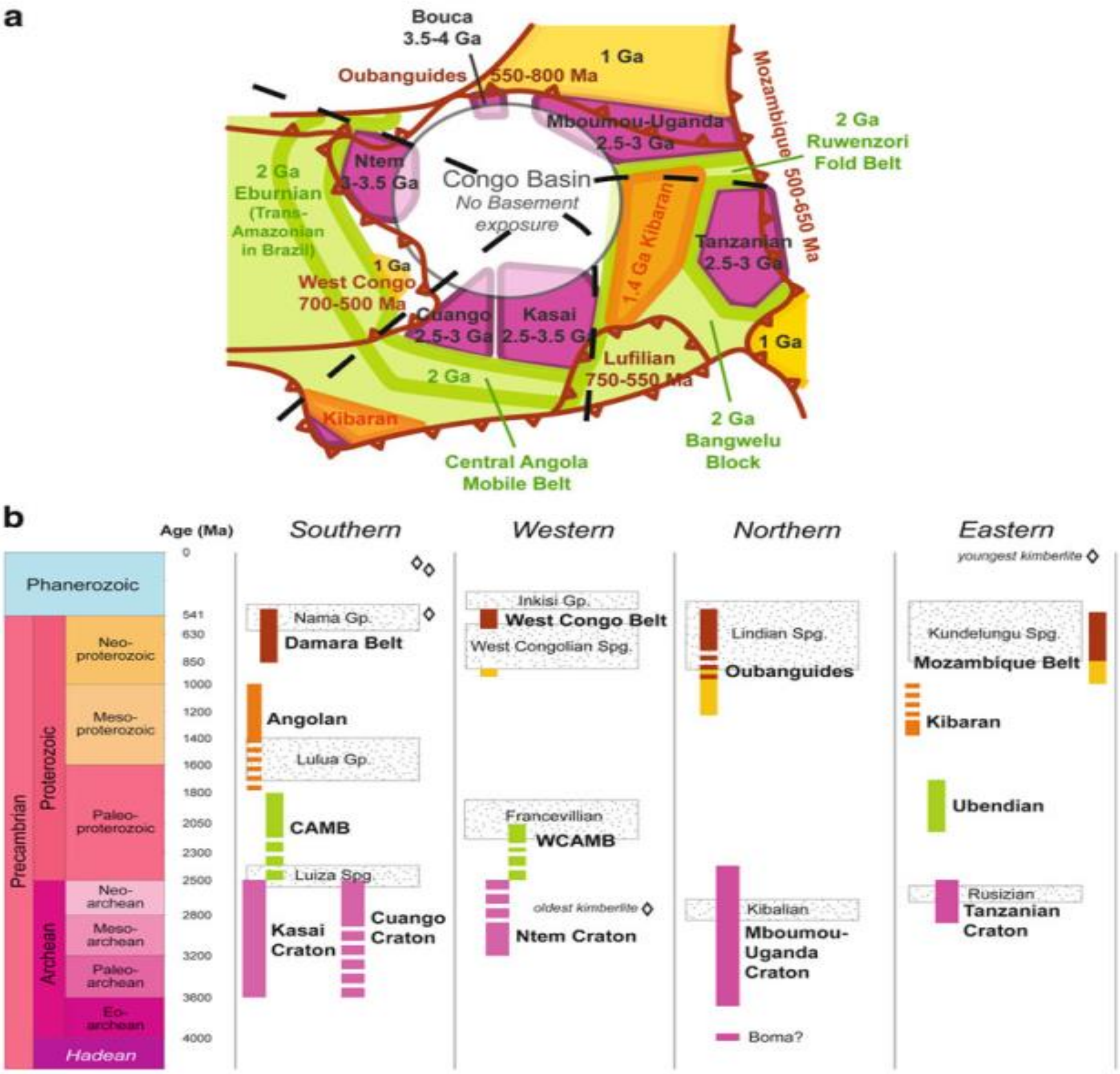


Fig. 4. Geochronology and Time–Space diagram of Precambrian basement around the Central Africa.

A: Geochronology: six Archean cratonic blocks (purple); Eburnian (green) and Kibaran terrains (orange and yellow), and tectonic fronts of Pan African fold-and-thrust belts (brown).

B: Time–Space diagram: dashed lines are regions and dotted rectangles are ¼ sedimentary sequences (De Wit and Lino, 2015).

Table III. Major soils type in Cameroon, Gabon and DR Congo (Anonymous 2, 2006).

Cameroon	Gabon	DR Congo
Xanthic-Ferralsols	Xanthic-Ferralsols	Xanthic-Ferralsols
Rhodic-Ferralsols	Ferralic-Arenosols	Rhodic-Ferralsols
Rhodic-Nitisols	Dystric-Fluvisols	Ferralic-Arenosols
Dystric-Gleysols	Dystric-Gleysols	Eutric-Gleysols
Rhodic-Nitisols	Haplic-Acrisols	-
Humic-Cambisols	Ferralic-Cambisols	-

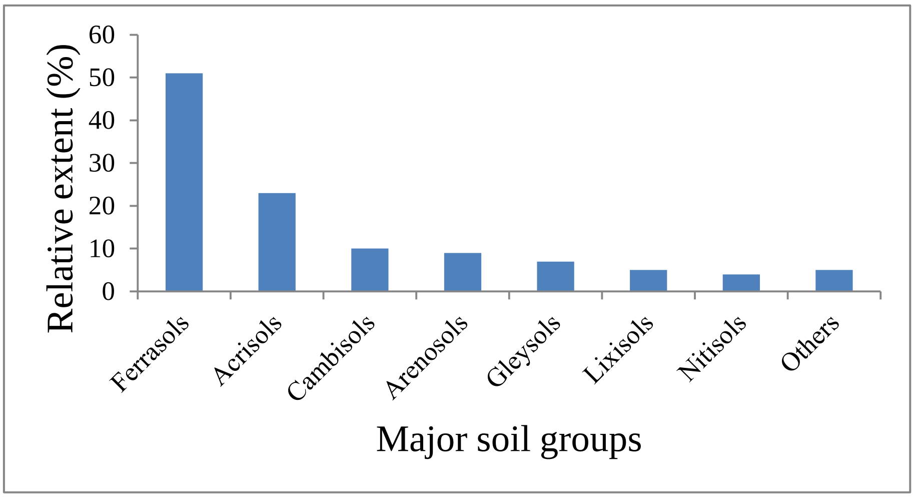


Fig. 5. Proportion of soil groups in Central Africa (Anonymous 2, 2006).

Fig. 6. Ferralsols with dark humus-enriched topsoil over uniform yellowish subsoil from Gabon (Jones *et al.*, 2013).

I.2.2. Choice of site and location of the Korup forest

The Korup forest (8°42′ N and 9°16′ E) is situated near the town of Mundemba at the south-western corner of Cameroon (Fig. 7) and covers a surface area of 1,260 km^2. It borders to the East by the Atlantic Ocean or approximately 50 km from the Bight of Biafra, 20 km from the mangrove swamps of the Rio Del Rey estuary linking Nigeria. The Korup forest zone is host to the Korup national park which was created since 1986 (*Presidential Decree No.86-1283*).

Data for the local scale study was specifically collected within the 50 ha (1000 m by 500 m) long-term Forest Dynamics Plot (FDP) in Korup (Fig. 7). The FDP was established since 1996 by national and international researchers, coordinated by the Centre for Tropical Forest Sciences (CTFS) of the Smithsonian Institution (Chuyong *et al.,* 2004; Thomas *et al.,* 2003). Since the plot was established all trees > one cm in diameter are being re-censured every five years.

The choice of the 50 ha FDP for local scale study was particularly motivated by a number of reasons:

- the FDP stands in an intact primary forest with no visible signs of anthropogenic disturbance such as commercial logging. Hence certainty to exclude anthropogenic influence in trait analysis. The forests also appear very ancient and rich in paleo-endemic species;
- the topography of the site shapes the plot into microhabitats that have been already described (Chuyong *et al.,* 2004);
- the existence of a wealth of historical ecological data following previous inventories All woody plant species in the plot with a diameter at breast height (dbh) equal or greater than 1 cm, is being monitored since 1996 (i.e. tagged, mapped and identified) (Kenfack *et al.,* 2007; Thomas *et al.,* 2003).

I.2.2.1. Climate and vegetation of the Korup forest

The climate in this area is bi-seasonal. The dry season is shorter, lasting for three months (December to February) and the driest month in January receives less than 100 mm of rain (Table IV). The rainy season is longer, lasting for nine months (March to November) with the peak in August receiving above 10 000 mm of rain and the mean annual rainfall can reach 5 300 mm (Thomas *et al.,* 2003).

The temperature of the area is relatively stable year round. The mean annual temperature settles around 27 °C with the maximum reaching 31.8 °C in the dry seasons and 30 °C during the rainy seasons (Thomas *et al.,* 2003).

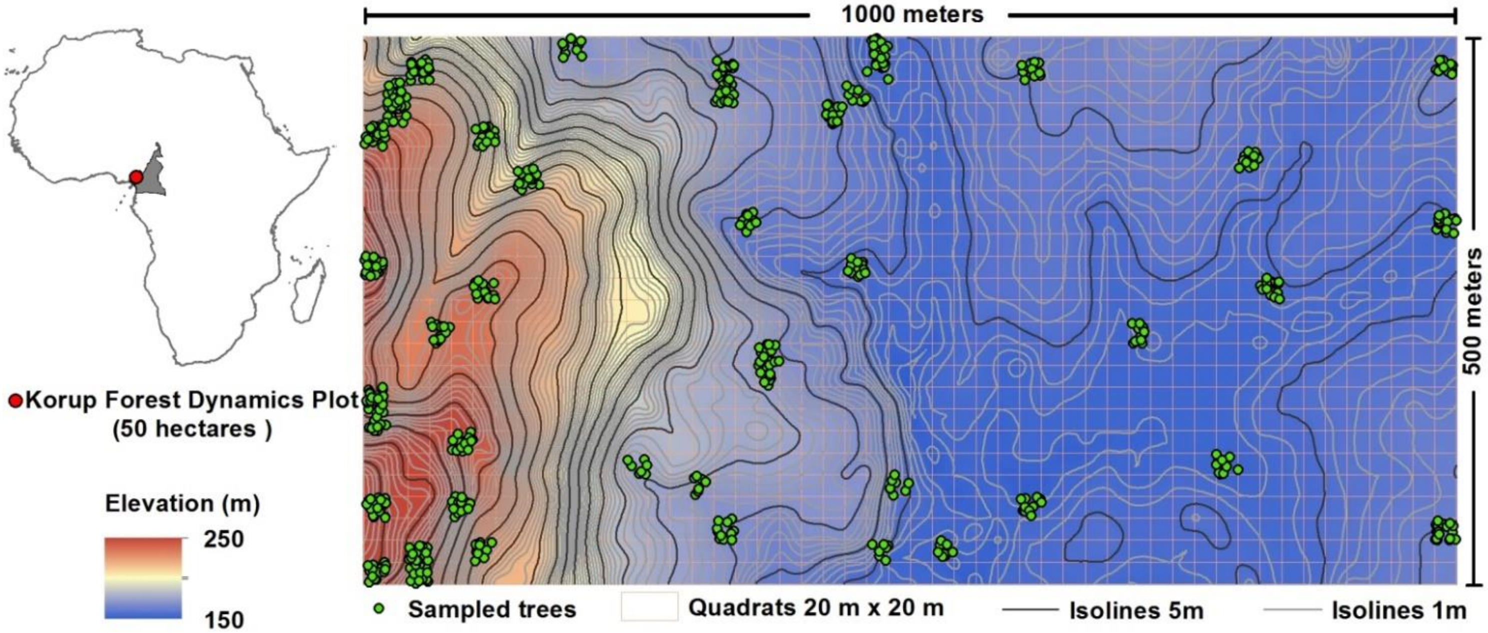


Fig. 7. Location of the 50 hectare Forest Dynamics Plot in Korup, southwestern Cameroon.

Table IV. Means of monthly rainfall and daily maximum and minimum temperature recorded 20 km from the Korup Plot over 21 years period. MDTMx is mean monthly maximum temperature; MDTMn is mean monthly minimum temperature. Data source is Thomas *et al.* (2003).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total means
Rainfall (mm)	38	58	221	329	459	564	913	914	691	668	341	76	5272
MDTMx (°C)	31.6	32.8	32.6	32	31.5	30.4	28.7	27.8	28.8	29.7	30.7	31.1	30.6
MDTMn (°C)	21.9	23	23.1	23	22.8	22.8	22.2	22.4	22.3	22.5	22.8	23.1	22.7

The rainforests of the Korup National Park are described as Biafran forest type; rich in species and dominated by gregarious stands of Fabaceae-Caesalpinioideae (Letouzey, 1985) and overlapped with a possible Pleistocene refuge of central African coastal forests (Maley, 1998). The floristic composition of the 50 ha FDP is diverse; is host to many rare and abundant species of the region (Kenfack *et al.,* 2007), and new species are discovered regularly (Ewango *et al.,* 2016; Kenfack *et al.,* 2015; Libalah *et al.,* 2014). The most important species in the 50 ha FDP are *Phyllobotryon spathulatum* (Salicaceae) with abundance reaching 26,741 trees and *Lecomtedoxa klaineana* (Sapotaceae) and *Oubanguia alata* with the largest basal area of 4 m^2 and 2 m^2 respectively in the 50 ha FDP (Kenfack *et al.,* 2007).

I.2.2.2. Geology and soil of the Korup forest

The geology of Korup forest is fairly known. The basement rock is traced back to Precambrian era with the soils being primarily derived from the *in situ* decomposition of granite and quartzite rocks (Gartlan *et al.,* 1986).

The soils are mostly sandy and nutrient-poor with a soil available phosphorus as low as 2 ppm (Gartlan *et al.,* 1986). The high rainfall is probably responsible for the porosity and soil nutrient depletion by mean of leaching. In the 50 ha FDP, the soils are ferralitic (or sometimes Arenosol) and may have developed from *in situ* weathering of granite bedrocks (Chuyong *et al.,* 2004). The FDP is also characterized by heterogeneous soil and topography; soils of the northern higher slope of the plot are dryer and thinner (presence of large embedded rocks) while at the southern lower plain, soils are wetter and deeper (almost absence of embedded rocks). Between these two extremes are boulders and gullies that channel streams and surface run-offs to the lower temporally flooded plane of the 50 ha FDP.

I.2.3. Community assembly

I.2.3.1. Definition

In the simplest term, community ecology is the study of patterns in the diversity, abundance, and composition of species in communities, and of the processes underlying these patterns (Vellend, 2010). Alternatively, it has been defined as the study of the processes that shape the identity (traits) and abundance of species within limited space (Kraft and Ackerly, 2014; MacArthur and Wilson, 1967; McGill *et al.,* 2006). Community assembly considers the mechanisms by which local communities are formed from a regional species pool which is equally more inclusive in geographic scope than the local community (Fig. 8). For a local community assemblage to be formed from the regional species pool, ecological processes such as. dispersal, biotic and biotic interactions (or an interaction of these processes) are expected to occur (Kraft and Ackerly, 2014). Thus, community assembly may unite evolutionary, biogeographical and environmental processes.

I.2.3.2. Processes explaining species co-occurrence

To understand why and how species co-occur within a given space without competitive exclusion, ecologists have postulated several processes. The underlying principle is that processes that shape local communities operate at a wide range of spatial and temporal scales (HilleRisLambers *et al.*, 2012). Though many of these processes have separately been developed, they can either be deterministic or stochastic in nature. According to Chase & Myers (2011) deterministic and stochastic processes simultaneously operate within a given community but act in opposition and are usually difficult to disentangle (Fig. 8). In addition, the resulting local communities are assumed to reflect the cumulative effects of these processes (Fig. 8).

Deterministic processes refers to all local processes (niche theory) imposed by the abiotic environment, biotic interactions and interspecific trade-offs, contrary to stochastic processes which emphasize the importance of randomisation (neutral theory) in colonization and extinction rates and ecological drift (Chave, 2004; Hubbell, 2001; Stegen *et al.,* 2012) but also disturbance, probabilistic dispersal and random birth-death events (Chase and Myers, 2011).

I.2.3.3. Niche theory

Among the several theories developed to explain co-occurrence of species and maintenance of biodiversity at different scales, the niche theory seems to be the oldest. The niche theory focuses on the interaction between a species or species' traits and its environment. Its prominence depends on the primary spatial scale under investigation. Its development (Elton, 1927; Grinnell, 1917) and later modification (Hutchinson, 1957) is thought to have inspired pioneering concepts. For instance, Robert MacArthur viewed the relationships between species or species' trait with the environment and also interspecific trade-offs as being paramount for co-occurrence at local scale (Macarthur and Levins, 1967; MacArthur, 1957).

These authors postulated that the diversity of co-occurring species at a local scale may results because of:

- limiting similarities; i.e. species may co-occur if there is a certain level of dissimilarities in their resource demands,
- competitive exclusion; i.e. species that compete for the exact same resources cannot stably co-occur.

From these pioneering concepts, it could be noted that modern niche theories in community ecology are explicitly focused on species–resource interactions and trade-off. For instance the

Resource-based trade-offs concept proposed that species co-occurrence is based on the minimum amount of a limiting resource that a species needs to persist in a given locality, and trade-offs among species in their abilities to use different resources (Tilman, 1980).

However, to understand patterns of compositional turnover and diversity at regional spatial scale, MacArthur & Wilson (1967) proposed the theory of "island biogeography"; the number of species on any island reflects a balance between the rate at which new species colonize it and the rate at which populations of established species become extinct. This theory seems very similar to and probably inspired the development of the neutral theory because it ignored any differences among species in their traits.

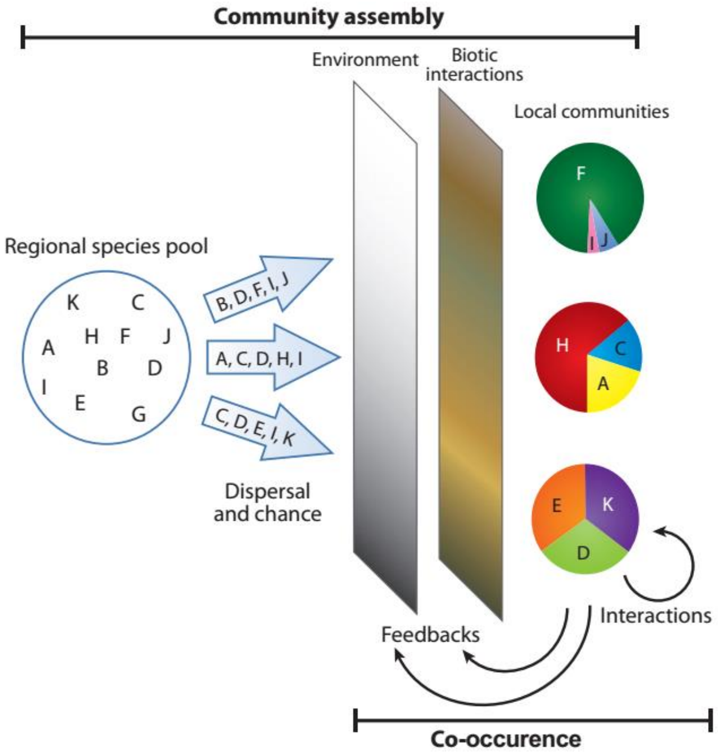


Fig. 8. Processes in community assembly operating at a wide range of spatio-temporal scales. Modified from HilleRisLambers *et al.* (2012).

I.2.3.4. Neutral theory

As an antithesis to the niche theory, neutral theory are dependent on the assumption that species are equivalent to each other in all important ecological respects (Hubbell, 2001). These theories are therefore formulated on the idea of "species-based equilibrium". That is, species in the simple version of the equilibrium concept are inherently equivalent, in that only colonization/extinction processes influence species diversity on an "island" or community, without consideration of their traits (Chase and Myers, 2011). According to Hubbell (2001) pervasive dispersal limitation, ecological drift and a balance between random extinction and speciation could explain a wide variety of ecological patterns:

- dispersal limitation; i.e. the capacity of a plant species to disperse its seeds to reach unoccupied sites (Ehrlen and Eriksson, 2000),
- ecological drift; i.e. the abundance of a particular species can either increase or decrease through time controlled by births, deaths and the outcome of competition (Purves and Turnbull, 2010; Vellend, 2010).

I.2.3.5. Evolutionary theory

On another view about theory underlying species diversity and co-occurrence, Ricklefs & Ricklefs (2003) points out the active role of natural speciation. According to McPeek (2017), speciation occur when all species engage in interactions with many other species, and these interactions regulate their abundances, define their trajectories of natural selection, and shape their movement decisions among different communities. Speciation is obviously an important determinant of the number and types of species found at regional scales such as entire continents, as well as on isolated islands (Ricklefs and Ricklefs, 2003). However speciation can also exerts an important influence on community patterns at comparatively small scales noted Vellend (2010). This author cited two of such scenarios where speciation can be the driving process of the species, and the number of species thus:

- equal-sized areas under very similar environmental conditions but in different geographical regions. Here, interplay of local diversity of processes, such as speciation and dispersal can determine the regional species pool;
- role of natural selection in the relationship between species diversity and local environmental drivers. For instance, species in lower diversity areas at the top of mountainside may not just be a subset of the species in higher diversity areas at the bottom of mountainside but also contain different sets of species.

I.2.4. Coexistence of the niche and neutral theories in community ecology

The publication of "the unified neutral theory" raised much debate in ecology as it was perceived as strong antithesis to the established niche theories. However, recent reviews [for e.g. (Adler *et al.,* 2007; Chase and Myers, 2011; Chave, 2004; Gravel *et al.,* 2006; Leibold and McPeek, 2006; Stegen *et al.,* 2012; Vellend, 2010)] have reconciled the coexistence between both sets of theories in explaining co-occurrence and maintenance of biodiversity. To begin with, Chase & Myers (2011) clarifies the schisms between both theories (see section I.2.3.2) and equally noted that it is sometimes difficult to detect the signal of niches when there are a lot of stochastic processes that emerge from local and regional factors (Chase and Myers, 2011). Chave (2004) further concluded that the strict assumption of species equivalence of neutral theories finds little empirical support in general but plays a pivotal role to demonstrate intraspecific variability in ecology.

I.2.5. Functional traits-based approach in community ecology

In its simplest definition, a trait is a proxy of an organism's performance. To reduce the misuse of the term and render it more functional, Violle *et al.* (2007) defined a trait as: "any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization" (Fig. 9). A trait in the strict sense therefore, does not require external information to the individual, i.e. environmental conditions or at any other level of organization, including the population, community or ecosystem. Despite the clarification of the term, the meaning and use of "function" added to "traits" hence "functional traits" has been widely applied in ecology. It has been used in the following ways: as a surrogate of function (e.g. Specific leaf area); as function itself (e.g. photosynthesis); as a trait that strongly influences organismal performance and/or individual fitness (see Violle *et al.* (2007) and references therein). Therefore, "functional traits" are any morphological, physiological or phenological trait which impacts fitness indirectly via its effects on "performance traits" (Fig. 9).

The trait-based approach to community ecology provides a means to characterize organisms in terms of their multiple biological functional traits and linking them to their external environment thus facilitating mechanistic prediction across environmental gradients (Ackerly and Cornwell, 2007; McGill *et al.,* 2006; Webb *et al.,* 2010; Westoby and Wright, 2006) (Fig. 9). In addition to being taxon-independent, this approach also has the ability to determine both intraspecific, interspecific and individual variation along environmental gradients (Auger and Shipley, 2013; Hulshof *et al.,* 2013; Siefert *et al.,* 2015).Trait-based approach has a long history. Its initial application focused on qualitative concepts describing life history traits and their variation along environment gradients (Grime, 1977). The follow-up was the development of quantitative models to predict trait-environment association (e.g. Ackerly and Cornwell, 2007; Brown *et al.,* 2014). More recently, the focus has been to bridge the historical gap between community and ecosystem ecology (e.g. Lepš *et al.,* 2011; McGill *et al.,* 2006; Westoby *et al.,* 2002). This recent revival is also stimulated by interest to predict community structure at different spatial scales (e.g. Ackerly and Cornwell, 2007), development of statistically robust methods to decompose the complex association between intraspecific and interspecific variation (e.g. Lepš *et al.,* 2011; de Bello *et al.,* 2011; Taudiere and Violle, 2015) and to understanding species distributions in the face of rapid environmental change (Thuiller *et al.,* 2004).

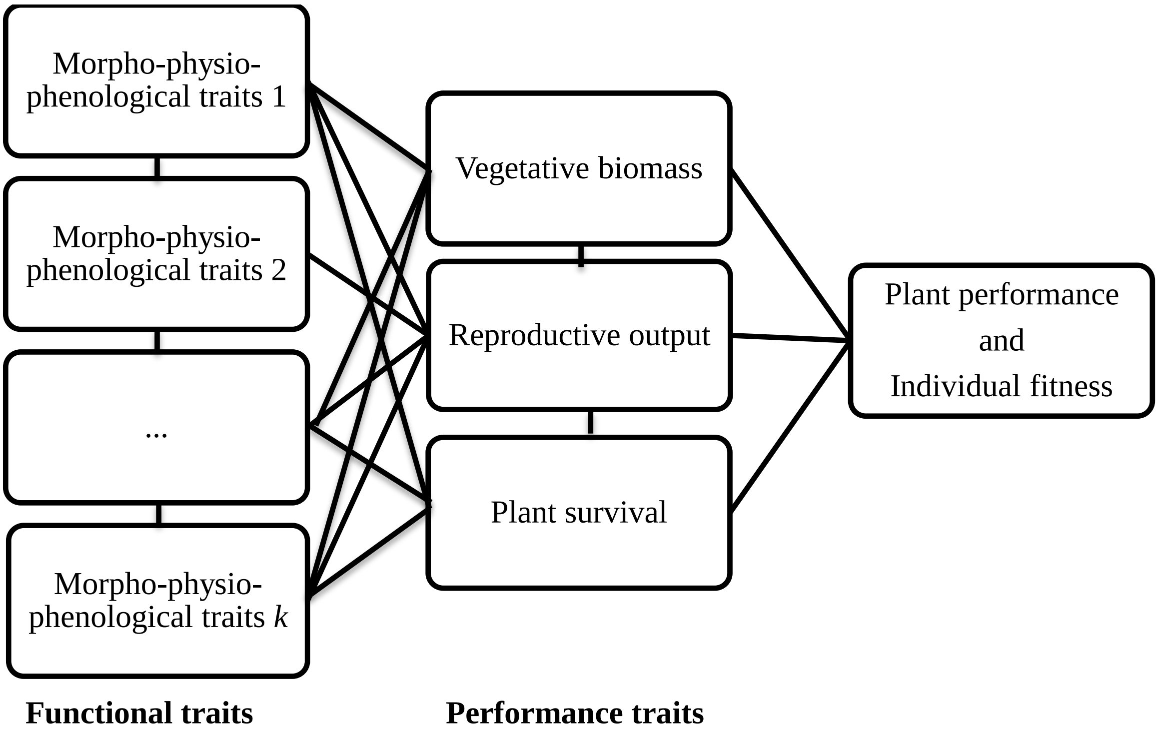


Fig. 9. Modulation of plant performance and individual fitness by various functional traits. Morpho-physio-phenological traits: Morphological-physiological-phenological traits from 1 to *k*; Performance traits: vegetative biomass, reproductive output and plant survival. Modified from Violle *et al.* (2007).

Table V. Association of some functional traits to four classes of environmental change.

Classes of environmental change: Response (climate, CO_2, soil and disturbance); competitive strength; plant ‘defense’; biogeochemical cycles and disturbance regimes. “*” is evaluated associations, “?” is unevaluated associations and “-” is unknown associations (Cornelissen *et al.,* 2003).

	Climate response	CO_2 response	Response to soil resources	Response to disturbance	Competitive strength	Plant defence	Effects on biogeochemical cycles	Effects on disturbance regime
Whole-plant traits								
Growth form	*	*	*	*	*	*	*	*
Life form	*	*	*	*	*	-	*	*
Plant height	*	*	*	*	*	*	*	*
Clonality	*	?	*	*	*	-	-	?
Spinescence v	*	?	-	-	*	*	-	?
Flammability	-	?	-	-	*	?	*	*
Leaf traits								
Specific leaf area	*	*	*	-	*	*	*	-
Leaf size	*	?	*	-	*	*	*	-
Leaf dry matter content	*	?	*	-	-	*	*	*
Leaf N and P concentration	*	*	*	*	*	*	*	-
Physical strength of leaves	*	?	*	*	-	*	*	-
Leaf lifespan	*	*	*	*	*	*	*	*
Leaf phenology	*	-	*	-	*	-	*	*

Photosynthetic pathway	*	*	-	-	*	-	-	-
Leaf frost resistance	*	-	-	-	*	*	-	-
Stem and belowground traits								
Stem specific density	*	?	?	*	-	*	*	*
Twig dry matter content	*	?	?	*	-	-	*	*
Twig drying time	*	?	?	?	-	-	*	*
Bark thickness	-	-	?	-	-	-	?	?
Specific root length	*	?	*	*	*	*	-	?
Diameter of fine root	*	?	*	-	-	*	-	-
Distribution of rooting depth	*	*	*	*	*	-	*	*
95% rooting depth	*	?	*	-	*	-	-	*
Nutrient uptake strategy	*	*	*	*	*	-	*	-
Regenerative traits								
Dispersal mode	-	-	-	*	-	-	-	-
Dispersule shape and size	-	-	-	*	-	-	-	-
Seed mass	-	-	*	*	*	*	-	-
Reproductive capacity	-	*	*	*	-	-	*	-

Chapter II

MATERIALS AND METHODS

Chapter II: MATERIALS AND METHODS

II.1. Materials for inventory

The establishment of a permanent plot requires the use of simple materials such as machettes, compasses, GPS, decameter tap as well as sophisticated materials such as the Trupulse ® and Trimble Geo7X®. The latter can be used to record data in the field but also serves as a high precision GPS devise. Table VI below presents a list of materials needed to ensure the successful collection of field data. This list is accompanied by a brief description of the material while details of each material are explained in the different satges.

Table VI. List of materials for establishment of a permanent plot and field inventory.

Materiels	**Quantity**	**Use**
Plot establisment		
Trimble (Geo7X 50cm)	1	This is a mini-computer for encoding data. It contains a very precise GSP allowing to geo-reference the plot
GPS (Gamin 62s)	1	Used for prospecting and locating geographic coordinates of parcels
TruPulse 360	1	Measure the slope of the ground and the heights of the trees
Digital camera	1	Digital camera 1 Photographing plants, botanical collections and landscapes
Supplementary batteries		3 for Trimble; 3 pairs for the GPS; 5 pairs for TruPulse; 2 for the camera
Compass	3	To orientate and give the azimuth of the transects
Machettes	3	To cut transects
Decameters	3	Mesurer the length/width of the transects
Plastic Ruban plastique	5	Preferably biodegradable, to serve as a topographic signal
DBH meter 3m	3	Measure the diameter of the trees
DBH meter 5m	2	Measure the diameter of the trees
Telescopic ladder 6-8m	1	Measure diameter of trees with buttresses or stilt roots and collect botanical specimens
Non corrosives nails (≥ 7 cm)	3 kg*	Fix tags on trees
Hammer	2	Hammer nails on trees

Metal tags (1-600)	1 lot de 600	Bearing a unique number to identify the different individuals trees within each plot
Pole de 1.60m	25	Wooden pole to mark the intersections between transects and quadrats
PVC pipes de 60 cm	4*	Mark the four corners of the plot
Pain 5 kg	1*	Red oil paint to mark the measurement height on the tree
Brush 1 cm	3*	Paint the heights of measurement
Forestry chalk	3*	Mark the heights of diameter measurements and the location of the label
Rope (> 100 m)	3	Materialize the boundaries of the plots
Botanical collections		
Secateurs	1	Cut leaf and small branches of botanical samples
Collection pole	1	Collect botanical samples for tall trees
News papers	10 kg	Presser/conserve botanical specimens
Paper tags	100*	Tagged specimens
Plant press	2	Press vouchers
Alcohol 70-95°	5 litre	Conserve specimens
Envelopes and silica gel	100	To dry the samples for genetic analysis, if desire
Markers, ordinary pencils, eraser	2	To mark and take notes
Notebook with hard cover	1	Take notes in the field
Soil collection		
Ziplock plastique papier bags	4*	Pack soil samples collected in the plot
50-100 liter plastic paper	50	Carrying botanical samples
Soil Auger	1	Soil sampling
Data sheet	15*	To record field data

*Average quantity per one hectare plot

II.2. Vegetation survey

The sampling of tree communities was realised through a stratified random design of permanent sampling plots (PSPs). Stratification here means the subsampling of tree communities from a given forest block which may correspond to a forest type and randomisation is the arbitrary placement of PSP around a forest block with the aim to capture the main geographic variation within the forest. Therefore, the stratified random design of PSP involved the subdivision of a PSP which is placed arbitrary within a forest block. However, each PSP was intentionally placed in mature forests with minimal human disturbance and on homogeneous terrain as to minimise intra-plot variation. The latter steps were feasible through a preliminary desktop GIS analysis using very high resolution optical imagery on a landscape map of specific sites (Fig. 10). The positions and the Geographic Positioning System (GPS) coordinates of the targeted sites were extracted from these maps.

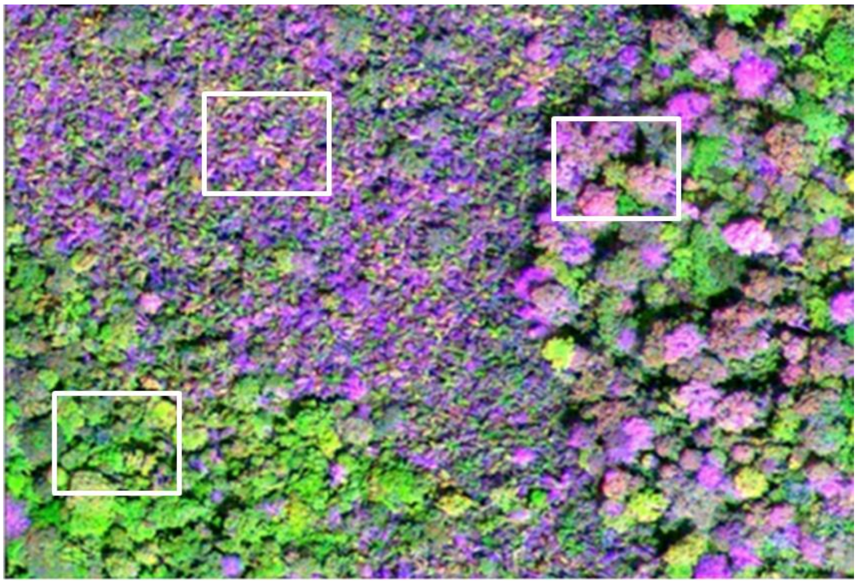


Fig. 10. Aerial view of forest types from very high resolution optical imagery of eastern Cameroon forests

Colours represent forest types, white frames are targeted sites for posterior sampling. Map modified from Henry *et al.* (2015).

Permanent sampling plots refer to sampling units where trees are individually and permanently identified and tagged. The use of PSP have received much attention as a tool to assessing plant diversity, carbon storage, forest exploitation or monitoring vegetation changes especially in tropical forests (Dallmmeier *et al.*, 1992; Libalah, 2017; Phillips *et al.*, 2003; Picard, 2007; Picard *et al.*, 2010) but also in temperate forests communities (Lutz, 2015). The size of PSP varies depending on the study objective and range in size from 50 ha (Losos and Leigh, 2004) to 1000 m^2 (Gentry, 1992). However, Alder & Synnott (1992) and Dallmmeier *et al*,. (1992) recommended one hectare PSP for monitoring biological diversity while one hectare PSPs have been the point of focus to estimating aboveground biomass in tropical forests (Djuikouo *et al.*, 2010; Kearsley *et al.*, 2017, 2013; Nascimento and Laurance, 2002). The PSP was therefore adopted, with modifications (Libalah, 2017), as the sampling unit for data collection because it does not only align with the objectives of this study but shall also contribute scientific data for regional and cross-continental forest research and serve for long term vegetation monitoring.

II.2.1. Design of Permanent sampling plots

In the present study, data were collected from two types of PSPs only differing in dimensions; 100 m by 100 m (one ha) PSP intended for studies at the CALF regional scale (Fig. 10 & Fig. 13), installed at least 500 m apart and the 50 ha Forest Dynamics Plot wherein the data collected were used for both regional and local scale studies (Fig. 7 & Fig. 11).

In the field, the dimension of the 50 ha FDP is 1 000 m long by 500 m wide (Fig. 7) which has been subdivided into 50 rectangular one ha plots of 500 m by 20 m. Each of these rectangular one ha plots was further subdivided into 20 m by 20 m quadrats, summing up to 1250 quadrats in the 50 ha. A computer based splitting of the 50 ha FDP was conducted to obtain fifty single 100 m by 100 m plots as shown in Fig. 11. This step was important to obtain plots of uniform dimension (100 m by 100 m) in Korup and in the other study sites. The procedures for data collection (specifically; taxonomy, dendrometry, climate and soil) were similar for the entire one ha PSPs.

All one ha PSP were orientated north–east and the geographical coordinates of the four edges of the plot were recorded using a high precision Trimble GeoExplorer® GPS (Fig. 14) to enable its spatial representation. In addition the coordinates after every 20 m along the border of the PSP were recorded.

Each one ha PSP was subdivided into 25 quadrats of 20 m by 20 m (Fig. 13) to facilitate data collect therein. Four permanent polyvinyl pipes of 60 cm long were planted at the edges and 32 wooden poles of 100 cm long were also planted at every intersection within the plot.

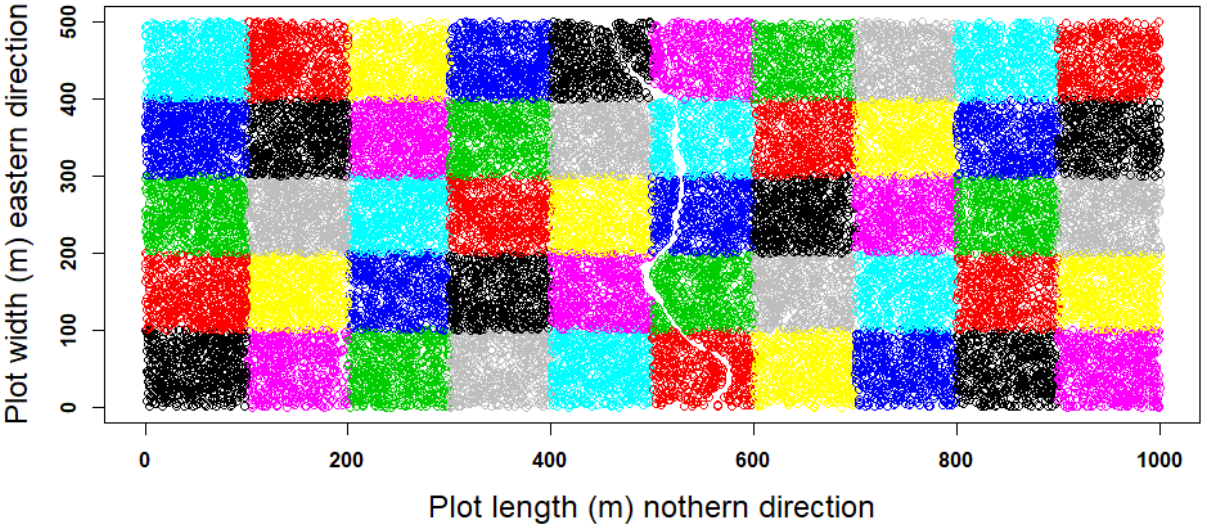


Fig. 11. Computer based splitting of the 50 ha rectangular forest block into fifty single 100 m by 100 m plots.

II.2.2. Plot demarcation

The demarcation of each one plot involves the use of a compass for orientation in a direction of preference. Following this direction indicated by the compass, two baselines of 100 m each are demarcated, one towards the North direction and the other towards the East direction. The two directions were named Y for the North-South axis and X for the East-West axis. In other words, these two baselines were the axes of an orthonormal frame and the insertion point is the origin of the frame (Fig. 12).

A 20 m distance was measured 20 m from the origin of the marker (point 0:0) and a pole was planted at this position. The pole was marked with a ribbon depending on the location along the XY position. Towards the X direction for example, the poles are successively numbered every 20 m thus: 0:0; 0:20; 00:40; 00:60; 00: 80 and 0: 100. Towards the direction Y, numbering was thus: 20:00; 40:00; 60:00; 80: 00 and 100: 00 as illustrated in Fig. 12 B. The position of the quadrat (a quadrat measuring 20 m x 20 m) in the space was numbered according to the XY coordinates of the southwest corner of the quadrat. PVC pipes (approximately 0.6 m long each) were planted at the 4 corners of the plot, precisely at 0:0; 100:00; 100:100 and 00:100. This allowed finding the plot after a certain time for the subsequent studies (remeasurement for example). The direction of movement in the parcel was systematic, starting with the 0:0 quadrat and moving eastward in the 00:100 directions (Fig. 13).

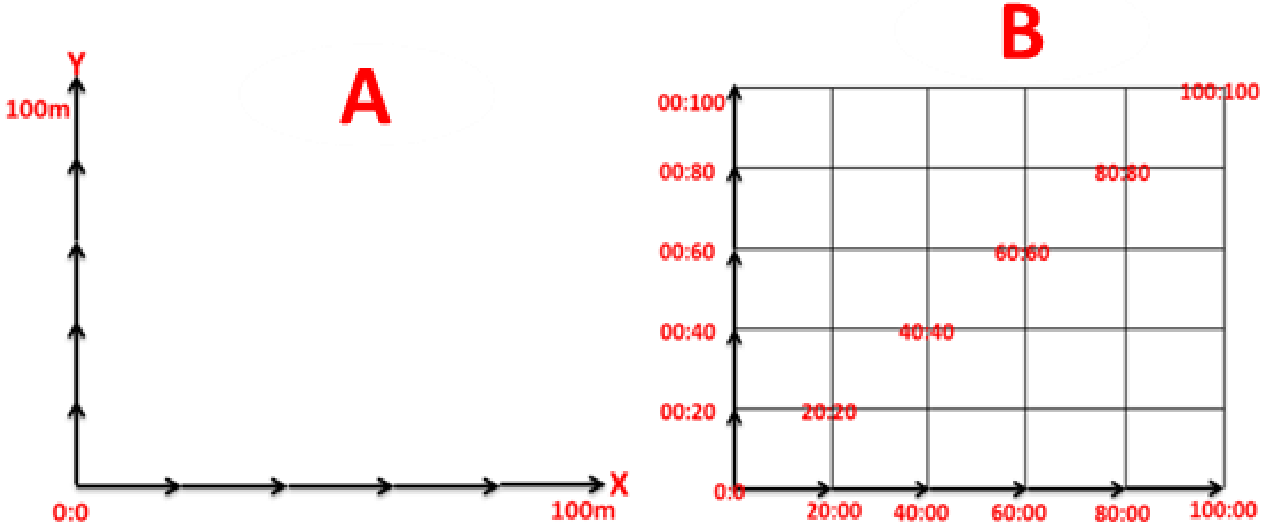


Fig. 12. Demarcation of a one ha plot.

A: length and direction of first baselines; B: complete demarcation of quadrats

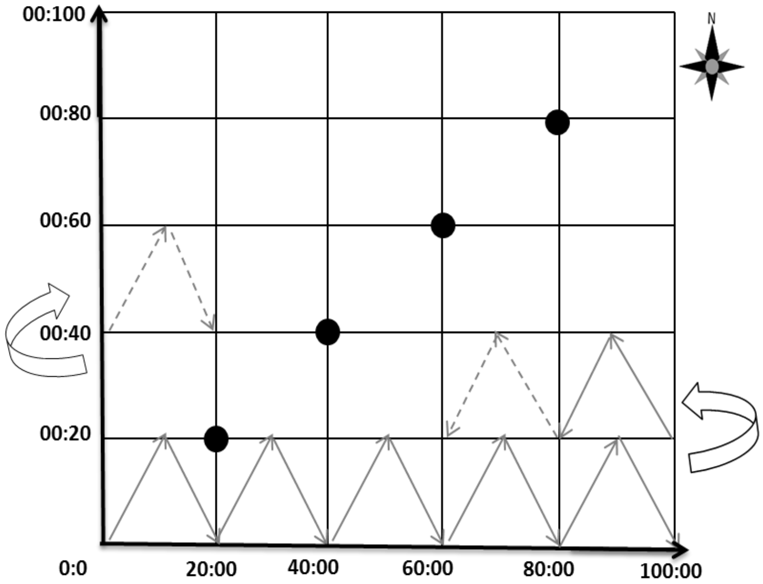


Fig. 13. Complete design of a permanent sampling plot for data collection.

Arrows: displacement with and between quadrat, black dots: soil collection positions

II.2.3. Geo-localisation of the plot

For a spatial location of the parcel, the GPS coordinates at the boundaries of the plot were recorded. That is, the GPS coordinates of each pole were recorded with the Trimble (Fig. 14) and the slope of the plots was also recorded using a TruPulse 360®.

Fig. 14. High precision Trimble Geo7X® GPS for data recording (A) and Trupulse 360® for tree heigh measurement (B) during field inventory data.

II.2.4. Procedure for data collection

By systematically passing from one quadrat to the next within the PSP (Fig. 13), all trees were censured following the modified protocol for the establishment of PSPs by Libalah, (2017). That is, the trees were measured at 1.3 m and assigned a tag (engraved number on a piece of metallic sheet), painted at the point of measurement and the taxonomic nomenclature determined or morphospecies code assigned to each tree. Within the PSP, data related to the taxonomy and dendrometry were obtained on all individuals; functional traits were measured on selected species; soil and topography data were collected within certain quadrats and climate data were obtained for each PSP.

II.2.4.1. Taxonomic data

Taxonomic data comprised species name or morphospecies code obtained during field inventories and herbaria studies. A first taxonomic identification was performed in the field at the time of tree measurement by observing the leaves, flowers, slash, habit and other diagnostic characters (Fig. 16). Trees were identified to the lowest taxon by experienced botanists assisted by local floras and identification guides. A unique morphospecies code was attributed to a tree if unidentified and this code was re-used whenever the same "species" was encountered within a locality. A herbarium specimen and vouchers including silica gel samples and photos were prepared for each individual if it was encountered for the first time. A second taxonomic identification was realized on the vouchers at three herbaria including the Plant Systematic and Ecology Laboratory (Higher Teachers' Training College, University of Yaoundé I) and at two official herbaria: National Herbarium of Cameroon (YA) and Herbarium of the Université Libre de Bruxelles (BRLU) [herbarium acronyms follow (Thiers, 2012)] (Fig. 16). The voucher specimens for each species were deposited in these herbaria. The names of the species were corrected/homogenized for synonymies and orthographic problems through major plant databases such as The Plant List (http://www.theplantlist.org/), The African Plant Database (version 3.4.0) (http://www.ville-ge.ch/musinfo/bd/cjb/africa/) and The Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/index.html). The nomenclature for Families and Genera are according to APG IV (2016).

II.2.4.2. Dendrometric data

Dendrometric data included the tree's diameter and height. The diameter at 1.3 m breast height (dbh) equal or greater than ten cm (≥ 10 cm) was measured on all trees using a diameter tap, plus a telescopic ladder for tall trees. This measurement was done on trees without deformation and for large trees with buttresses or deformations at dbh 10 cm, measurements were done at 30 cm above the deformations (Fig. 15). A red band of paint about 5 mm wide was applied around the tree at the

1.3 m point of measurement (Fig. 15). Each stem was treated as an individual tree for those with multiple stems.

The total height and the trunk height (height between the ground and first branch) were measured with a TruPulse 360® irrespective of the species (Fig. 15). This measurement was realised on at least five trees per diameter class (10–20; 20–30; 30–40; 40–50; 60–70 cm, etc.) selected randomly within the PSP. The total minimum number of tree heights measured per PSP was maintained at 18 trees for statistical validity.

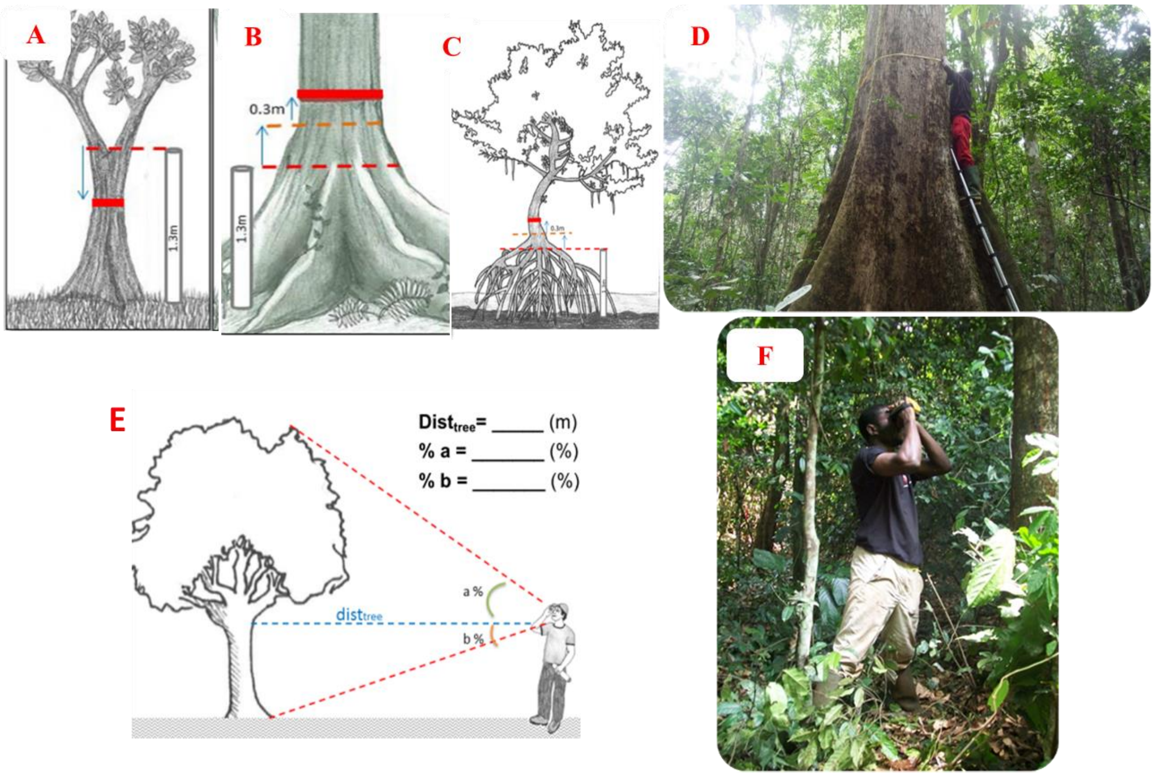


Fig. 15. Principles and field measurement of dendrometric parameters.

A-D: Tree diameter measurement at different positions; E-F: Illustration of tree height measurement (A, B, C and E anonymous).

II.2.4.3. Wood density

The wood density of each tree was obtained from DRYAD global wood density database (Chave *et al.*, 2009; Zanne *et al.*, 2009). Not all species sampled in the field were found to have wood density values in the database. Therefore, wood density values were allocated at the species level whenever available. If not found, the Genus-level or Family-level or plot-level averages were computed and assigned to the individual.

II.2.5. Soil and topography data

Soil samples were obtained using an AMS soil auger®. From each one ha PSP, soils were collected at four specific locations along the diagonal of the plot (see illustration on Fig. 13). In the

50 ha FDP, soils were collected from the centres of the 44 randomly selected 20 m x 20 m sub-quadrats. For each point of soil collection, four soil cores (excluding litters: Fig. 17) were dug at 10 cm depth intervals (0–10; 10–20; 20–30 and 30–40 cm). The cored samples were separately air-dried (Fig. 17) and a pooled sample was constituted from equal proportions of the respective samples.

Within each of the one ha PSP, data for the altitude and the Height Above Nearest Drainage (HAND) index (Rennó *et al.*, 2008) were extracted from the Shuttle Radar Topography Mission (SRTM version 3: Farr *et al.*, 2007). Both SRTM and HAND topographic data were aggregated at 30 arc-second (900 m) from an initial resolution of 3 arc-second (90 m).

Fig. 16. Some stages involved in botanical identification.

A-C: Field collection of vegetative material; D-E: Tree slash for identification; F-G: pressing of specimen; H-J: Herbarium identification.

Because the rectangular 50 ha FDP covers a significant surface area, intra-quadrat variation was expected to occur contrary to the one ha PSPs which were intentionally installed on homogenous terrain. Therefore three topographic data were used from the 44 randomly selected quadrats of the 50 ha FDP including the elevation, slope and convexity (Chuyong *et al.*, 2011, 2004; Thomas *et al.*, 2003). The elevation was measured on-site to the nearest 0.1 m at each corner of the quadrat and the value added to the absolute elevation got from the published survey map of the area. The slope was measured by forming three angles and measuring the deviation from the horizon of each of the triangular planes. Convexity was calculated as the difference between the mean elevation of the focal quadrat and the mean elevation of the eight surrounding quadrats. For quadrats at the edge, convexity was calculated as the difference between the elevation of the centre of the focal quadrat and the mean elevation of the four corners. Using these three topographic attributes for each quadrat, Chuyong *et al.* (2011) assigned each quadrat to one of five habitat types. Out of the 44 randomly selected quadrats, 8–10 of these belonged to one habitat type.

II.2.6. Laboratory analysis of soil composition

The pooled soil samples were analysed for ten soil composition variables. To analyse these variables, each sample was first air-dried and ground to pass through a 2 mm sieve using a motorized – Retch RM200® – grinder and further fine-ground to pass through a 0.5 mm sieve for Nitrogen and Carbon analyses. Soil pH in water was determined in a 1:2.5 (w/v) soil: water suspension. Total nitrogen and total phosphorus were determined from a wet acid digest and analysed by colorimetry (Anderson and Ingram, 1998; Buondonno *et al.,* 1995) and total phosphorus was further determined using the molybdate blue procedure described by Murphy and Riley (1962). Cation exchange capacity was determined using ammonium acetate at pH 7. Moisture content was determined by gravimetry after sample drying at 105 °C. Organic carbon was determined by chromic acid digestion and spectrophotometric analysis using a Genesys 10S UV/Vis spectrophotometer. Soil organic matter was then obtained by multiplying organic carbon value by 1.72 (Heanes 1984). Particle sizes (Sand, Silt and Clay) were determined by the Bouyoucos hydrometry (Bouyoucos, 1951; Day, 1953). The analyses of soil mineral resources were conducted in the Plant and Soil laboratory of the Institut de la Recherche Agricole pour le Dévelopement (IRAD)-Yaoundé and the Soil & Plant laboratory of the International Institute of Tropical Agriculture (IITA)-Yaoundé. The detailed protocol for the analysis of soil samples in the laboratory is presented in Appendix 1.

Fig. 17. Major steps to collect soil sampling in the field

A-B: Sample collection; C: packaging; D: air-drying (D: Yamina Pressler).

II.2.7. Bioclimatic data

The bioclimatic data were extracted only for the regional scale analysis (i.e. one ha PSPs). To extract these data the GPS coordinates (centroid of each one ha PSP) served to extract remotely sensed bioclimatic data at 30 arc-seconds (900 m) from an initial resolution of three arc-seconds (90 m).

Ten bioclimatic variables were extracted from Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA v1.2: http://chelsa-climate.org/). These bioclimatic variables are based on a quasi-mechanistical statistical downscaling of the ERA interim global circulation model (Karger *et al.,* 2017). The bioclimatic variables include Annual Mean Temperature, Temperature Annual Range calculated as maximum temperature warmest month – minimum temperature coldest month, Annual Precipitation, Precipitation Seasonality calculated as a coefficient of variation of monthly precipitation, Mean Temperature of Warmest and Coldest Quarters and Precipitation of Wettest and Driest Quarters. To account for variation in the radiative budget, data was obtained for cloud frequency (mean and yearly standard deviation) from Wilson and Jetz' EarthEnv dataset (Wilson and Jetz, 2016), derived from 15 years of Moderate Resolution Imaging Spectroradiometer satellite optical data. The bioclimatic stress index (ChavE) proposed by Chave *et al.,* (2014) which is derived from Climate Water deficit (CWD), Temperature and Precipitation seasonality thus: $(0.178\ \times \mathrm{TS} - 0.938\ \times \mathrm{CWD} - 6.67\ \times \mathrm{PS}) \times 10^{-3}$ was equally extracted.

II.2.8. Functional traits data

Within the 50 ha FDP, a subsample of 44 quadrats was randomly selected from the overall quadrats wherein data collected. These quadrats represented habitat heterogeneity of the 50 ha FDP.

Four leaf traits were sampled on tree species (≥ 10 cm) in the selected quadrats of the 50 ha FDP. Leaves were collected in the field and analysed in the laboratory to obtain the trees' leaf area, specific leaf area, leaf nitrogen content and leaf phosphorus content following the procedure below. Trees which presented physiological deformation or obvious symptoms of pathogen or herbivore attack were not sampled. Integrating such individuals in the analysis may reflect the modified physiological status of the plants rather than the ecological functioning (Cornelissen *et al.,* 2003). Trees with tall inaccessible canopies were also not sampled for practical reasons.

In the field, three fully opened exposed leaves (leaf blade plus petiole) from each tree were harvested for healthy trees by means of a collecting pole and ladder each measuring 5 m long. The fresh leaves were spread in-between a 25 cm × 50 cm white surface (below) and a transparent sheet (above) to take a high-resolution photograph without shadow (Fig. 18A). The photograph was analysed with TOASTER; an ImageJ software plugin (Borianne and Brunel, 2012), to obtain automatically leaf area values for the three leaves (Fig. 18B). Each set of leaves were preserved in a labelled envelop and dried.

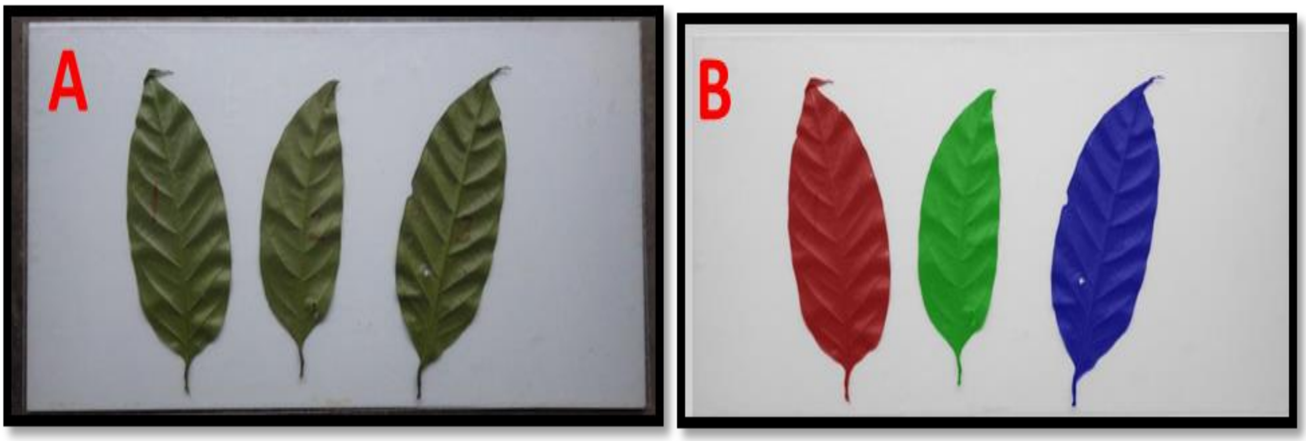


Fig. 18. Photographic image analysis by TOASTER software.
A: Leaves image of *Strombosiopsis tetrandra* before analysis; B: after analysis.

In the laboratory, the leaf samples were oven-dried with a Genlab OV/50® oven at 70 °C to constant weight and weighed with an OHAUS scout® *pro* sp202 balance (mass precision of 0.01 g), to obtain their dry masses. The leaf area (cm^2) per tree was determined as the average area of the three leaves; specific leaf area ($mm^2.mg^{-1}$) was calculated as the ratio between leaf area and the average mass of the three leaves. These analyses were conducted at the Plant Systematic and Ecology Laboratory, University of Yaoundé I, Cameroon.

The phosphorus and nitrogen concentrations of the leaves were measured by cutting equal fractions from each of the three leaves, crushed and homogenized using a Retch RM200® grinder and dried at 105 °C for 48 h to exclude moisture. Then, 0.2 g of the powder was weighed using a Sartorius R200D® balance (mass precision of 1×10^{-6}g) and further calcinated at 450 °C in a Lenton ARF® furnace.

The phosphorus concentration ($\mu g.g^{-1}$) of the calcinated sample was determined by acid dissolution of the ashes followed by a colorimetric determination with the molybdenum blue method (John, 1970). From another 0.2 g powder, leaf nitrogen content ($\mu g.g^{-1}$) of the sample was determined by flash combustion at 950 °C in a C-N elemental analyser (Dumas method). LPC and LNC analyses were conducted at the Plant Ecology and Biogeochemistry Unit, Université Libre de Bruxelles, Belgium.

II.3. Statistical analyses

II.3.1. Multivariate analysis

Multivariate analysis (or multivariate ordination) has become a well-established framework mainly for exploratory data analysis rather than testing hypothesis. It facilitates the arrangement of objects that are characterised by multiple variables (i.e., multivariate objects) so that similar objects are closer each other and dissimilar objects are farther from each other (Dray *et al.*, 2012; Gauch, 1982; Ter Braak and Prentice, 1988). The result of a multivariate analysis is a matrix of relationships between objects on different dimensions or axes that can be numerically and/or graphically represented. The purpose of multivariate analyses in this study was first of all to identify the main gradients and reduce the number of dimensions from the large number of bioclimatic data and soil composition (as explanatory variables) and floristic composition (as response variables) and secondly to resolve collinearity problems that usually arise with multiple variables in data analysis. Also, the multivariate analysis was applied as unconstrained ordination or as constrained method.

II.3.1.1. Unconstrained ordination

Unconstrained ordinations techniques are based on species composition expressed as site-by-species matrix. It is intended to bring out the main trends in the data in the form of continuous axes. The Principal Component Analysis (PCA) and Correspondence Analysis (CA) are widely used unconstrained ordination techniques in community ecology. The PCA is the main eigenvector-based method that works on raw and quantitative data and it preserves the Euclidean distance among sites (Legendre and Legendre, 1998). The CA is mainly used to analyse species data tables in the form of frequencies or frequency-like. It accepts dimensionally homogeneous and non-negative data and preserves the chi square distance among rows or columns (Legendre and Legendre, 1998).

Two specialised forms of the CA have been developed to integrate species diversity indices in a multispecies (plot-by-species floristic table) framework with the aim to capture the prominent features of the species composition of a community (Couteron and Pélissier, 2004; Pélissier *et al.*, 2003). The first is the symmetric CA which integrates the species richness as a measure of species diversity and gives more weight to scarce species in the floristic table. The second is the Non-symmetric correspondence analysis (NSCA) which integrates the Simpson-Gini index as a measure of species diversity and emphasises on abundant species in the floristic table (Pélissier *et al.*, 2003).

II.3.1.2. Identification of gradients in soil composition and bioclimatic variables

Two independent PCAs were run on the soil composition and bioclimatic variables in order to identify the orthogonal gradients in these datasets. The elevation and slope were included as supplementary quantitative variables in the PCA to interpret their correlation with the main PCA axes.

Because the output of a PCA produces many ordination axes, one serious problem is to decide on the number of interpretable PCA. Often, selection of the number of interpretable PCA axes is based on visual selection but two other sophisticated approaches to overcome this problem have been proposed (Borcard *et al.*, 2011):

- Kaiser–Guttman criterion (Yeomans and Golder, 1982); computes the mean of all eigenvalues and interpret only the axes whose eigenvalues are larger than that mean,
- Broken-stick model (MacArthur, 1957); divides a stick of unit length into the same number of pieces as there are PCA axes, arrange the pieces in order of decreasing length and compare to the eigenvalues. Only the axes whose eigenvalues are larger than the length of the corresponding piece of the stick are retained as interpretable axes.

II.3.1.3. Identifying patterns in multispecies distribution

The Symmetric correspondence analysis was used to capture the gradients contributed by scarce while the Non-symmetric correspondence analysis is necessary to determine the proportion abundant species in the community (see II.3.1.1). Mathematically, a species was determined as being scarce within a given locality when the average was ≤ 1 tree.ha^{-1} while an abundant species had an average of > 1 tree.ha^{-1} (Pitman *et al.*, 2001).

II.3.1.4. Constrained ordination

Constrained ordinations techniques are based on species composition, expressed as site-by-species, and on environmental factors, expressed as site-by-predictors matrices by means of variance partitioning. Variance partitioning quantifies the relative influence of several environmental factors on multispecies floristic pattern (Dray *et al.*, 2012). In other words, the constrained ordination techniques attempt to explain differences in species composition between sites by differences in environmental predictors via multivariate linear models. Therefore, inter-site variances of the species composition can be equated to diversity metrics (Couteron and Pélissier, 2004). The proportion of explained variance on the species composition is considered to originate from the measured environmental factors while the proportion of unexplained variance is interpreted as the result of unmeasured environmental factors or stochastic effects (Legendre *et al.*, 2005).

The Symmetric Correspondence Analysis with Instrumental Variables (CAIV; Couteron *et al.*, 2003), synonymous to the Canonical Correspondence Analysis of (CCA; ter Braak, 1986), and the Non-Symmetric Correspondence Analysis with Instrumental Variables (NSCAIV; Couteron *et al.*, 2003), which is a particular version of redundancy analysis, have been developed as the constrained analogues of the CA and NSCA. Just like the unconstrained analogues, the CAIV and NSCAIV are complementary strategies that refer to two popular metrics of diversity (i.e. species richness and Simpson-Gini index), via two different weighting of individual species (Pélissier *et al.*, 2003).

II.3.1.5. Accounting for the influence of environmental gradient on floristic patterns

The CAIV and NSCAIV permitted to analyse how environmental gradients influence patterns in species distribution. Specifically, the CAIV was used to account for the extent to which soil and/or climate gradients explain the distribution of scarce species while the NSCAIV was used to determine the extent to which these gradients explain the distribution of abundant tree species. Therefore the extent to which soil gradient ($\mathrm{S_{IV}}$) and climate gradient ($\mathrm{C_{IV}}$) independently and jointly ($\mathrm{S_{IV}} + \mathrm{C_{IV}}$) influence species distribution were apportioned on the floristic tables using the CAIV and NSCAIV approaches.

Because the CAIV and NSCAIV strategies require the two datasets (plot-by-species and plot-by-environmental predictors) to have equal number of rows or plots (Couteron *et al.*, 2003; Dray *et al.*, 2012; Pélissier *et al.*, 2001), a full floristic table of 82 one ha PSP versus 541 species and morphospecies was built to assess the overall patterns in species distribution. Further, the full floristic table was subdivided to have a reduced floristic table containing 60 one ha PSP versus 449 species and morphospecies, to match the table of 60 one ha plots for which soil data were available. Only the reduced floristic table was then subjected to the constrained ordinations (i.e. CAIV and NSCAIV).

II.3.1.6. Accounting for redundancy in constrained ordination

To determine the extent to which the soil and climate gradients were redundant in predicting species distribution, a partial ordination was performed. That was by calculating the proportion of variance explained by soil after factoring-out the effects of climate ($\mathrm{S_{IV}} - \mathrm{C_{IV}}$) and the other hand, the proportion of variance explained by climate after the soil effects were factored-out ($\mathrm{C_{IV}} - \mathrm{S_{IV}}$). Also, the shares of total variance explained by the soil and climate gradients on each species were calculated as in equation 1;

$$\mathrm{s}^2 = \frac{\sum(x-\bar{\mathrm{x}})^2}{n-1} \qquad \text{………………….. ………………..} \quad \text{Equation 1}$$

II.3.2. Descriptive statistics

II.3.2.1. Mean

The means or average is calculated by dividing the total of all values (x) by the number of values (n) as in equation 2;

$Mean = \frac{\sum_{i=1}^{n}(x)}{n}$ ………………….. ……………….. Equation 2

II.3.2.2. Root mean square error

The root-mean-square error (RMSE; equation 3 is a frequently used measure of the differences between sample and population values, predicted by a model or an estimator and the values actually observed. In this study, the RMSE serves to measure the error associated to different linear models;

$RMSE\ (\%) = \left[\sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(H_{Eco,i} - H_{Obs,i}\right)^{2}}\right] \times 100$ …………………… Equation 3

where n is the total number of trees, H_{Obs} is the height of tree i measured in the field and H_{Eco} is the predicted height of tree i from a model.

II.3.2.3. Bias

The Bias measures the difference between an expected value and the observed or true value of the parameter being estimated. This Bias was applied in this study to account for difference in the observed tree height and the predicted tree height from an improved model. It was calculated for each PSP thus:

$Bias\ (\%) = [mean\ (H_{Eco} - H_{Obs}) \div H_{Obs}] \times 100$ ………………………….. Equation 4

II.3.2.4. Variance analysis

The variance (equation 5) measures the spread of values (x) from their mean value (x̄):

$\text{Variance} = \frac{\sum(x-\bar{x})^{2}}{n-1}$ ……………………….…….. ……………….. Equation 5

The analysis of variance analyzes the differences among group means and can be accompanied by a Post Hoc test of multiple comparisons. One suitable Post Hoc test of multiple comparisons is the Bonferroni Correction to account for unequal sample means (Dunn, 1961).

II.3.3. Statistical relationships

II.3.3.1. Regression analysis

Regression analysis is widely used as a statistical method to model and estimate the relationship among variables for explanatory or predictive purposes. Linear regression estimates the relationships between one dependent and one (simple regression) or more (multiple regression) independent variables. The ordinary least square repression is a specific method for estimating unknown parameters in a linear regression model. The goal of an ordinary least squares regression is to minimize the differences of the sum of the squares between the dependent and independent variables.

The purpose of linear regressions in this study was mainly to:

- quantify the strength of the relationships between soil and climate gradients versus parameters of forest structure and functional traits and
- predict the heights of trees from their respective diameter measurements.

II.3.3.2. Correlation analysis

Correlation analysis serves to evaluate the strength of relationships between two, numerically measured, continuous variables such as soil and climate gradients versus parameters of forest structure. The Pearson correlation coefficient was used throughout the analysis to report results of correlation.

II.3.4. Resampling and significance tests

II.3.4.1. Monte Carlo Permutation test

Monte Carlo Permutation test (otherwise randomization test) is a type of statistical test that rely on repeated random sampling of the observed data, calculate the test statistic of the random sample distribution and compare for difference with the test statistic of the observed sample (Dwass, 1957).

In this study, randomization permitted to test the significant influence of the environmental variables on the floristic patterns. The null hypothesis (H_0) was that the species distribution patterns are independent of the environmental variables. That is, the soil and climate gradients do not significantly influence species distribution. If the observe species distribution is different from H_0, H_0 is rejected and consider that the soil and climate gradients influence the patterns in species distribution. Each test test considered statistically significant at a P – value less than 0.05 after 999 simulations. Graphically (Fig. 19), if the test was significant, the observe value was found at the extreme with respect to the simulated distribution.

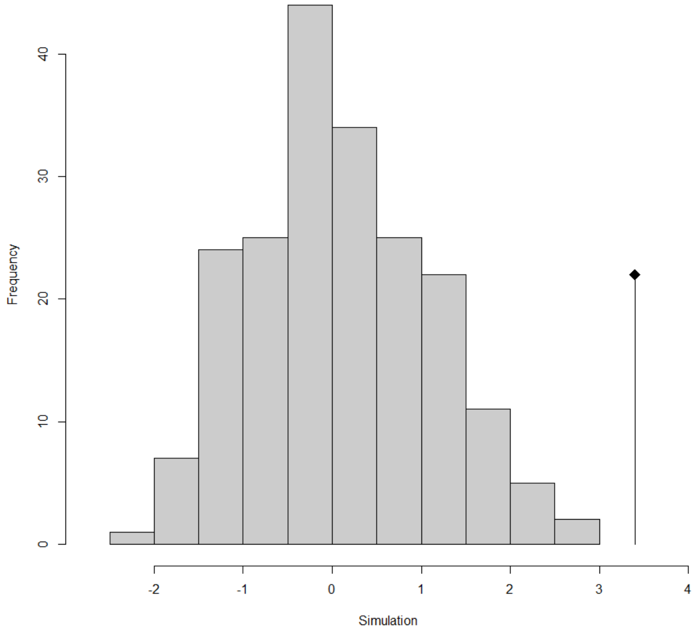


Fig. 19. Exemplary graph of a Monte Carlo randomization test after 999 simulated values. Right vertical line: indication of significance zone and rejection of the null hypothesis.

II.3.4.2. The Jackknife analysis

This is a common resampling technique based on omitting the *i*-th observation from a dataset and calculating the estimate and then finding the average of these calculations (Efron and Stein, 1981). In this study, the mean of community-weighted trait was computed from subsamples consisting of all but the *i*-th data point. The Jackknife mean was computed from *n* subsamples thus:

$$\text{Jackknife mean} = \frac{1}{n-1}\sum_{j=1, n\neq i}^{n} x_j \quad i = 1, \ldots, n \ldots\ldots\ldots\ldots\ldots \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{Equation 6}$$

II.3.4.3. Forward selection

The forward selection approach permits to reduce the number of variables to be included in a model by selecting only variables that would improve the model. For each explanatory variable, this test calculates whether the addition of a new variable ameliorates the model considering that other variables already exist in the model.

II.3.4.4. Cross validation

Cross-validation is a statistical method intended for validating a predictive model, that is, how the results of a statistical analysis will generalize to an independent data set (Geisser, 1993). Subsets of the data are held out for further use as validating sets (Leave-one-out procedure); a model is fitted to the remaining data (a training dataset) and used to predict for the validation dataset. The leave-one-out cross validation procedure is particularly important in testing the robustness of a new model, developed on the training dataset and tested on the validating dataset. Its particularity is to avoid "self-influence".

II.3.5. Forest structure

The following parameters were calculated at the level of each plot to describe the structure of the forest.

II.3.5.1. Stem density

The stem density (D_S) is the number of individual tree-stems counted within a one ha PSP.

II.3.5.2. Basal area

The basal area is a classical parameter used by foresters and is simply the cross-sectional area of a tree stem measured at breast height (1.3 m). It is closely related to the volume occupied by a tree in a given area. The basal area was expressed in m^2 and was calculated for a tree in a one ha PSP (or 10 000 m^2) as: pi * D^2 / 40000. The sum of all tree's basal area in a one ha PSP yields the plot's basal area.

II.3.5.3. Quadratic mean diameter

Quadratic mean diameter (D_g) is another proxy of the volume occupied by a tree. It is expressed in cm and calculated as the average square root of squared diameter per ha^{-1} as show below:

$$D_g = \sqrt{\sum_{i=1}^{n} \frac{(D)^2}{n}} \quad \text{…………………. ………………..} \quad \text{Equation 7}$$

II.3.5.4. Wood density weighted basal area

The wood density weighted by basal area (D_W ; equation 8) can be used to represent forest dynamics; young forests would have greater proportion of pioneers species (low wood density) compared to old forests with greater proportion of oldgrowth species (high wood density). This parameter is important to weigh plots based on the volume of phytomass so that plots with large trees will be weighted more than those with small trees (Gourlet-Fleury *et al.*, 2011). It is expressed in g $cm^{-3}$and calculated using the formula below:

$$D_W = \frac{\sum_{i=1}^{Ds}(BA_i \times WD_i)}{\sum_{i=1}^{Ds} BA_i} \quad \text{. ………………..} \quad \text{Equation 8}$$

where WD is the mean wood density of species i , BA is the basal area and D_S is stem density.

II.3.6. Trait-gradient analysis

This analysis focused on interspecific and intraspecific variation in leaf trait values across soil gradient at local scale. The trait-gradient approach (Ackerly and Cornwell, 2007) permits the computation of three trait metrics (species mean trait, community-weighted mean trait and functional divergence) to evaluate species and community traits response to soil gradient.

II.3.6.1. Computing functional trait metrics

Species mean trait (t_i) is a functional trait metric to measure the performance of species via their traits (Ackerly and Cornwell, 2007). The t_i computes trait average of the species *i* and sums species' traits irrespective of the quadrats where it was sampled (Equation 9).

Community-weighted mean is a commonly used functional trait metric to measure community performance via traits (Lavorel *et al.,* 2008). Traits were measured within quadrats hence quadrat-level weighted mean traits (q_k). The q_k computes the quadrat mean trait and sums quadrat trait values irrespective of species (Equation 10).

$$t_i = \frac{\sum_{k=1}^{P} a_{ik} \times t_{ik}}{\sum_{k=1}^{P} a_{ik}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 9}$$

$$q_k = \frac{\sum_{i=1}^{S} a_{ik} \times t_{ik}}{\sum_{i=1}^{S} a_{ik}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 10}$$

where t_i represents the *i*th species mean trait and q_k abundance-weighted quadrat-level mean values, t_{ik} being the trait value of species *i* in quadrat *k* and a_{ik} is the abundance of species *i* in quadrat *k*. The total number of species and quadrats in the study is *S* and *P*, respectively.

II.3.6.2. Computing functional divergence

The functional divergence (FDiv_k) is derived from the Rao's diversity index (Botta-Dukát, 2005). The FDiv_k expresses the trait dissimilarities between quadrats such that quadrats with relatively high FDiv_k would indicate a high degree of niche differentiation, and thus low resource competition and vice versa (Mouchet *et al.,* 2010). It is calculated as the sum of pairwise trait dissimilarities between species within a quadrat, weighted by the species relative abundance (Botta-Dukát, 2005; Mouchet *et al.,* 2010). The unstandardized FDiv_k was computed for each trait independently, using the formula in Equation 11 below;

$$FDiv_k = \sum_{i=1}^{S} \sum_{j=i+1}^{S-1} d_{ij}\, a_i\, a_j \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 11}$$

where d_{ij} is the trait dissimilarity between each pair of species *i* and *j* ($d_{ik} = d_{ki}$ and $d_{ii} = 0$), a_i and a_j are the relative abundance vectors of species *i* and *j* and *S* is the total number of species.

II.3.6.3. Accounting for traits-soil gradient relationship

To examine how a shift in the edaphic gradients may be associated with functional traits, linear regressions were fitted for each trait separately by using the quadrat-level weighted mean trait ($\mathrm{q_k}$) and functional divergence ($\mathrm{FDiv_k}$) vs. the scores of the main soil PCA axes. Significant correlations between the main soil PCA axes vs. q_k, were interpreted as the effect of abiotic filtering, and vs. $\mathrm{FDiv_k}$ as the effect of competitive interaction (Ackerly and Cornwell, 2007; Botta-Dukat, 2005).

II.3.6.4. Determining non-random community trait distribution

To determine whether the trait-soil gradient associations were non-random, a null model approach was used; which assumes that traits are randomly distributed within quadrats. Null communities were generated by randomizing species traits values within each quadrat-by-species matrix. Species abundances within each quadrat were kept constant but traits were shuffled across species. A null $\mathrm{q_k}$ and null $\mathrm{FDiv_k}$ were estimated for each quadrat and the 95% confidence intervals (CI) were calculated after 999 simulations of the null model. We computed the differences between the observed communities and the null (i.e. observed $\mathrm{q_k}$ – null $\mathrm{q_k}$ and observed $\mathrm{FDiv_k}$ – null $\mathrm{FDiv_k}$). Positive differences were interpreted as the effects of trait convergence while or negative differences were interpreted as the effects of trait divergence.

II.3.6.5. Assessing trends of intraspecific trait variation across soil gradients

Intraspecific trait variations relative to the quadrat-level mean trait ($\mathrm{q_k}$) were assessed via linear regressions by using individual trait values of the ith species in a quadrat ($\mathrm{t_{ik}}$) vs. the $\mathrm{q_k}$. The slopes of the linear regressions were interpreted to reflect intraspecific trait variation.

Note that there is lack of mathematical independence in the computation of $\mathrm{t_{ik}}$ and $\mathrm{q_k}$. That is, $\mathrm{t_{ik}}$ is included in the computation of $\mathrm{q_k}$. This may lead to false correlation even in the absence of any ecological association. To correct for this, a Jackknife analysis (Equation 6) was used to recalculate the $\mathrm{q_k}$ but without accounting for focal species in the quadrat (Cornwell and Ackerly, 2009). Further, linear regressions were performed between $\mathrm{t_{ik}}$ and the scores of the main soil PCA axes to assess intraspecific trait response to the gradient. We used the abundance-weighted ordinary least squares regression to examine the trends of intraspecific trait variation across the gradients.

II.3.7. Modelling Height–diameter relationship

More than 20 model forms are commonly used to fit Height–diameter (*H–D*) relationship of trees (Mehtatalo, 2017). Here, a second order polynomial model was used to model tree *H–D* relationship:

$$\ln(H) = a + b \times \ln(D) + c \times \ln(D)^2 + \varepsilon \quad \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots. \text{ Equation 12}$$

where H is total tree height (in m), D is diameter (in cm), a is the coefficient of intercept and b and c are the coefficients of slope and ε is the error term. This model form was selected as it accounts for the general increase in H prediction error with D (i.e. Mascaro *et al.,* 2011) and this model has been shown to perform well in tropical forests (Chave *et al.*, 2014; Feldpausch *et al.*, 2011; Réjou-Méchain *et al.,* 2015), such as in central Africa (Fayolle *et al.*, 2013).

II.3.7.1. Height prediction not integrating environmental predictors

Using the model form of (Equation 12 above, two sets of tree heights were predicted from diameter: $\mathrm{H_{gen}}$ based on the overall data irrespective of plots and $\mathrm{H_{Ref}}$ based on plot-specific data. For $\mathrm{H_{Ref}}$, plots were introduced as factors in the model (Equation 13) to account for site effects on the H–D relationship. The model coefficients (i.e. Equation 13) for each plot were extracted and observed for variability among sites.

$$H_{Ref} = \exp(a + b \times \ln(D) + c \times \ln(D)^2 + Plots + \varepsilon) \dots\dots\dots\dots\dots\dots\dots\dots\dots \text{ Equation 13}$$

where $Plots$ represent the plots’ coefficients expressed as factors.

II.3.7.2. Height prediction integrating ecological factors

To identify the ecological factors which are likely to influence the prediction of H from D, several linear regression models were built by considering each dependent variable to all combinations of N independent variables. Specifically, the plots’ coefficients (obtained from Equation 13), were used as the dependent variables (total of 78) and the ecological factors as independent variables (total of 12; Table VII), to construct several regressions models (Equation 14) each time taking a plot’s coefficient versus all possible combinations of the biotic and abiotic factors (4096 linear models in total). The leave-one-out cross-validation procedure was then employed to estimate the accuracy of the linear models. That is, the linear models were calibrated on all other plots except the focal one and later validated the models using this focal plot. The later procedure was necessary to ensure mathematical independence between the calibration and validation datasets (for cross validation procedure, see section II.3.4.4). A Null model was equally built (coefficient ~ 1) where no ecological factors were integrated in the model.

$$H_{Eco} = \exp(a + b \times ln(D) + c \times ln(D)^2 + x_i + \varphi + \varepsilon) \ldots\ldots.\ldots\ldots\ldots\ldots\ldots\ldots. \text{Equation 14}$$

where x_i is the coefficient of the ith plot and φ represents a combination of 1-12 predictors (ecological factors). Note that H_{Eco} represent the predicted height of tree i and therefore the intercept coefficient a is corrected with a correction factor of 0.5×RSE^2 (RSE of the regression) to account for the bias associated to back-transformation of logarithmic models (Baskerville, 1972).

Table VII. List of twelve ecological factors used for the prediction of tree height–diameter relationship.

	Factors	Code
Abiotic factors	Soil PCA axis1	SAxis1
	Soil PCA axis2	SAxis2
	Soil PCA axis3	SAxis3
	Climate PCA axis1	CAxis1
	Climate PCA axis2	CAxis2
	Climate PCA axis3	CAxis3
	Bioclimatic stress variable	ChavE
	Height Above Nearest Drainage	HAND
	Altitude	SRTM
Biotic factors	Basal area	BA
	Stem density (count)	Ds
	Wood density	Dw

II.3.7.3. Selection of best height – diameter models

For each linear model, a root-mean-square error [RMSE (%): Equation 15] was calculated as criterion accounting for the error introduced in the model by the driver(s). For a driver(s) to be retained as likely to influence the H–D model, the RMSE should be lower than the Null model that has no driver. The selection of a linear model was based on the forward selection procedure, that is, starting with linear models with one driver and choosing the lowest RMSE and later to linear models with two drivers but containing the first driver and choosing the one with lowest RMSE and until all the linear combinations are checked.

$$RMSE = \left[\sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(H_{Eco,i} - H_{Obs,i}\right)^2}\right] \times 100 \ldots\ldots\ldots\ldots\ldots\ldots\ldots.. \text{Equation 15}$$

II.3.7.4. Model comparison

The newly developed H–D model was compared with two existing pantropical H–D models developed in Central Africa. Together, the three models all used similar linear model forms but differ in the height prediction approaches. That is:

- $\mathrm{H_{Eco}}$ is predicted height values where the the best ecological factors were integrated in the H–D model;
- $\mathrm{H_{ChE}}$ is the pantropical predicted height where the bioclimatic stress variable was integrated in the H–D model (Chave *et al.*, 2014) and
- $\mathrm{H_{Fel}}$ is pantropical predicted height where an average tree height for Central African forests was is used (Feldpausch *et al.*, 2011).

The relative root-mean-square error ($\mathrm{RMSE_{rel}}$: Equation 16) and a [Bias (%) : Equation 17] were calculated and used to compare the three predicted height models.

$$RMSE_{rel}: RMSE \div mean(H) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 16}$$

$$Bias = [mean\ (H_{Eco} - H_{Obs}) \div H_{Obs}] \times 100 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 17}$$

II.3.8. Aboveground biomass estimation and error propagation

II.3.8.1. Estimating aboveground biomass

Aboveground biomass (AGB) for each one ha PSP was estimated by summing individual tree biomass ($\mathrm{AGB_{tree}}$: Equation 18) calculated using data on wood density (WD), diameter (D) and height (H).

$$AGB_{tree} = \alpha * (WD * D^2 * H_\Theta)^\beta \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 18}$$

where α = 0.0673 and β = 0.976 are the coefficients of the pan-tropical AGB model (Chave *et al.*, 2014) and $\mathrm{H_\Theta}$ represents four alternative height predictions : $\mathrm{H_{Ref}}$ or $\mathrm{H_{Eco}}$ or $\mathrm{H_{ChE}}$ or $\mathrm{H_{Fel}}$, all leading to four sets of AGB estimates.

It is worthy to note that any differences in AGB estimates is only linked to the H–D models ($\mathrm{H_{Eco}}$, $\mathrm{H_{ChE}}$ and $\mathrm{H_{Fel}}$) since WD and D are the same. The reference allometric model employed the in-filed measured tree heights values.

II.3.8.2. Accounting for error propagation in aboveground biomass

To determine the uncertainty associated with each set of AGB estimates, the Markov chain Monte Carlo scheme error propagation procedure was performed (Chave *et al.,* 2014; Molto *et al.*, 2013; Réjou-méchain *et al.,* 2017). This procedure calculates the AGB (Equation 18) by simulating 999 iterations and assigning random errors independently to wood density, diameter and tree height values. The error on the AGB model (Equation 18) is systematic i.e. the parameters of the AGB model are randomly set up by picking a single vector of posterior parameters and apply simultaneously to all the trees. A single error term is considered for all trees in a stand independently from the distribution. Finally, a 97.5 % credibility interval following the error propagation of the stand AGB value is calculated.

II.3.9. Statistical tools

All statistical analyses were performed in R software version 3.2.2 (R Development Core Team 2015), using the following packages: FactoMinR (Lê *et al.*, 2008) and ade4 (Dray and Dufour, 2007) to perform PCA; taxonstand (Cayuela *et al.*, 2012) to correct taxonomy; diversity.R (Pélissier, 2013) for CA, NSCA, CAIV and NSCAIV analyses; vegan (Oksanen *et al.*, 2012) to generate null communities; FD (Laliberté *et al.*, 2014) to compute q_k and $FDiv_k$; BIOMASS (Réjou-méchain *et al.*, 2017) to retrieve wood density values, compute AGB and perform Monte Carlo Permutation test.

Chapter III

RESULTS AND DISCUSSIONS

Chapter III: RESULTS AND DISCUSSION

III.1. Results

III.1.1. Variation of species diversity between sites in Central African lowland forests

A total of 183 one ha permanent plots were studied including the 50 ha single one ha in Korup. These plots together hosted 86,009 trees with diameter ≥ 10 cm. The number of species sampled per one plot ranged from 28 species in Lomie, Cameroon to 121 species in Deng Deng, Cameroon. Based on the Bonferoni multiple comparison tests, species diversity were significantly different between sites both for Shannon diversity index and the number of species (Fig. 20). In terms of the Shannon diversity index, the Lomie site in Cameroon was significantly different from six other sites (Korup, Mindourou 1, Mindourou 2, Deng Deng, Somalomo and Uma) while the Azingo site in Gabon was not significantly different from any of the 10 sites studied (Fig. 20 A). In terms of the number of species, Mindourou 2 site in Cameroon was significantly different from three sites (Azingo, Lomie and Mabounie) while the Uma site in the Democratic Republic of Congo was significantly different from the Mabounie site in Gabon (Fig. 20 B).

The Bonferoni multiple comparison tests also showed that, in term of Shannon diversity index, only a slight difference was observed between the evergreen forest types (either on hydromorphic or Terre Firme soils) and the Semi-deciduous or mixed forest types (Fig. 21 A). In terms of the number of species of each forest types, the Evergreen forest type on hydromorphic soils were significantly different from the mixed forest type on Terre Firme soils both of which were only slightly different from the other three forest types (Fig. 21 B).

III.1.2. Role of soil and climate gradients on regional floristic patterns in the moist forests of eastern Cameroon

III.1.2.1. Floristic composition

In total, 82 one ha PSP were established within seven localities in the moist forests region of Cameroon (Fig. 22). These plots together hosted 38,871 trees ≥ 10 cm in dbh from 536 species and morphospecies belonging to 265 genera, grouped in 60 families. Among these, 1024 trees (2.63 %) remain unidentified and were therefore excluded from further analysis. The five most important species in terms of number of trees were *Tabernaemontana crassa* Benth. (Apocynaceae; 1,561 trees), *Greenwayodendron suaveolens* (Engl. & Diels) Verdc. (Annonaceae; 1,508 trees), *Anonidium mannii* (Oliv.) Engl. & Diels (Annonaceae; 1,442 trees), *Petersianthus macrocarpus* (P.Beauv.) Liben (Lecythidaceae; 870 trees) and *Strombosia grandifolia* Hook.f. ex Benth. (Olacaceae; 826 trees); together representing 15.9 % of all trees sampled. The three most diverse families were Fabaceae (77 species), Rubiaceae (40 species) and Malvaceae (38 species). The list of all sampled species and their relative abundance are presented in Appendix 2.

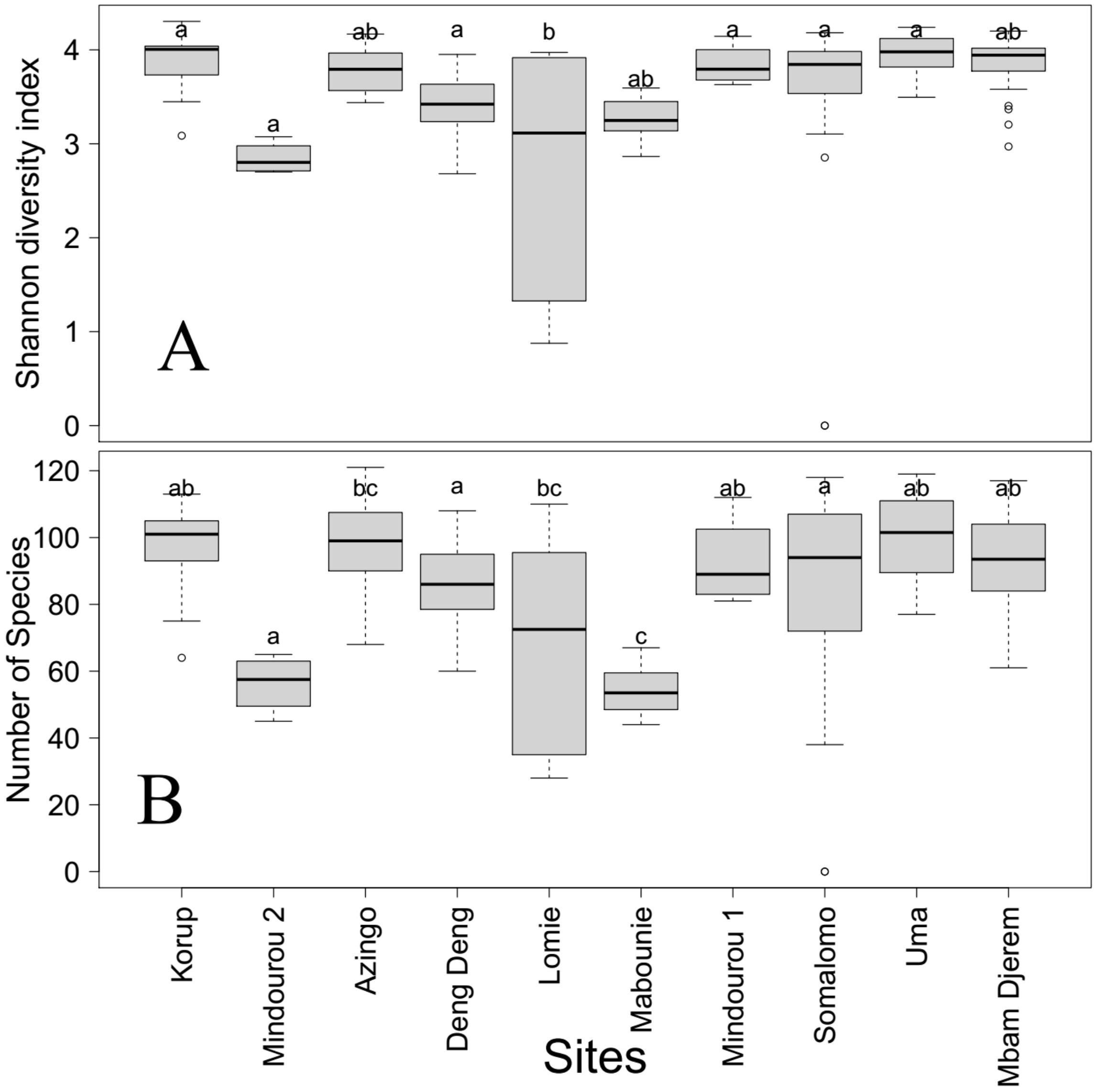


Fig. 20. Variation in species diversity between sites in Central African lowland forests.

A: diversity expressed as Shannon diversity index; B: diversity expressed as number of species. Sites with the same letter are not significantly different.

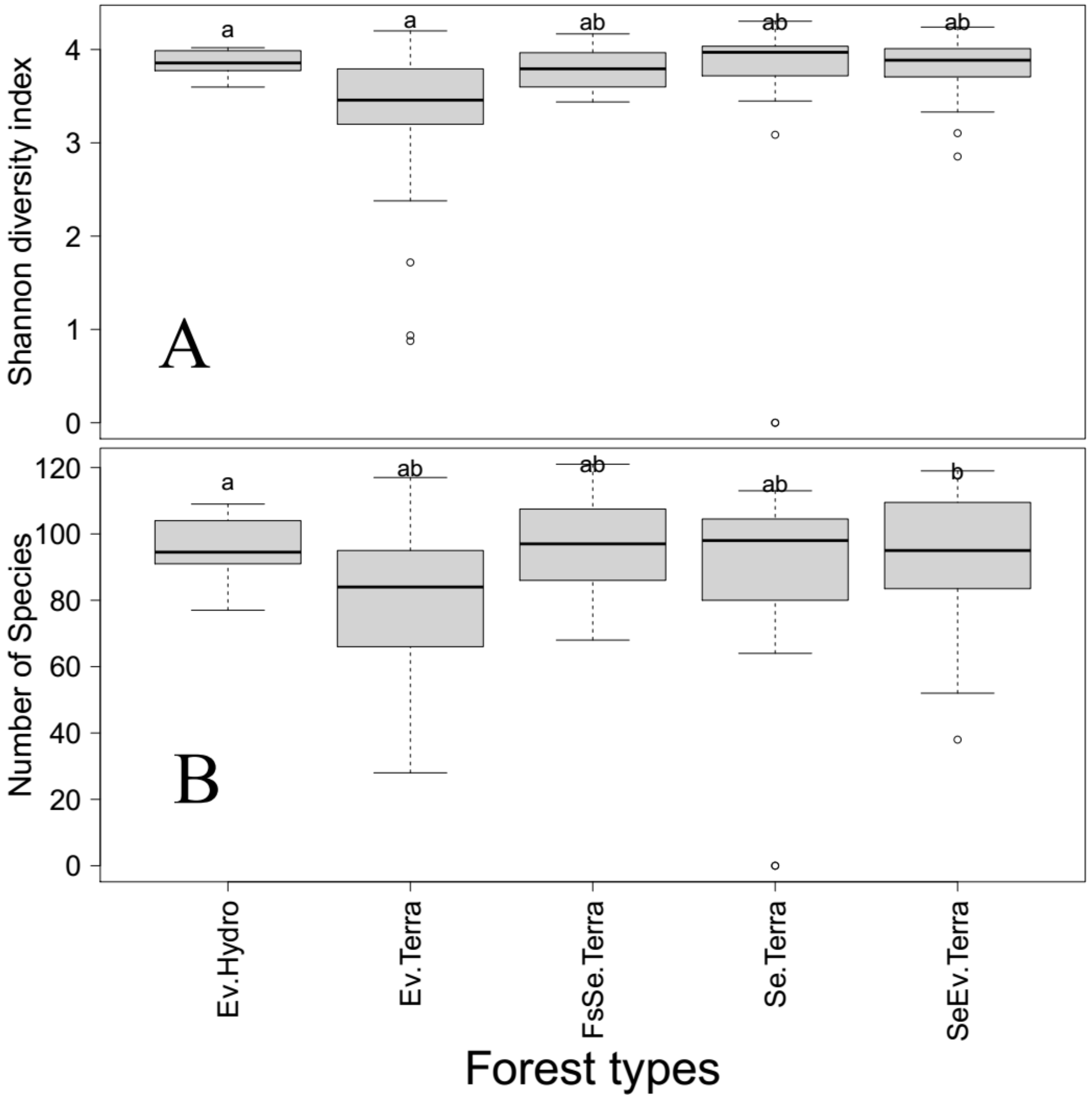


Fig. 21. Variation of species diversity between forest types of Central African lowland forests. Ev.Hydro: Evergreen forests on hydromorphic soils; Ev.Terra: Evergreen forests on Terra firme soils; FsSe.Terra: Forest-savanna forests on Terra Firme soils; Se.Terra: Semideciduous forests on Terra Firme soils; SeEv.Terra: Mixed Semi-deciduous/Evergreen forests on Terra Firme soils.

Among the seven localities in the entire study sites, 116 species and morphospecies were “abundant”. That is, 21.64 % of the species scored densities > 1 tree.ha^{-1} while the majority 78.35 % (420 species) recorded densities ≤ 1 tree.ha^{-1} and were quantified as “scarce”. *Tabernaemontana crassa* Benth, *Strombosia grandifolia* Hook.f. ex Benth., *Funtumia africana* (Benth.) Stapf, *Trichilia welwitschii* C.DC. and *Cola lateritia* K.Schum. were abundant in all seven localities while 18 species were abundant in six localities. Within each locality, the number of abundant species varied between 70 in Mbam Djerem to 108 in Mindourou 1 while most of the species were scarce i.e. between 46 species in Ngoila to 215 species in Mindourou 2 (Table VIII). The two most abundant species characterising each locality included *Greenwayodendron* *suaveolens* (Engl. & Diels) Verdc. and *Funtumia africana* (Benth.) Stapf in Deng-Deng; *Plagiostyles africana* (Müll.Arg.) Prain and *Strombosia grandifolia* Hook.f. ex Benth. in Lomie; *Uapaca guineensis* Müll.Arg. and *Cola lateritia* K.Schum. in Mbam Djerem; *Desbordesia insignis* Pierre and *Greenwayodendron suaveolens* in Mindourou I; *Tabernaemontana crassa* Benth. and *Trichilia welwitschii* C.DC. in Mindourou II; *Millettia sanagana* Harms and *Tabernaemontana crassa* Benth. in Ngoila and *Tabernaemontana crassa* and *Anonidium mannii* (Oliv.) Engl. & Diels in Somalomo.

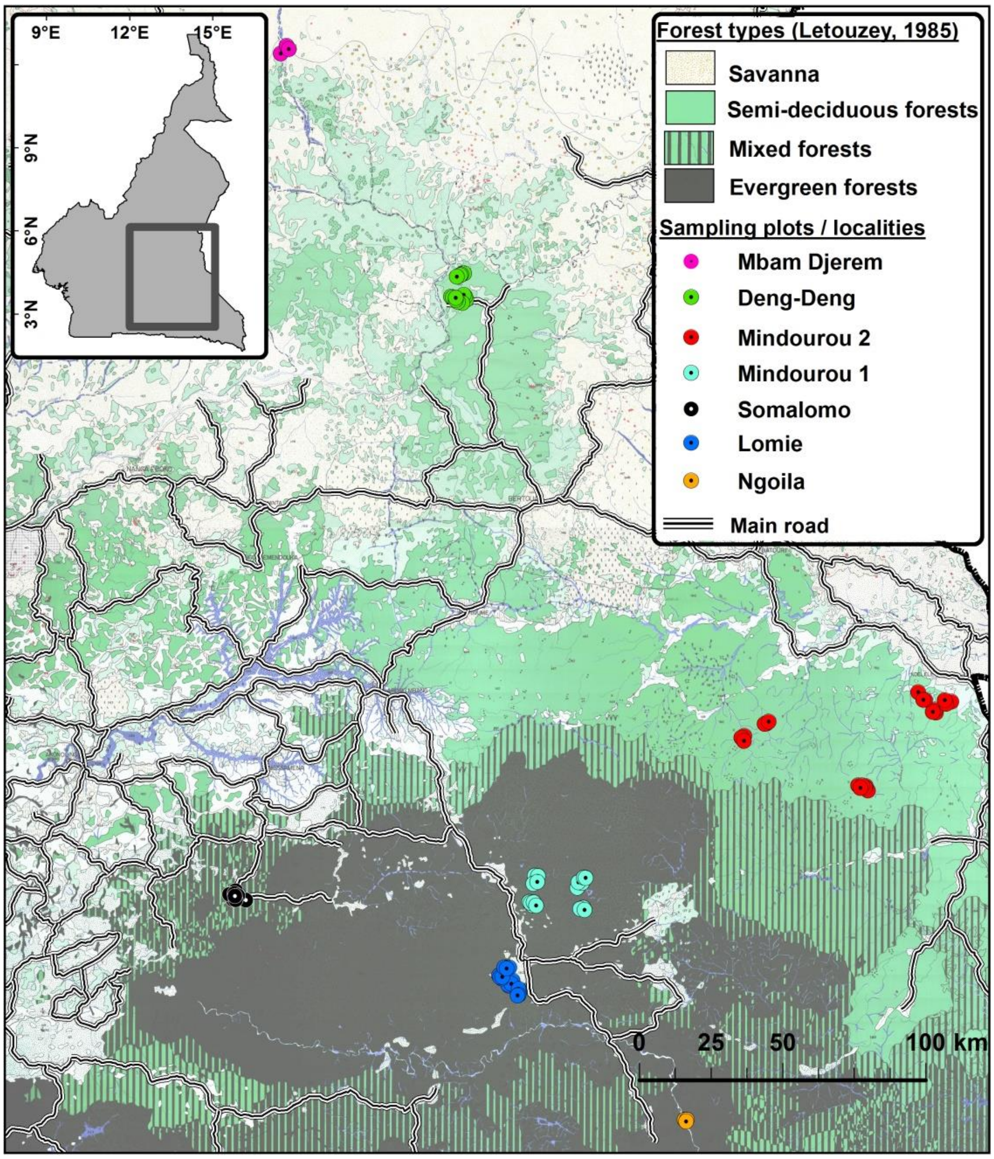


Fig. 22. Spatial distribution of permanent sampling plots and forest types in eastern Cameroon.

Constrained ordination requires equal dimensions (number of rows or plots) of the plot-by- species and plot-by-environmental variables. Therefore, when the 82 one ha (i.e. the full floristic table) were reduced to 60 one ha (i.e. the reduced floristic table), the floristic data changed to 28,429 trees, 493 species, 247 genera but the number of families remained unchanged. Also, the number of localities reduced from seven to six with the exclusion of Ngoila where soils samples were not analysed.

Table VIII. Summary statistics of the floristic data from the seven localities in eastern Cameroon

Localities	Number of one ha plots	Number of species	Abundant species	Scarce species	% Abundance	% Scarce
Deng-Deng	15	306	107	199	34.97	65.03
Lomie	14	308	96	212	31.17	68.83
Mbam Djerem	4	144	70	74	48.61	51.39
Mindourou I	17	309	108	201	34.95	65.05
Mindourou II	21	312	97	215	31.09	68.91
Ngoila	3	132	86	46	65.15	34.85
Somalomo	8	247	96	151	38.87	61.13

III.1.2.2. Regional patterns in species distribution

Non-symmetric correspondence analysis on both the reduced floristic table and full floristic table revealed similar geographical patterns of species distribution (Fig. 23; Fig. 24, respectively). For the reduced floristic table, the gradient revealed by the first axis of the NSCA (11.49 %) was strongly influenced by the Lomie and Deng-Deng localities while the second and third axes (9.41 % and 8.13 %, respectively) were not well defined but included mostly Mindourou I, Mindourou 2 and Mbam Djerem sites (Fig. 23). A similar structure in the floristic gradient was observed with the full floristic table (Fig. 24) except for the proportion of variance on species diversity that changed along the first three axes (9.84 %, 8.68 % and 7.77 % respectively). On both the reduced floristic table and full floristic table, the first three axes revealed the main floristic gradients characterized by species that were either scarce or abundant. For example, species such as *Greenwayodendron suaveolens* and *Anononidium mannii* were found to be abundant in Deng-Deng and *Strombosia grandifolia* and *Desbordesia insignis* were abundant in Lomie while *Parkia biglobosa*, *Olax subcopioides* and *Markhamia lutea* were qualified as scarce but characterized the locality of Mbam Djerem (Fig. 23; Fig. 24). Resubmitting the two floristic tables to CA, the gradient in species distribution and geographic patterns were similar to the results obtained for NSCA with only slight differences in the proportion of variance explained by species diversity (Fig. 25; Fig. 26). For instance, percentage variance of the CA explained in the first three axes was respectively 8.27 %, 5.40 and 5.01 % for the full floristic table, and 10.33 %, 6.56 and 6.25 % for the reduced floristic table.

III.1.2.3. Gradients in soil composition and bioclimatic variables

Based on the Broken-stick model and Kaiser–Guttman criterion applied on the PCA, the major gradients in both soil composition and bioclimatic variables were summarized at the first three axes of the respective PCAs (Fig. 27). The variances summarized on each of the first three axes were 64.5 % for soil composition and 84.7 % for bioclimatic variables

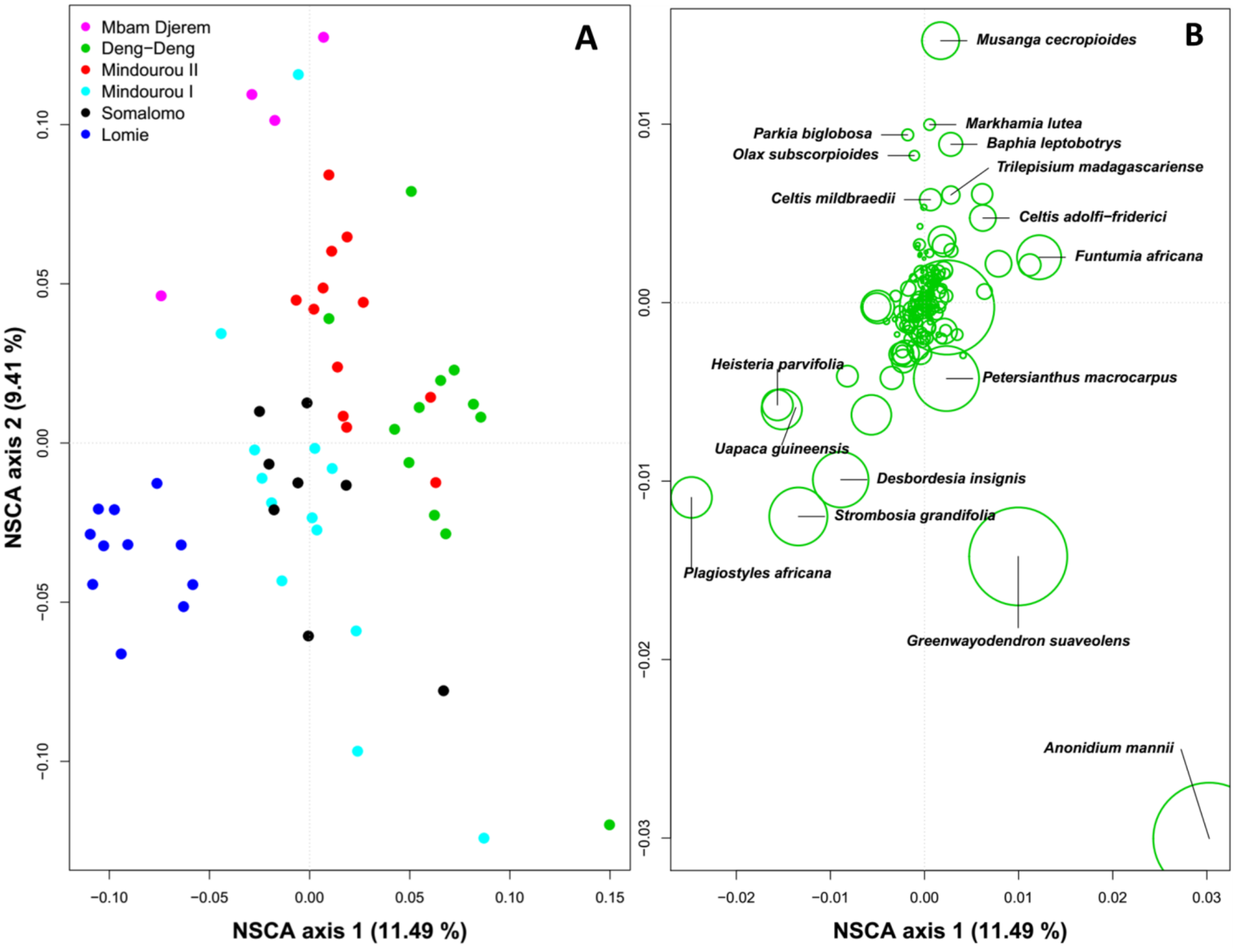


Fig. 23. Floristic patterns in eastern Cameroon depicted by first two axes of a Non-symmetric Correspondence Analysis on the reduced floristic table.

NSCA: Non-symmetric Correspondence Analysis; A: Site plan and coloured dots are plots within sites; B: Species plan and circles and their sizes are proportionate to species abundance. Only representative species are shown for readability.

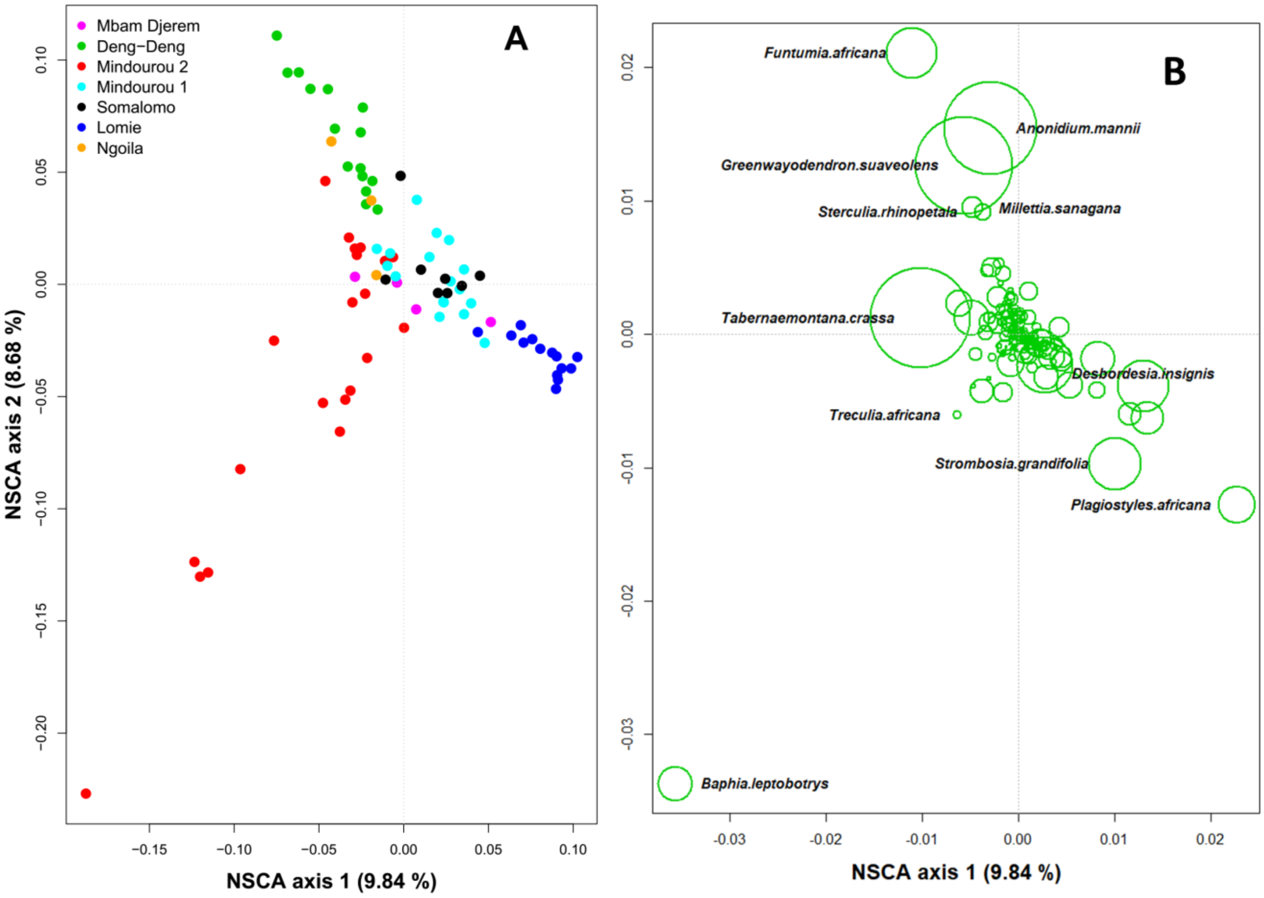


Fig. 24. Floristic patterns in eastern Cameroon depicted by first two axes of a Non-Symmetric Correspondence Analysis on the full floristic table.

A: Site plan and coloured dots are plots within sites; B: Species plan and circles and their sizes are proportionate to species abundance. Only representative species are shown for readability.

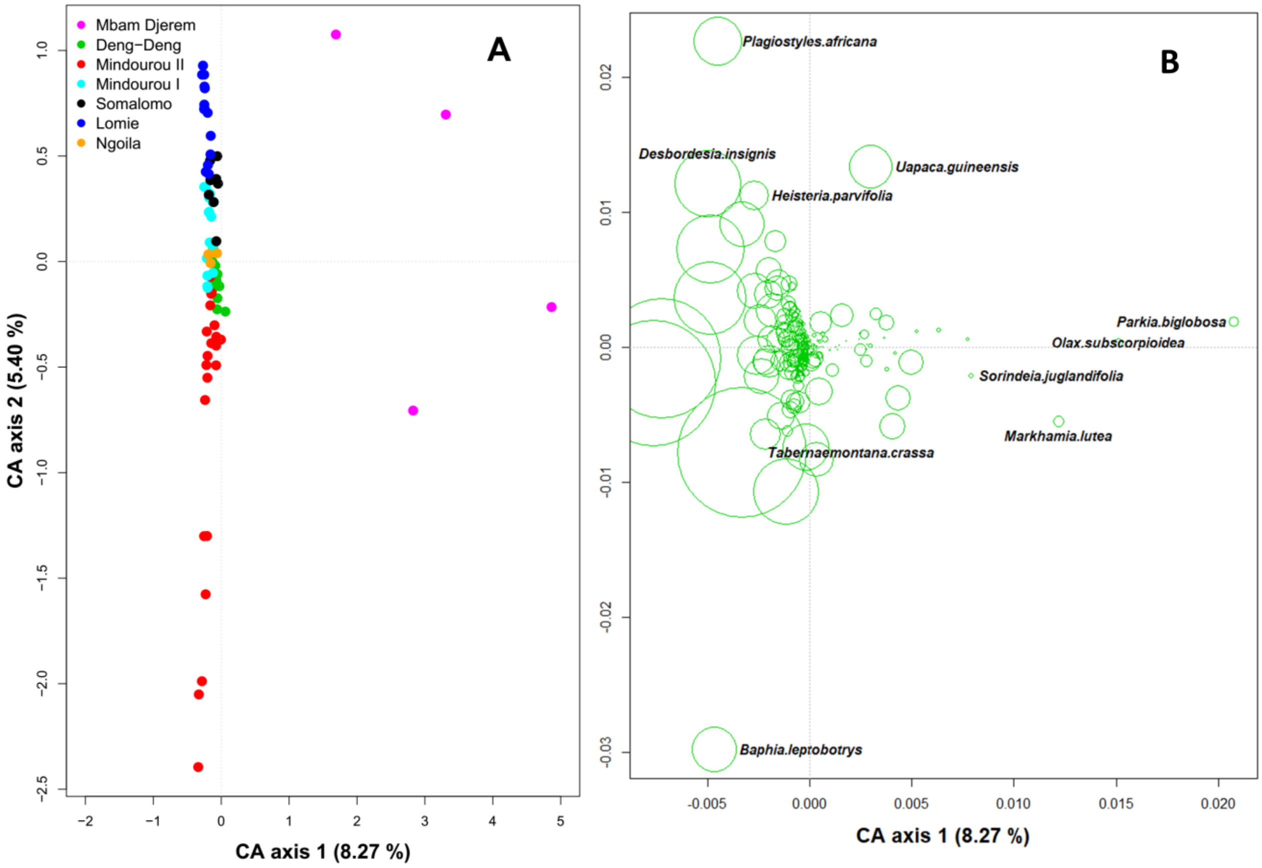


Fig. 25. Floristic patterns in eastern Cameroon depicted by first two axes of a Correspondence Analysis on the full floristic table.

CA: Correspondence Analysis; A: Site plan and coloured dots are plots within sites; B: Species plan and circles and their sizes are proportionate to species abundance. Only representative species are shown for readability.

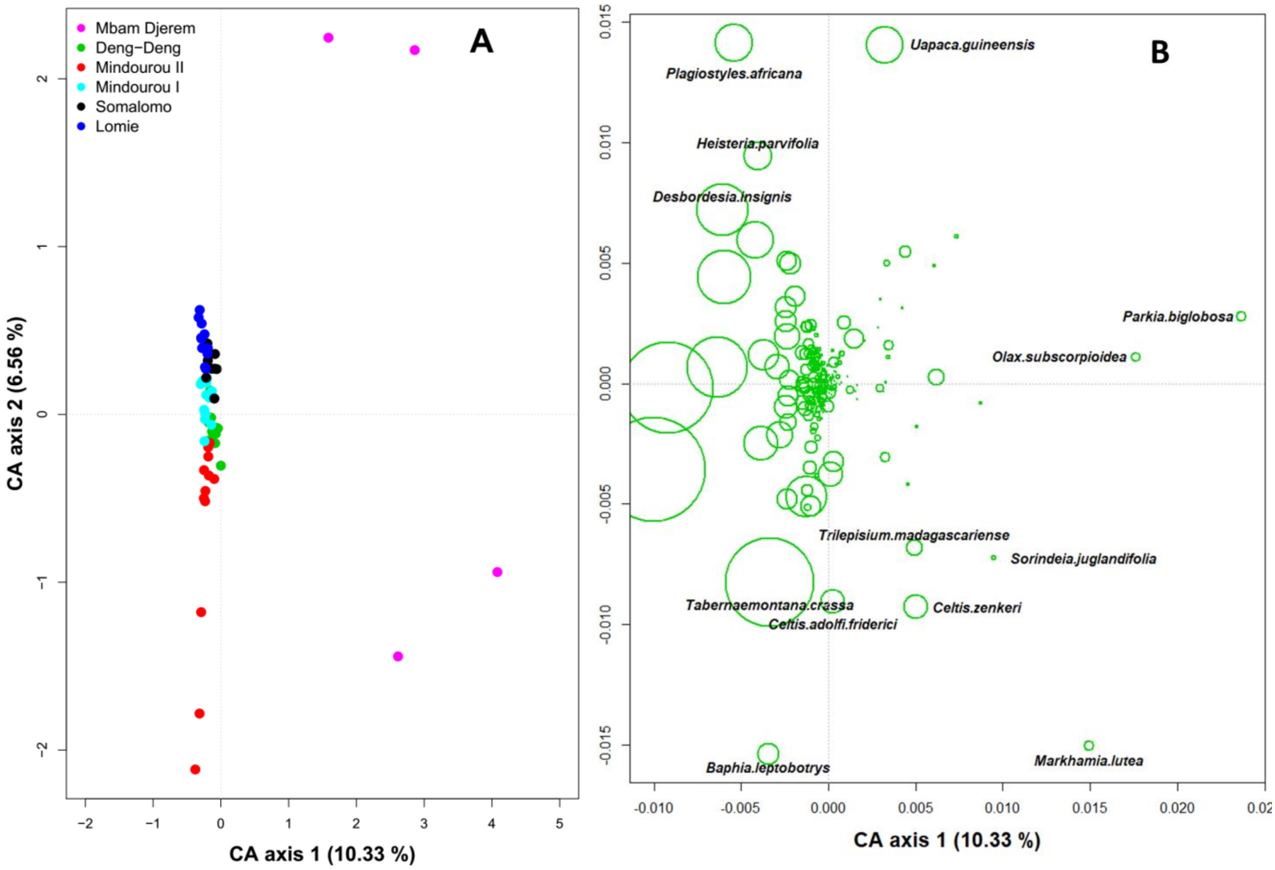


Fig. 26. Floristic patterns in eastern Cameroon depicted by first two axes of a Correspondence Analysis on the reduced floristic table.

A: Site plan and coloured dots are plots within sites, B: Species plan and circles and their sizes are proportionate to species abundance. Only representative species are shown for readability.

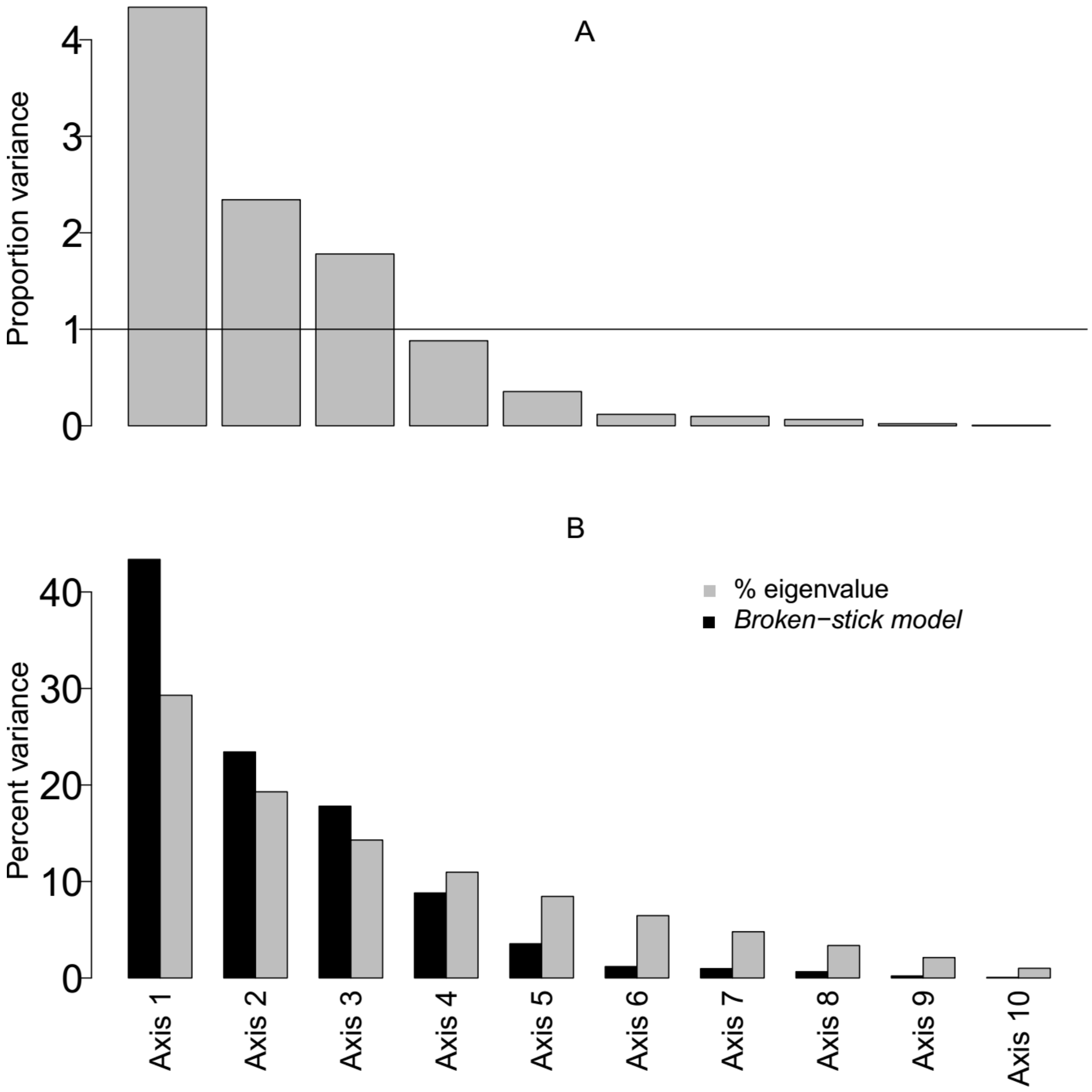


Fig. 27. Eigenvalue barplots to assess the number of interpretable PCA axes.
A: Assessment based on Kaiser–Guttman criterion; B: Assessment based on Broken-stick method.

Soil axis 1 (27.56 % variance) was positively correlated with clay content, C:N ratio, moisture, available phosphorus , but negatively correlated with pH, Silt, total nitrogen and sand; soil axis 2 (22.3 % variance) was positively correlated with total phosphorus, moisture, total nitrogen, available phosphorus, pH but negatively correlated with C:N ratio; soil axis 3 (14.7 % variance, not illustrated) was positively correlated with organic carbon, silt, total nitrogen, available phosphorus but negatively correlated with total phosphorus and pH. To increase visibility, each axis was interpreted based on correlation ($r > 0.5$) with the variables that are most characteristic of the gradients. Hence, soil axis 1 was interpreted as texture (Texture) gradient (Clay: $r = 0.84$; Sand: $r = - 0.61$); soil axis 2 as phosphorus fertility (P-fertility) gradient (Phosphorus: $r = 0.75$) and soil axis 3 as organic fertility (Organic fertility) (organic carbon: $r = 0.81$). The ten soil composition variables were also significantly different between localities considered in the study (Fig. 28).

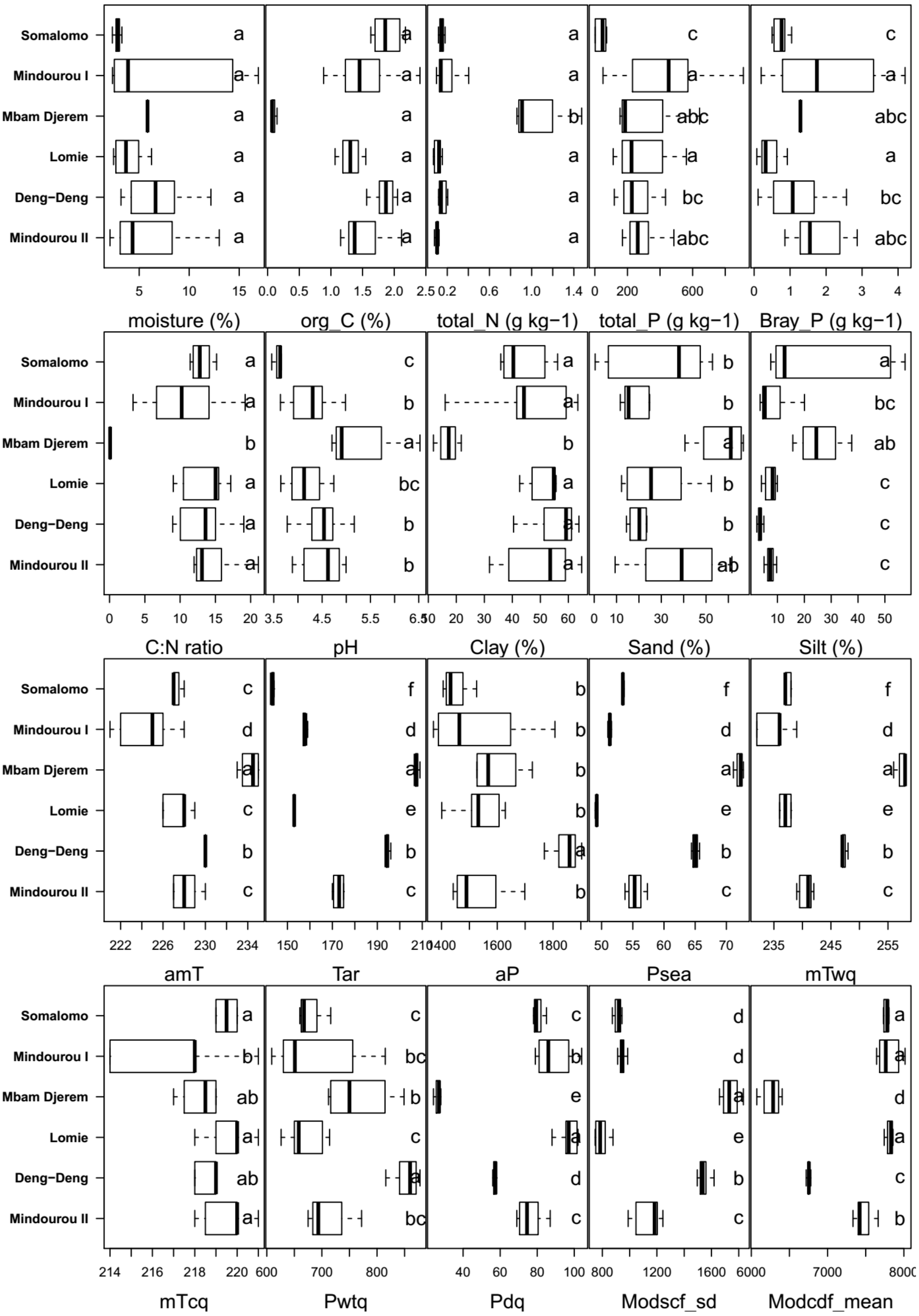


Fig. 28. Variation of individual elememts of soil composition and bioclimatic variables between six localities in eastern Cameroon.

Soil composition = 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.

Bioclimatic variables = 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. ModscfCF_mean: mean of cloud frequency; Modscf_sd: standard deviation of cloud frequency.

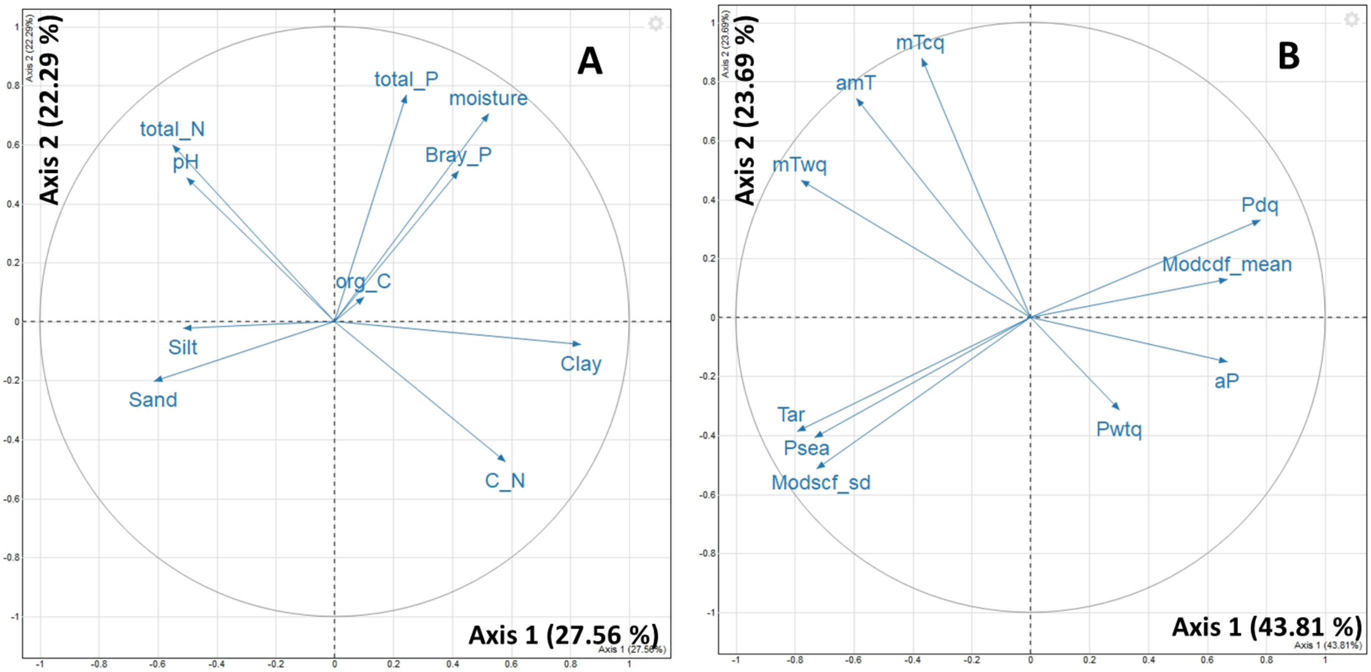


Fig. 29. Correlation circles of the main gradients in soil (A) and bioclimatic variables (B). Variables are defined in Fig. 28.

PCA on the bioclimatic variables revealed a first axis (43.81 % variance) that strongly correlated (r > 0.5) with precipitation-related variables such as annual precipitation, precipitation of the driest quarter of the year and precipitation seasonality and cloudiness (Modcdf_mean). This first axis was therefore interpreted as a precipitation gradient (Fig. 29 B) and coincided with the equatorial rainfall gradient drifting from west to east of the equatorial forests region (Fig. 30). The second axis (23.69 % variance) correlated with temperature-related variables [minimum temperature of coldest and minimum temperature wettest quarter of the year and annual range temperature and was interpreted as a temperature gradient. Axis 3 (17.38 % variance) correlated with precipitation seasonality and variation in cloud frequency (Fig. 30). The latter axis was therefore, interpreted as a gradient of precipitation seasonality. These bioclimatic variables also vary individually and significantly between the studied localities (Fig. 28).

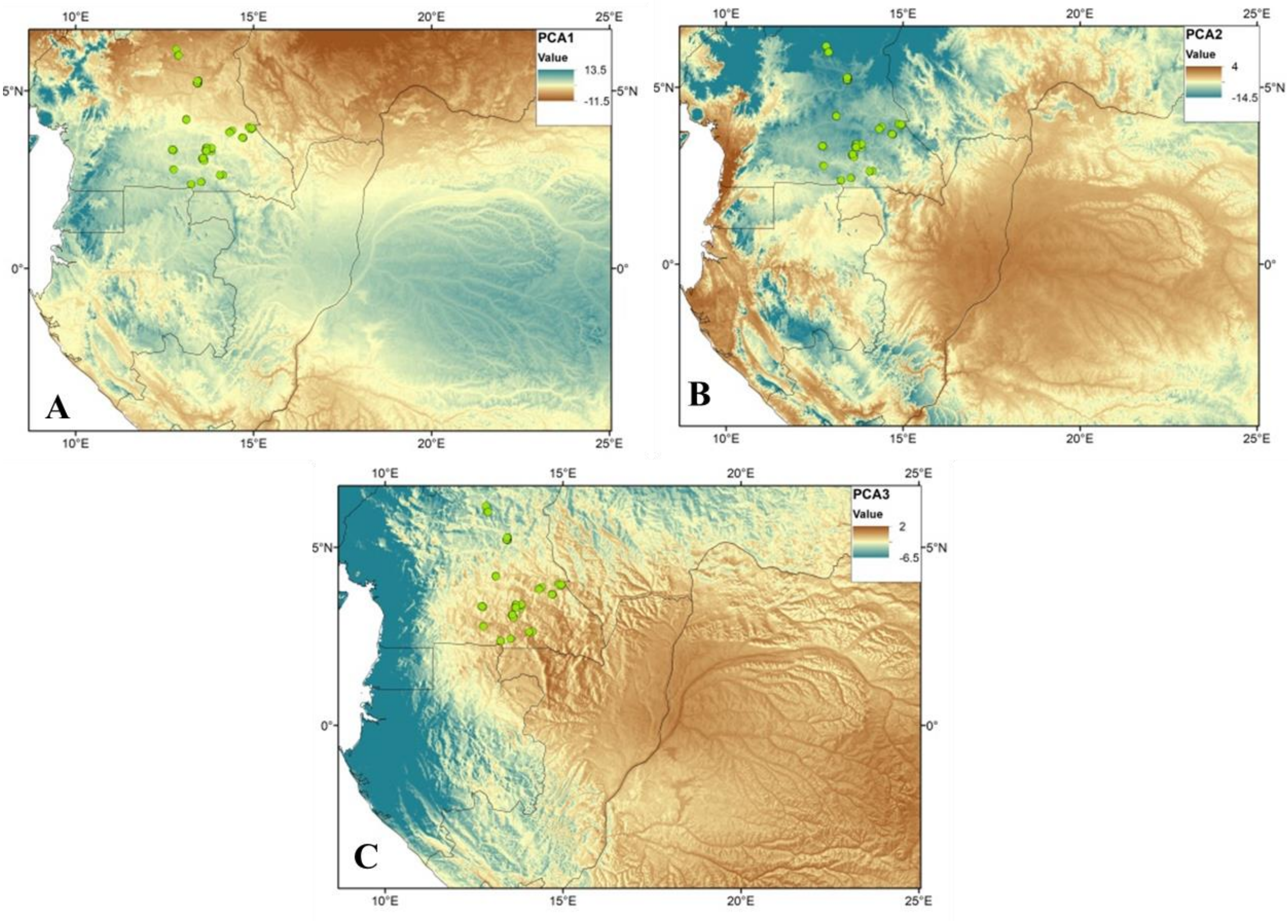


Fig. 30. Main gradients in bioclimatic variables projected across equatorial forests region.

A: PCA1 rainfall gradient projected; B: PCA2 temperature gradient and C: PCA3 precipitation seasonality gradient. Green dots: sampled plots.

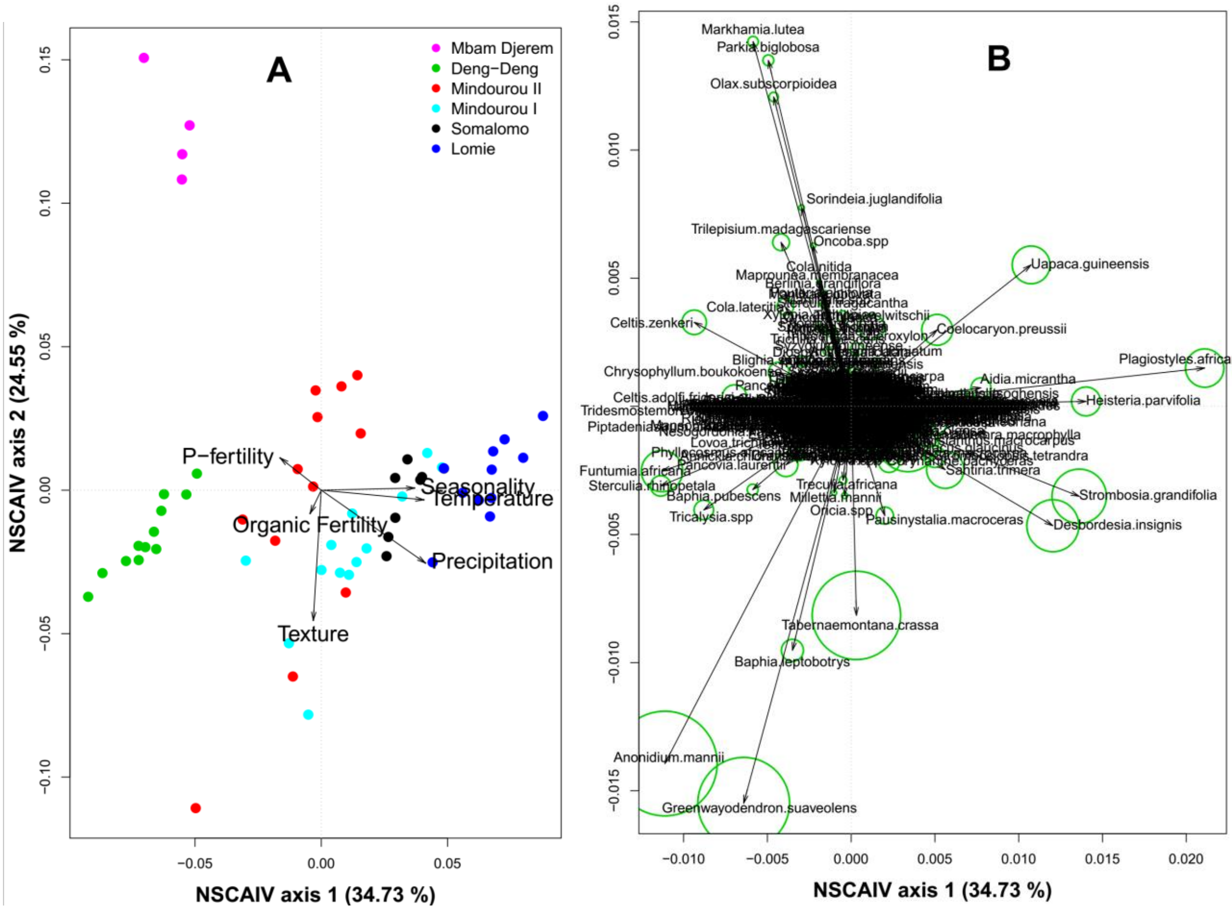


Fig. 31. Influence of main soil and bioclimate gradients on tree species distribution in eastern Cameroon.

A: Site plan with coloured dots as plots within sites; soil and climate gradients derived from independent PCA analyses in Fig. 29; B: Species plan and circles and their sizes are proportionate to species abundance.

III.1.2.4. Variance apportioning of environmental predictors

Apportioning the variances from the soil and/or climate gradients on the floristic patterns via the NSCAIV and CAIV approaches revealed the significant contributions of either one or both environmental predictors (Fig. 31; Fig. 32). For the NSCAIV approach, the total variance explained by climate alone was slightly higher (14.5 %) than soil alone (11.5 %) and both jointly explained 25.2 % variance of the species distribution. Considering the CAIV approach, climate and soil independently explained 12.5 % and both joint effects explained 22.3 % variance of the species distribution. Overall, the proportion of variances explained by both environmental predictors was 1 to 3 times higher for NSCAIV compared to the CAIV (Table IX).

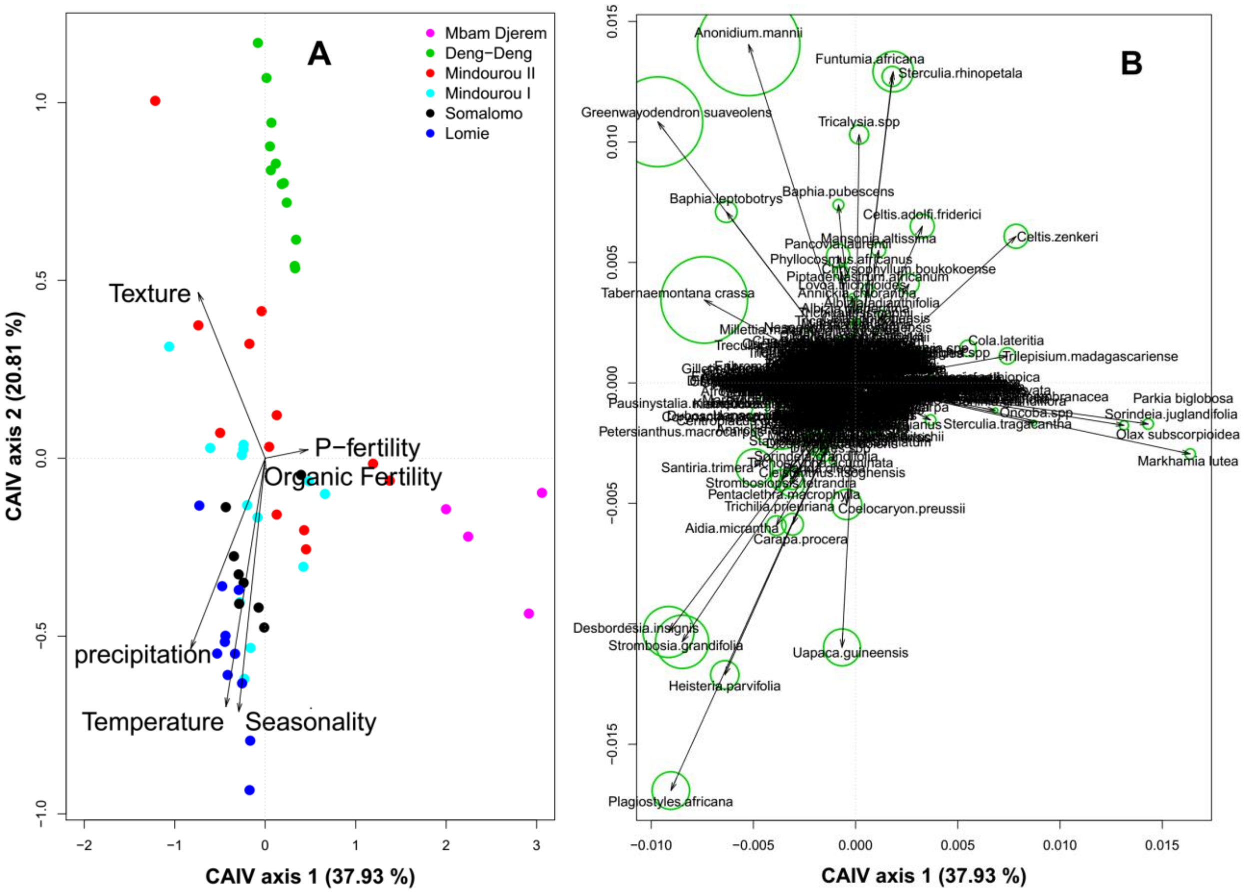


Fig. 32. Influence of main environmental gradients on scarce and abundant tree species distribution depicted by Correspondence Analysis with Instrumental Variables.

CAIV: Correspondence Analysis with Instrumental Variables.

The proportion of unexplained variance of the floristic patterns when either the effects of soil or climate were factored-out revealed that soil and climate gradients were strongly complementary (i.e. limited variances shared) in explaining the tree species distribution. Focusing on the NSCAIV approach for instance, factoring-out the effects of soil, climate explained 10.8 % of variance on species distribution while factoring out the effects of climate, soil explained 8.2 % on species distribution considering the NSCAIV approach (Table IX).

Examining the proportion of species that significantly revealed the effects of one or both predictors through variance apportioning (Monte Carlo Permutation test, *P*-value < 0.05), it was noticed that soil influenced the distribution of 15.42 % (76/493) while climate explained 26.37 % (130/493) of the inventoried species (Fig. 33). In addition, the soil effects influenced those tree species which were qualified as scarce in the study (e.g. *Tessmannia africana* Harms, *Leplaea thompsonii* Sprague & Hutch, *Monodora myristica* (Gaertn.) Dunal) meanwhile climate mostly explained distribution of those species which were qualified as abundant in the study (e.g. *Strombosia gradifolia*, *Desbordesia insignis*, *Piptadeniastrum africanum* (Hook.f.) Brenan, *Celtis zenkeri*

Engl.). Approximately only 7.1 % (35/493) of the tree species most of which were qualified as scarce in the study area appeared to be influenced by both soil and climate predictors (e.g. *Greenwayodendron suaveolens*, *Berlinia grandiflora*, *Olax subscorpioides* Oliv., *Panda oleosa* Pierre and *Sorindeia juglandifolia* (A.Rich.) Planch. ex Oliv.) (Fig. 33).

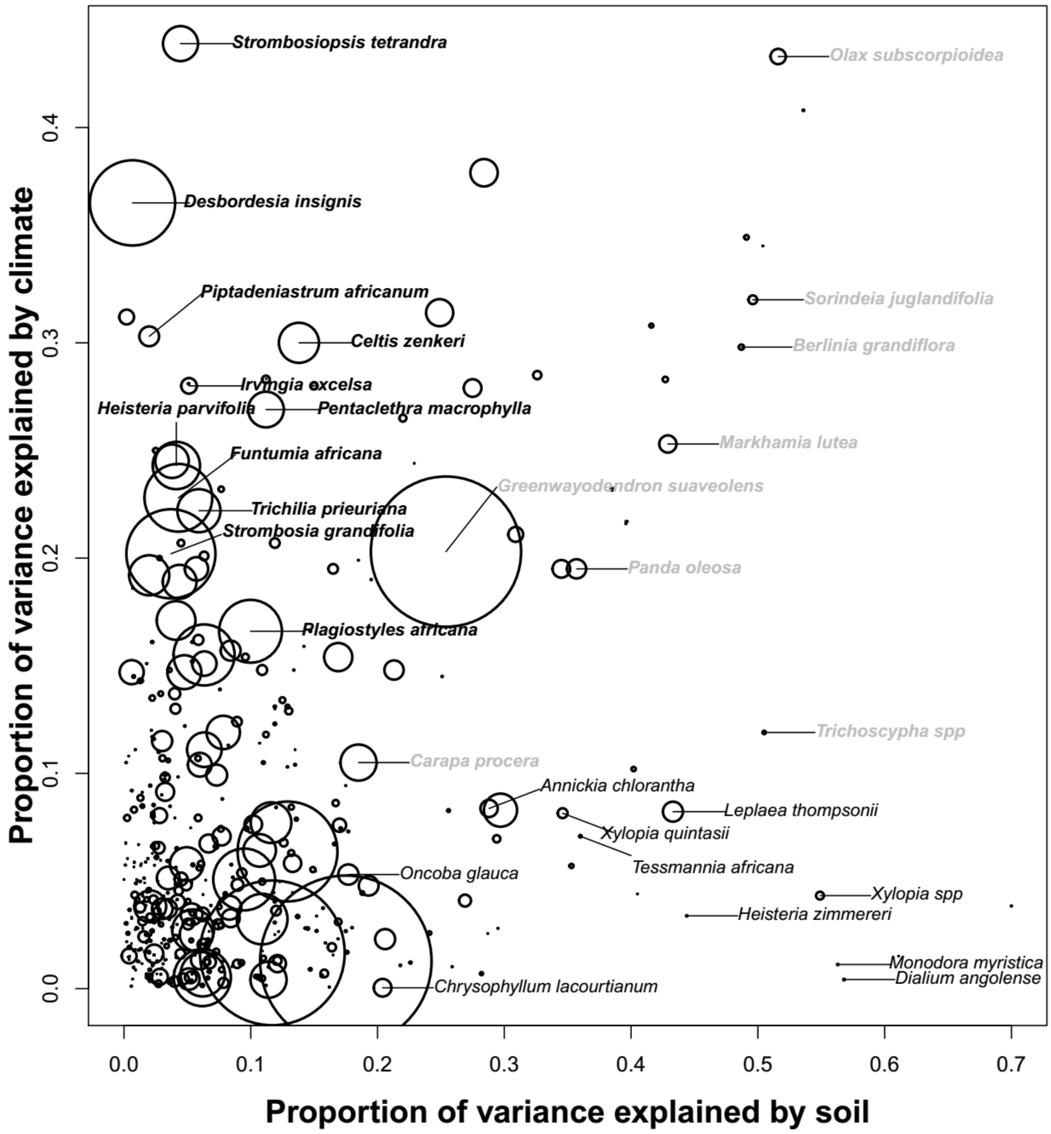


Fig. 33. Proportion of individual species variance explained by soil gradient and/or climate gradient.

Circles: Species and circle sizes are proportional to species abundance

Uunbold-faced: species explained mainly by soil; bold-faced: species explained mainly by climate; gray: species explained by both soil gradient and climate gradient.

Table IX. Proportion of species variance and diversity apportioned with respect to soil and/or climate gradients.

S_{IV}: soil gradients, C_{IV}: climate gradient. Levels of significance by Monte-Carlo permutation test: *= $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

		Constrained ordination						Partial ordination				Residual ordination	
		S_{IV}		C_{IV}		$S_{IV} + C_{IV}$		$C_{IV} - S_{IV}$		$S_{IV} - C_{IV}$		$total - (S_{IV} + C_{IV})$	
	Total diversity	% variance	diversity	% variance	diversity	% variance	diversity	% variance	diversity	% variance	diversity	% variance	diversity
CA	5.93	12.4	0.74**	12.5	0.738**	22.3	1.32**	7.9	0. 47**	7.4	0.442***	77.7	4.61**
NSCA	0.28	11.5	0.005**	14.5	0.004**	25.2	0.007**	10.8	0.003**	8.2	0.002**	74.8	0.021*

Note: Total diversity for species richness in the CA is total number of species minus 1 (493-1) while total diversity for Simpson-Gini diversity in the NSCA is 1.

III.1.3. Contribution of ecological factors in modelling tree height–diameter relationship

III.1.3.1. Data summary

The data used to model tree heights from their diameters while intergrating into the model, the influence of ecological factors at the regional scale comprised of 71,146 trees (all diameter measured) from which the heights of 4,510 trees were measured in the field (Table X). In all, nine sites from three countries (Cameroon, Gabon and DR Congo) were sampled comprising 127 one ha permanent sampling plots. Soil samples were collected from 78 of the 133 one ha plots and 312 soil samples (ten variables analysed per sample) were analysed and 78 bioclimate data point (each data point corresponded to 10 bioclimatic variables) were extracted fron remotely sensed satellite data. The ecological data comprised of 12 predictors: six axes from PCA analyses realised on soil and bioclimatic variables (see section III.1.3.2); four parameters of forests structure (Table X) and two variables related to local topography and the bioclimatic stress of Chave *et al.*, (2014) (Table XI).

Table X. Data summary employed for the development of regional tree height-diameter allometric model

Country	Sites	Total tree height measured	Number of plots where height measured	Total one ha plots in sites	Forest type
Cameroon	Deng-Deng	185	5	15	semideciduous
Cameroon	Korup	132	2	52	evergreen
Cameroon	Somalomo	250	5	8	evergreen
Cameroon	Mondourou II	996	12	21	semideciduous – savanna transition
Cameroon	Mondourou I	618	10	17	evergreen
Cameroon	Lomie	495	10	18	evergreen
DR Congo	Uma	1549	26	30	evergreen/ monodominant
Gabon	Azingo	100	3	4	evergreen
Gabon	Mabounie	185	5	12	evergreen

Table XI. Data ranges of the ecological variables.

Max.: Maximum; Min.: Minimum; BA: Basal Area; D_s: Stem density; D_g: Quadratic mean diameter; D_w: wood density weighted by BA; HAND: Height Above Nearest Drainage and *ChavE*: Bioclimatic stress index of Chave *et al.*, (2014).

	Forest structure				Local topographic index	Bioclimatic stress index
Sites	BA (m^2): Min–Max	D_s (count): Min–Max	D_g (cm): Min–Max	D_W (g cm^{-3}): Min–Max	HAND Min–Max	*ChavE* Min–Max
Deng-Deng	20.48–44.73	423–591	23.28–33.88	0.43–0.58	66–73	0.088–0.097
Korup	30.4–44.73	394–559	31.34–31.92	0.49–0.69	128–174	-0.089– -0.09
Somalomo	21.09–32.71	391–511	23.93–30.74	0.56–0.66	6–25	-0.082– -0.08
Mindourou II	17.06–57.61	342–604	22.91–39.42	0.45–0.64	13–83	-0.08– -0.07
Mindourou I	24.59–37.92	395–619	24.2–31.59	0.43–0.71	28–75	-0.04– -0.10
Lomie	24.85–40.09	323–622	24.12–35.9	0.58–0.71	34–77	-0.09– -0.08
Uma	22.73–39.58	322–557	27.26–35.51	0.59–0.72	15–176	-0.05– -0.04
Azingo	27.74–34.95	422–480	28.37–32.47	0.68–0.77	13–59	-0.06–0.06
Mabounie	17.66–31.42	222–492	23.69–37.02	0.66–0.8	52–103	-0.07– -0.06

III.1.3.2. Regional gradients in soil composition and bioclimatic variables

Based on the Kaiser Guttman criteron applied on the PCAs to select interpretable axes, three axes were retained to summarize the main gradients in the soil composition and bioclimatic variables (Fig. 34 A). The first soil axis (SAxis1: 21.96 % of total variance) was interpreted as a gradient of soil texture because of the positive correlation ($r > 0.8$) of sand and negative correlation ($r > 0.7$) of clay, while soil axis 2 (SAxis2: 16.76 % of total variance) was interpreted as a gradient of phosphorus fertility because of the negative correlation ($r > 0.7$) of total phosphorus and nitrogen contents) and Soil axis 3 (CAxis3: 14.63 % of total variance) was interpreted as a gradient of Silt because of the positive correlation ($r > 0.7$) of silt content (Fig. 34 B).

The first PCA axis of bioclimatic variables (Fig. 34c) (CAxis1: 33.67 % of total variance) was interpreted as a gradient of interannual temperature variation because of the positive correlation (r> 0.9) of mean temperature of coldest and driest quarters of the year, and annual mean temperature. The second bioclimatic axis (CAxis2: 28.38 % of total variance) was interpreted as a gradient of precipitation because of the negative correlation (r > 0.8) of precipitation seasonality and positive correlation of precipitation of the driest quarter of the year. Bioclimatic axis 3 (CAxis3: 15.3 % of total variance) was interpreted as a gradient of inter-annual precipitation seasonality because of the negative correlation (r >0.5) of precipitation of wettest quarter of the year.

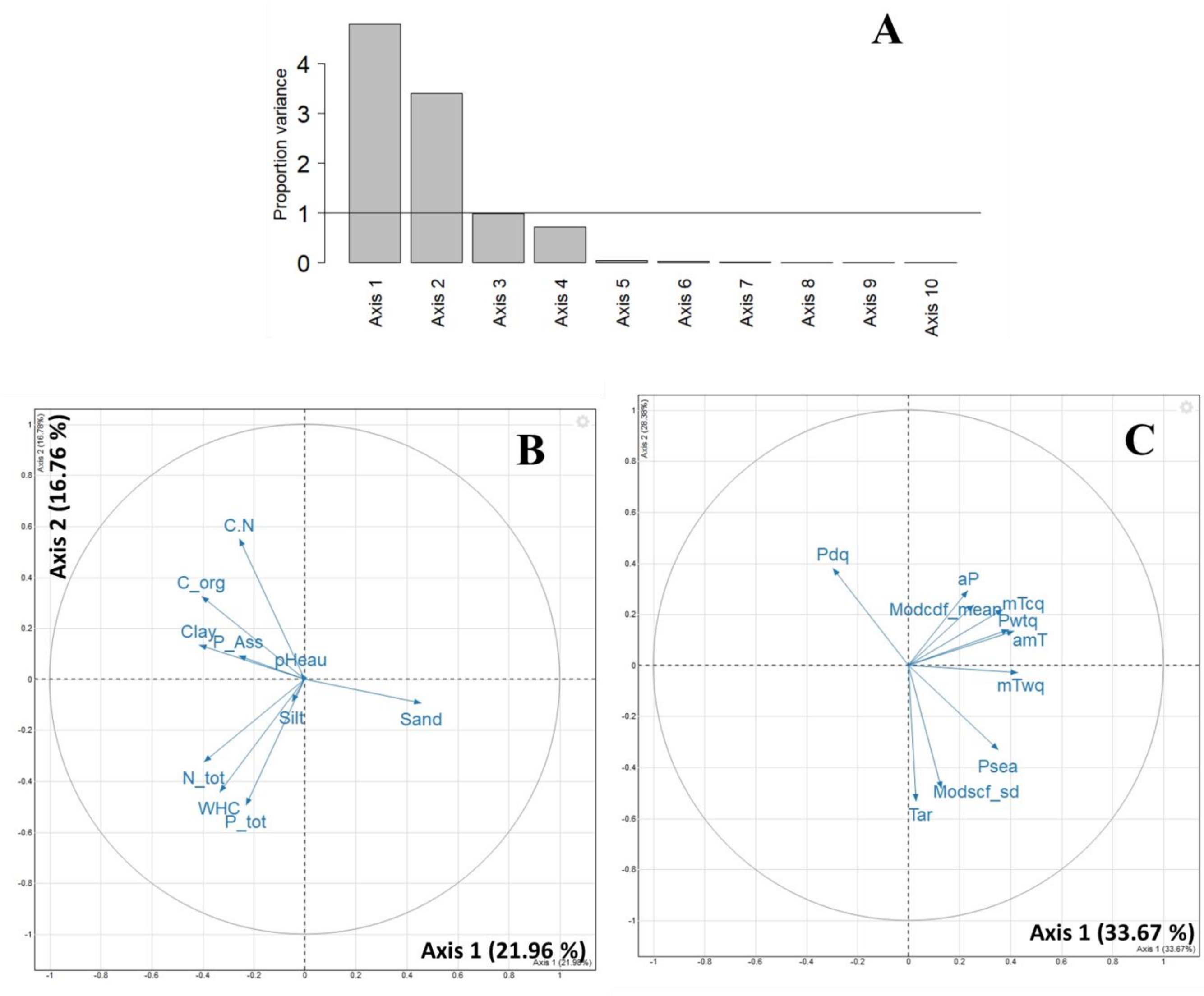


Fig. 34. Correlation circles of Principal Component Analyses on soil composition and climate variables.

A: Eigen value barplot depicted from Kaiser-Guttman method; B: Soil composition variables: 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. C: Bioclimatic variables: 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. ModscfCF_mean = mean of cloud frequency; Modscf_sd = standard deviation of cloud frequency.

III.1.3.3. Patterns of tree height in Central African lowland humid forests

The plots' coefficients extracted from the H–D model in equation 13 captured the site-effect (R^2 27.6 %; p-value = 0.0001) on H–D relationship among the different sites and the level of site-effect also vary from one site to the other in Central African forests (Fig. 35). Site-effect was strongest in Lomie (a semi-deciduous forest type in Cameroon), Azingo (an evergreen forest type in Gabon) and Uma (an evergreen/monodominant forest type in DR Congo).

For a given diameter, trees were generally taller for sites in the semi-deciduous forests than in evergreen forests, and were taller than plots in the monodominant forest type in Uma (Fig. 36). For a given site, trees in plots were either taller or shorter than the regional average (i.e. average tree height from all trees irrespective of the plot). Trees in plots from the Mindourou I site were generally taller than the regional averaged tree height and a similar pattern was observed for most plots in the semi-deciduous forest types. Contrarily, trees in plots from Azingo, Mabounie and Korup which are also evergreen forest sites, were often shorter compared to the regional averaged tree height (Fig. 36). The heights of trees in plots from the Uma site were either taller (in some plots) or shorter (in other plots) than the regional averaged height.

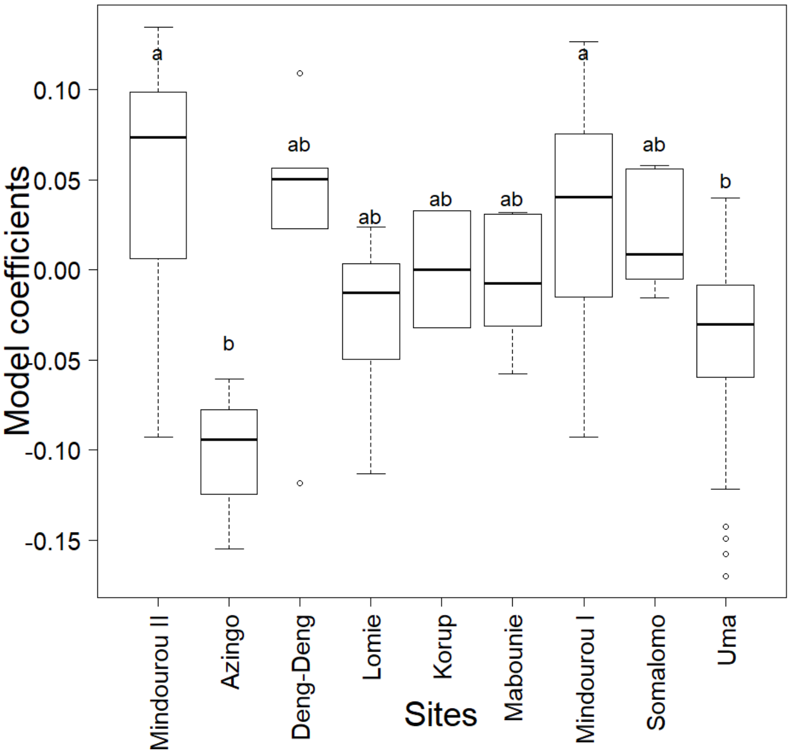


Fig. 35. Variation between sites of plot coefficients of height-diameter model.
Sites with the same letters are not significantly different.

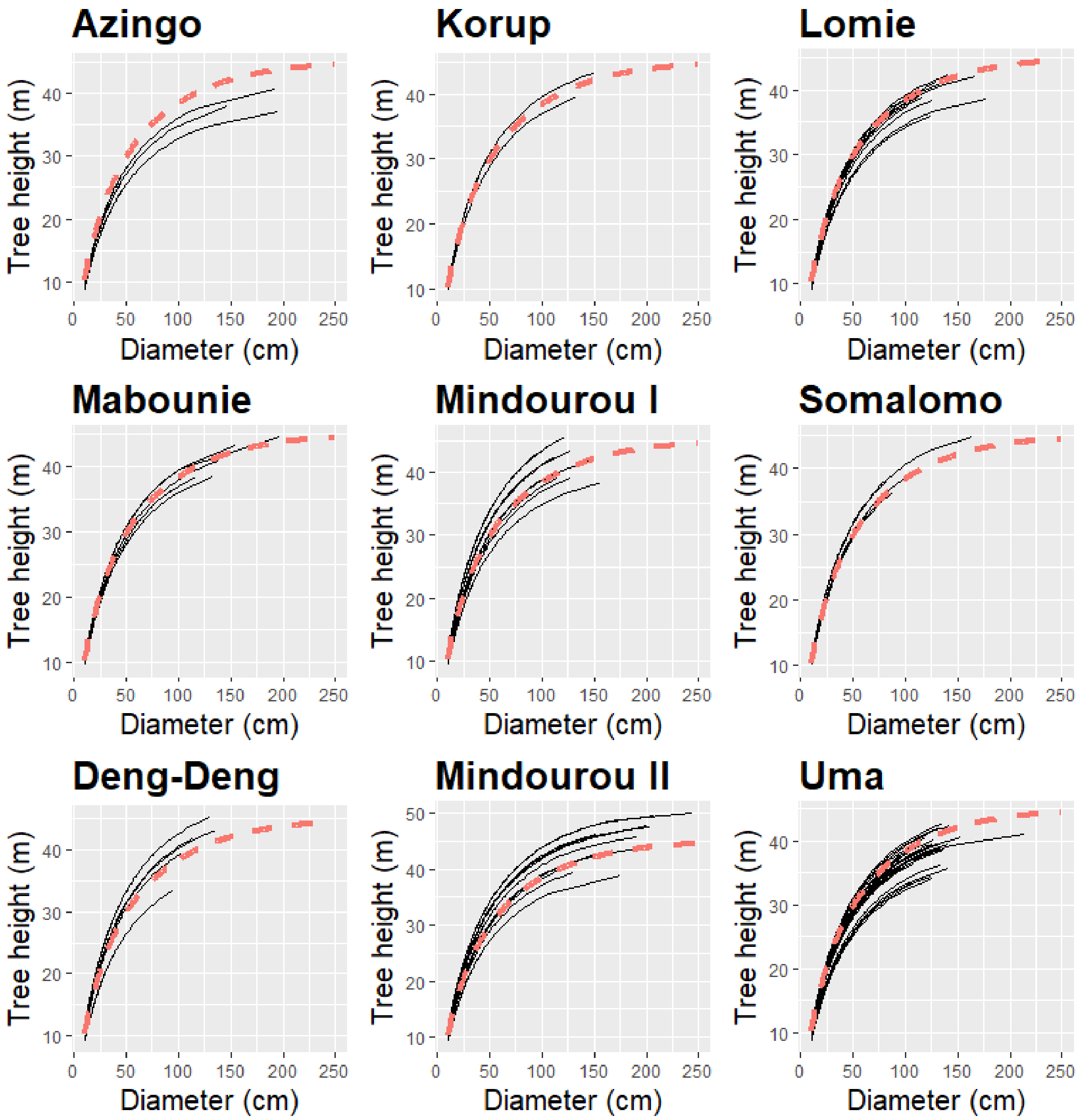


Fig. 36**.** Tree height-diameter relationship curves among sites in Central African lowland forests. Black full lines: plot-specific height-diameter curves; Red broken lines: regional height-diameter curves.

III.1.3.4. Influence of biotic and abiotic factors on height–diameter model

A total of 4096 H–D models were built, integrating all possible combinations of the 12 biotic and abiotic factors. Forward selections of models with the lowest root-mean-square error (RMSE) retained nine models which had lower RMSE relative to the Null H–D model (i.e. model that integrated no factors) (see Fig. 37 & Table XII) With respect to the Null H–D model (RMSE = 0.0763), the lowest RMSE of 0.0660 was obtained from the model integrating Basal area plus the first PCA axis for climate (BA + CAxis1). Eight other models integrating either one driver (CAxis1) or a combination of nine biotic and abiotic factors (see Fig. 37 & Table XII) also yielded RMSE lower than the Null H–D model. RMSE higher than the Null H–D model was obtained whenever the bioclimatic stress variable of Chave *et al.*, (2014) was integrated into the *H–D* model either as a single variable or in combination with other factors.

Table XII. Top nine linear regression models with relative root-mean-square-error.
$RMSE_{rel}$: relative root-mean-square-error; Regressions were performed between 78 Plots' coefficients and 12 ecological factors.

Regression	$RMSE_{rel}$	Number of factors
coeffPlots~ 1 (Null model)	0.076378685	0
coeffPlots~ CAxis1	0.068584042	1
coeffPlots~ CAxis1+BA	0.066044475	2
coeffPlots~ CAxis1+SAxis1+BA	0.066149254	3
coeffPlots~ CAxis1+SAxis3+Ds+Dw	0.065690714	4
coeffPlots~ CAxis1+SAxis1+SAxis3+Ds+BA	0.066413444	5
coeffPlots~ CAxis1+SAxis1+SAxis3+SRTM+Ds+BA	0.067051474	6
coeffPlots~ CAxis1+SAxis1+SAxis3+SRTM+Ds+BA+Dw	0.067742216	7
coeffPlots~ CAxis1+CAxis3+SAxis1+SAxis2+SAxis3+SRTM+Ds+BA+Dw	0.073359898	9

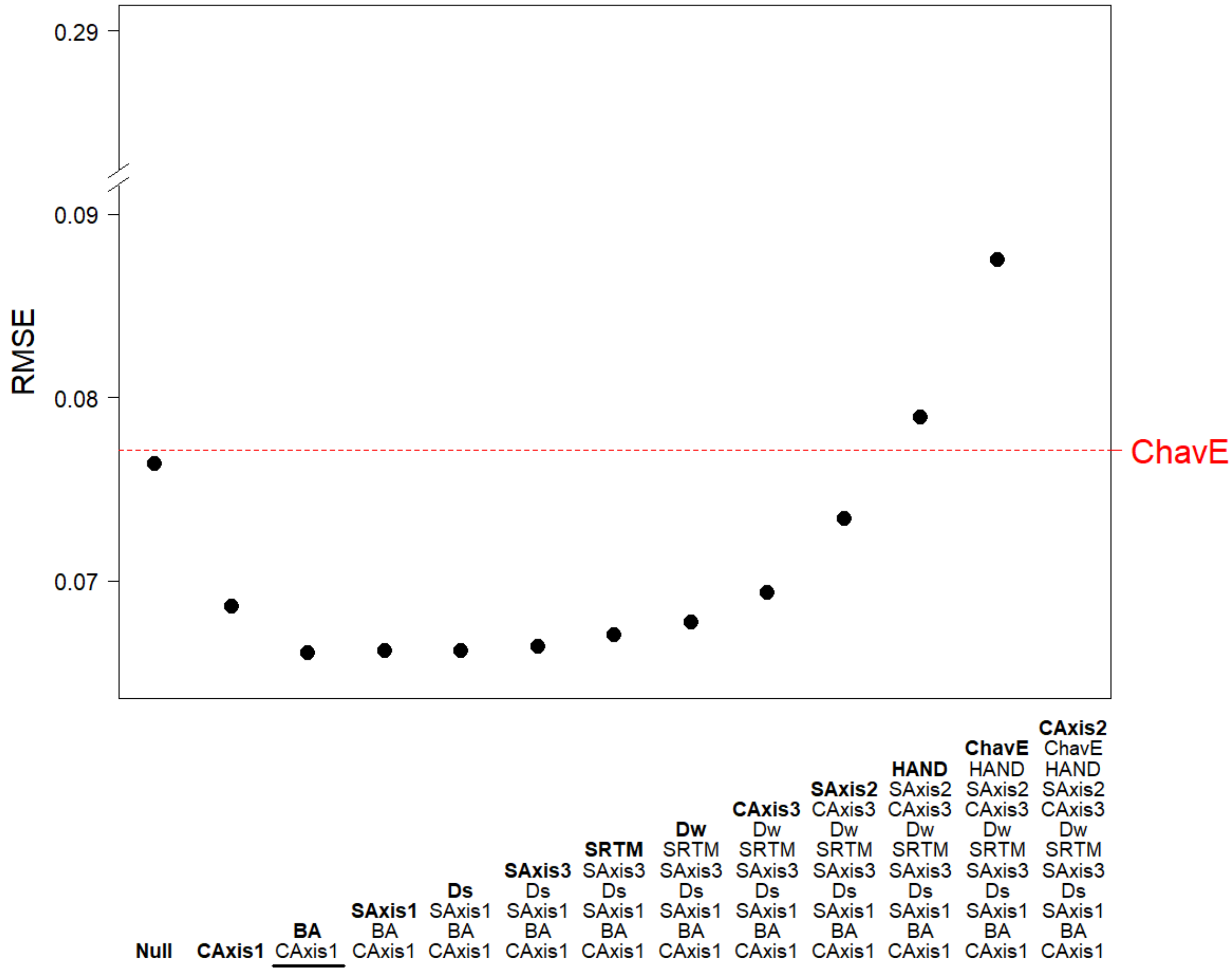


Fig. 37. Error associated with height–diameter models when different combinations of ecological factors are integrated in the model.

RMSE: Root-mean-square error from height–diameter models when no driver was integrated in the model (Null) and when combinations of 1-12 drivers were considered. Ecological factors are defined in Table VII.

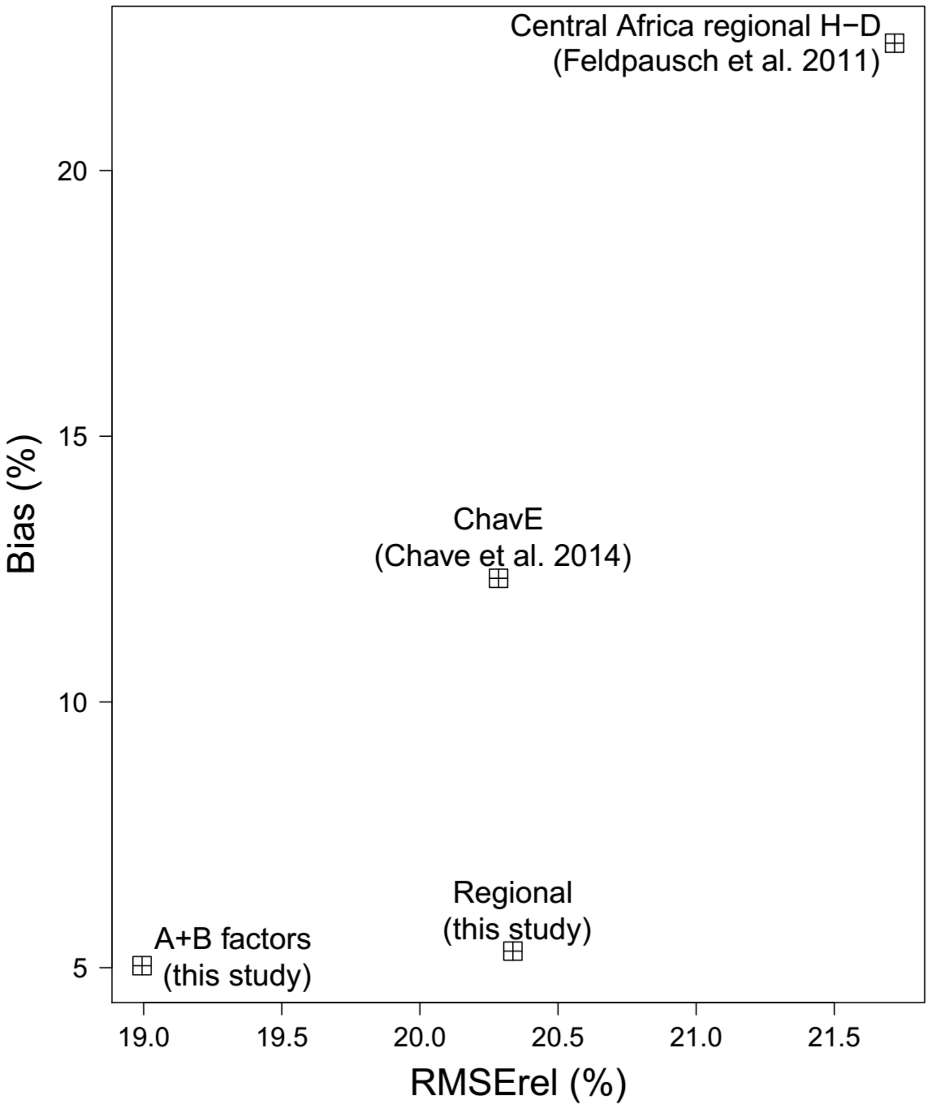


Fig. 38**.** Relative root-mean-square error and bias associated with tree height prediction using different height-diameter models.

A+B factors: best height prediction model from this study; ChavE: model integrating bioclimatic stress variable of Chave *et al.*, (2014), Central Africa regional H–D: model integrating the regional height-diameter model for Central Africa (Feldpausch *et al.,* 2011).

III.1.3.5. Error and bias reduction in tree height prediction

The relative RMSE and Bias associated with tree height prediction was lowest for the H–D model integrating the best biotic and abiotic drivers (BA + CAxis1: equation 14b) compared to the H–D model accounting for the bioclimatic stress variable (Chave *et al.,* 2014) and Central African regional $H–D$ model (Feldpausch *et al.,* 2011) (Fig. 38).

$$\ln(H_{Eco}) = \exp(a + b \times \ln(D) + \mathrm{c} \times \ln(D)^2 + x_i + \ BA \ + CAxis1 + \varepsilon) \ldots\ldots\ldots\ldots \text{ Equation 14b}$$

The relative RMSE associated with H_{Eco} was 18.9 % opposed to 20.2 % and 21.7 % RMSE associated with H_{ChE} and H_{Fel}, respectively. Also, the H_{Eco} had a 5.0 % bias which was 2.5 folds and 4.3 folds lower than H_{ChE} and H_{Fel}, respectively (Fig. 38).

III.1.3.6. Reducing uncertainty in biomass estimation

The reference allometric model (i.e. H_{Ref} as height value) estimated AGB of between 157 to 664 Mg ha^{-1} with a mean of 375 Mg.ha^{-1} and an s.d. of 92 Mg.ha^{-1}. Because the wood density and diameter values were similar in the reference AGB allometric model and in the other pantropical models, differences in AGB can only originate from differences in the predicted tree height or H–D models. Hence the allometric model that used H_{Eco} (eqn 4b in this study) estimated AGB of 175–658 Mg.ha^{-1} (mean: 376 Mg.ha^{-1}, standard deviation of 89 Mg.ha^{-1}) for trees of diameter ≥ 10 cm. The allometric models which used either H_{ChavE} or H_{Fel} consistently overestimated AGB to the order of 25 to 55 Mg.ha^{-1}, respectively (Fig. 39).

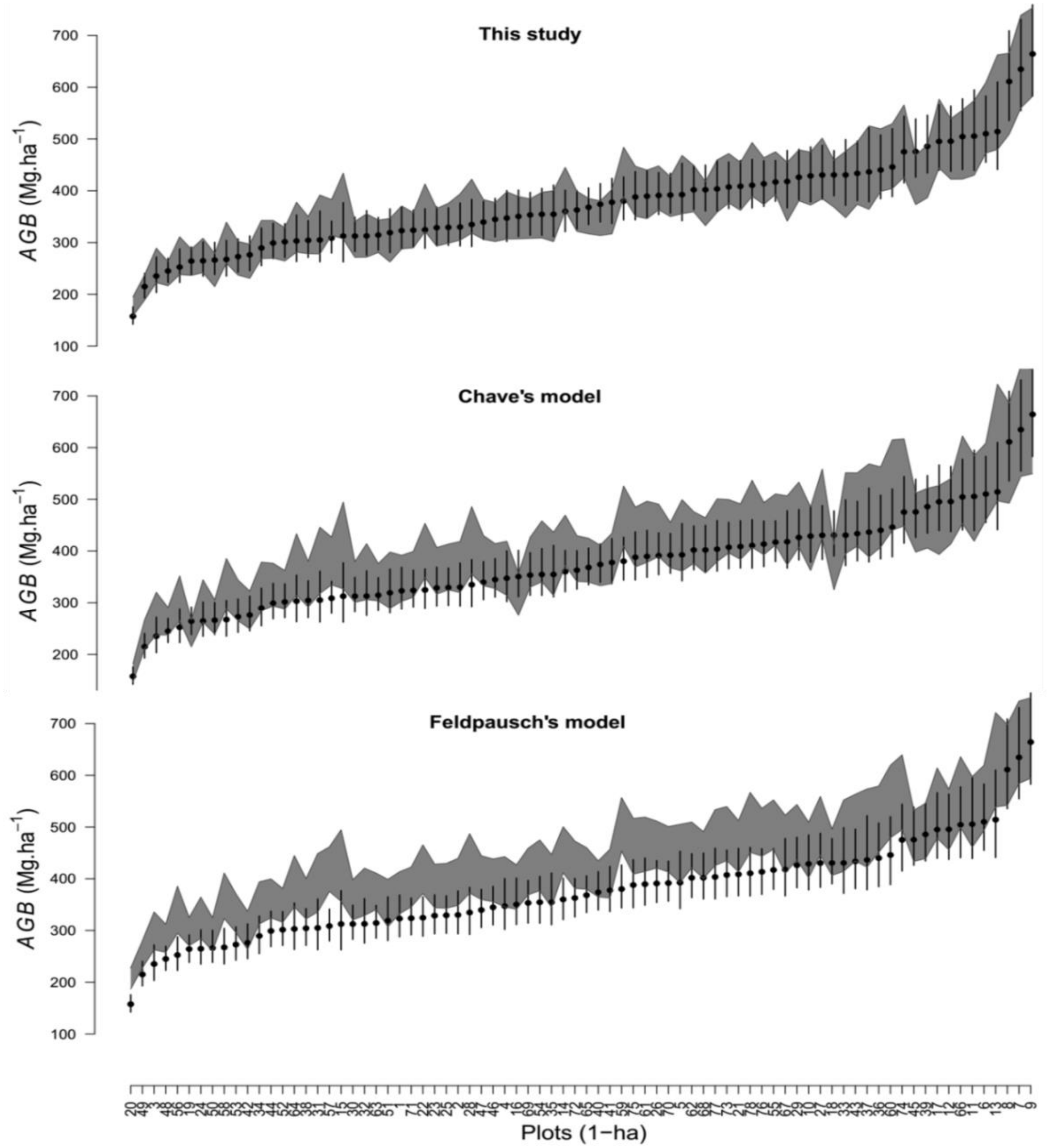


Fig. 39**.** Uncertainty in biomass estimates based on three height-diameter models.

AGB: Aboveground biomass in Mg.ha^{-1}; This study: based on best height prediction model for this study; Chave's model: based on bioclimatic stress variable by Chave *et al.,* (2014); Feldpausch's model: based on the Central Africa regional height model by Feldpausch *et al.*, (2011). Black points: reference AGB based on measured tree heights; Gray background is upper 95 % and lower 5 % credibility intervals; black vertical lines are the credibility range of respective models.

III.1.4. Influence of soil gradient on community leaf functional traits

III.1.4.1. Soil data summary

A summary statistics of the soil and topography variables measured from the 50 ha Forest Dynamics Plot in Korup is presented in Appendix 3.

III.1.4.2. Floristic overview

A total of 489 individual trees (dbh ≥ 10 cm) from 98 species (75 genera and 37 families) were sampled from 44 quadrats of 0.04 ha each. Five species had the highest number of individuals in the dataset: *Oubanguia alata* Baker f. (75); *Drypetes staudtii* (Pax) Hutch. (42); *Hymenostegia afzelii* (Oliv.) Harms (24); *Cola rostrata* K.Schum (23) and *Strombosiopsis tetrandra* Engl. (15), which are also among the most dominant species in the 50- ha FDP in Korup. Seventeen species were common in at least seven quadrats (16%), 46 species were sampled in one quadrat only and 14 quadrats hosted more than ten species. The list of studied species and their abundance are provided in Appendix 4.

III.1.4.3. Main edaphic gradients

Using Kaiser-Guttman’s criterion, three PCA axes were retained to summarize the main gradients from the soil variables and accounted for 67 % of the total variance (Table XIII & Appendix 5). The first PCA axis explained approximately 34 % of total variance, was related to soil mineral resources and topography. Thus this first axis described a soil gradient of increasing cation exchange capacity, organic matter, Clay, total phosphorus and total nitrogen, and strongly and positively correlated to elevation (r = 0.71, p-value < 0.001) and to slope (r = 0.61, p-value < 0.001) (Table XIII). Dim.1 was interpreted as a gradient of soil fertility because of the higher proportion of cation exchange capacity, organic matter and Clay which are all fertility-related soil properties. The second axis (Dim.2), accounting for 20 % of total variance and was interpreted as a soil texture gradient because of the strong correlation with sand (r = -0.71, p-value < 0.0001) and silt contents (r = 0.77, p-value < 0.0001). This axis was also negatively correlated to total nitrogen but positively correlated to soil moisture content. The third axis, explaining 13 % of the total variance, was interpreted as a gradient of phosphorus content. Total phosphorus was positive while total nitrogen was negatively correlated to this axis. The latter two gradients were not significantly correlated with elevation and slope (Table XIII). The soil fertility gradient was retained to explore further trait-gradient analysis since the second and third soil gradients were not significantly correlated to quadrat-level mean trait values and functional divergence (Table XIV). It should be acknowledged, however, that some important constituents of fertility, namely phosphurus and to some extent nitrogen were partly independent from the first gradient. Elevation and slope were also strongly correlated to first axis and were therefore not considered in further trait-gradient analyses. The later result is reported in Appendix 5.

Table XIII. Identification of the main gradients in topography and soil-related variables in the 50-hectare Forest Dynamics Plot in Korup

Dim. 1, Dim. 2 and Dim. 3: main axes of principal component analysis. Pearson correlation and level of significance: n.s. = not significant, *p < 0.05, **p < 0.01, ***p < 0.001) between the main axes and measured variables are provided.

	Dim. 1	**Dim. 2**	**Dim. 3**
Eigenvalues	3.07	1.82	1.13
% of variance	34.17	20.28	12.62
Cumulative % of variance	34.17	54.45	67.07
Sample size	44	44	44
Interpretation	**Soil fertility gradient**	**Soil texture gradient**	**Soil phosphorus gradient**
Nitrogen, (g kg^{-1})	0.69***	-0.45**	-0.44**
Phosphorus, (g kg^{-1})	0.37***	0.33**	0.79***
Sand content, (%)	-0.37*	-0.71***	0.31*
Silt content, (%)	-0.4**	0.77***	-
Cation exchange capacity, (cmol kg^{-1})	0.87***	-	-
Organic matter, (%)	0.83***	-	-
Clay content, (%)	0.77***	-	-
Moisture content (%)	-	0.49***	-
Elevation (m)	0.71***	0.1 *n.s.*	0.21 *n.s.*
Slope (°)	0.61***	0.08 *n.s.*	0.25 *n.s.*

Table XIV. Linear regression for the second and third principal component axes four traits.

r: Pearson correlations; *P*: degree of significance; LPC : leaf phosphorus content; LNC: leaf nitrogen content; LA: leaf area; SLA: specific leaf area.

Trait metrics	Traits	Dim. 2 (Soil texture gradient)		Dim. 3 (Soil phosphorus gradient)	
		r	*P*	r	*P*
Quadrat-level weighted mean	LPC	-0.1	0.4	0.05	0.57
	LNC	0.21	0.31	-0.05	0.81
	LA	-0.15	0.32	-0.04	0.79
	SLA	-0.05	0.72	-0.01	0.9
Functional divergence	LPC	0.5	0.8	-0.24	0.29
	LNC	0.2	0.92	-0.16	0.44
	LA	-0.12	0.42	0.05	0.7
	SLA	-0.02	0.88	-0.25	0.1

III.1.4.4. Association of functional traits with soil fertility gradient

The association between functional traits and the soil fertility gradient was significant for three quadrat-level mean trait and four functional divergence traits (Fig. 40). Of the two functional trait metrics, trait association with the soil fertility gradient was highly variable among the traits. For example, quadrat-level mean trait for LPC, LNC and LA was positively correlated (from $r = 0.32$ to $r = 0.40$) with the soil fertility gradient while no significant association was observed for SLA versus soil fertility (Fig. 40: A–E). Functional divergence (i.e. within quadrat dissimilarities between species' trait) showed two patterns: species were either more dissimilar for LA and SLA or less dissimilar for LPC and N:P ratio, as the gradient in soil fertility increases (Fig. 40: F–J). However, no correlation was observed for functional divergence of LNC along the soil fertility gradient (Fig. 40: G).

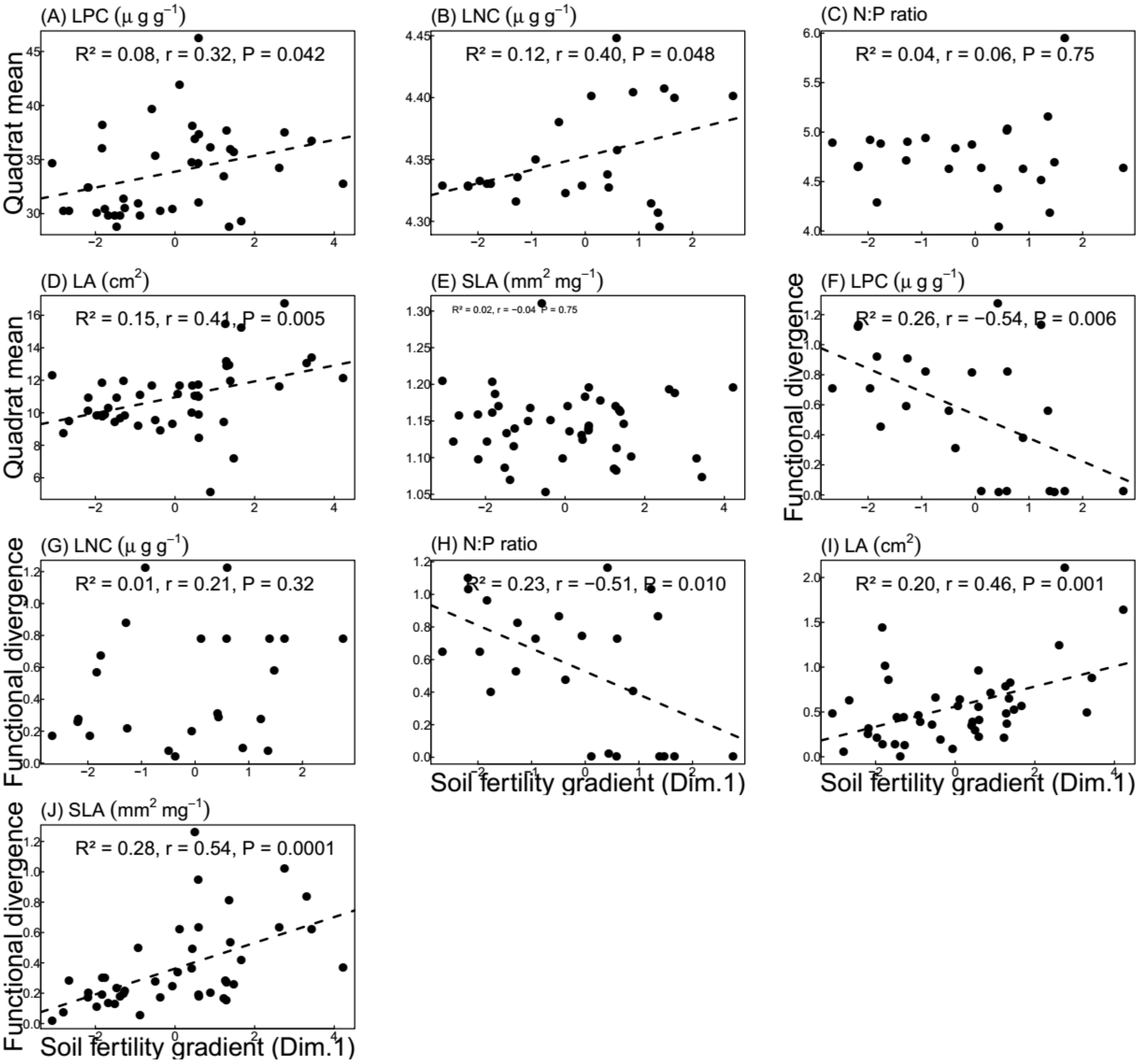


Fig. 40. Association of leaf functional traits with soil fertility gradient for quadrat weighted mean and functional divergence.

Dim.1: First axis of principal component analysis; LA: leaf area; SLA: specific leaf area; LPC: leaf phosphorus content; LNC: leaf nitrogen content. Dashed lines: slope of linear regression; R^2: adjusted coefficient of variation; r: Pearson correlations coefficient.

III.1.4.5. Non-random community trait distribution

Quadrat-level weighted mean trait distribution and functional divergence along the soil fertility gradient were significantly different from the null assumption of random trait distribution. These differences varied among the traits and were either positive (trait convergence) or negative (trait divergence) (Fig. 41). Quadrat-level weighted mean for LPC, LNC and LA but not N:P ratio increased toward the more fertile end of the soil gradient, i.e. trait variation based on species' mean trait values was higher than expected in these traits for quadrats on more fertile soils and lower than expected for quadrats on less fertile soils (Fig. 41: A, B & D). Functional divergence of LPC, LA and SLA showed two patterns: divergence of LPC decreased as the gradient in soil fertility increased (Fig. 41-E) while divergence in LA and SLA increased as the gradient in soil fertility. More divergence, therefore, occurred in quadrats on less fertile soils than those on more fertile soils for LPC contrary to LA and SLA. Non-random trait distribution also changed depending on the trait. For instance, non-random trait distribution accounted for 13 % and 33 % of species' dissimilarity between quadrats and 15 % and 30 % of species' mean trait variation between quadrats for LA and LPC, respectively (Fig. 41).

III.1.4.6. Trends in intraspecific trait variation

Results of the Jackknife analysis showed that intraspecific trait variations differed from the quadrat-level mean trait variation in strength and direction (Fig. 42). Overall, the slopes of intraspecific trait variation ranged from -8.33 to 3.94 but these variations changed between the traits and were either in the same direction or in the opposite directions relative to the quadrat-level mean trait (Fig. 42). The slope of intraspecific variation ranged between -0.19–0.0 for LPC, -0.51–0.26 for LNC, -0.23–0.54 for N:P ratio, -5.12–3.89 for LA and -8.33–3.94 for SLA. Five species showed significant intraspecific trait variation for SLA and three for LA. No species showed any significant intraspecific trait variation among the four species on which LPC, LNC and N:P ratio were analysed. When the quadrat-level mean trait values were substituted by Dim.1 (i.e. PCA scores related to quadrats), the results obtained for intraspecific trait variation were similar to the one above (Fig. 41). The values obtained from the intraspecific slope are presented in Appendix 6 for each species and traits.

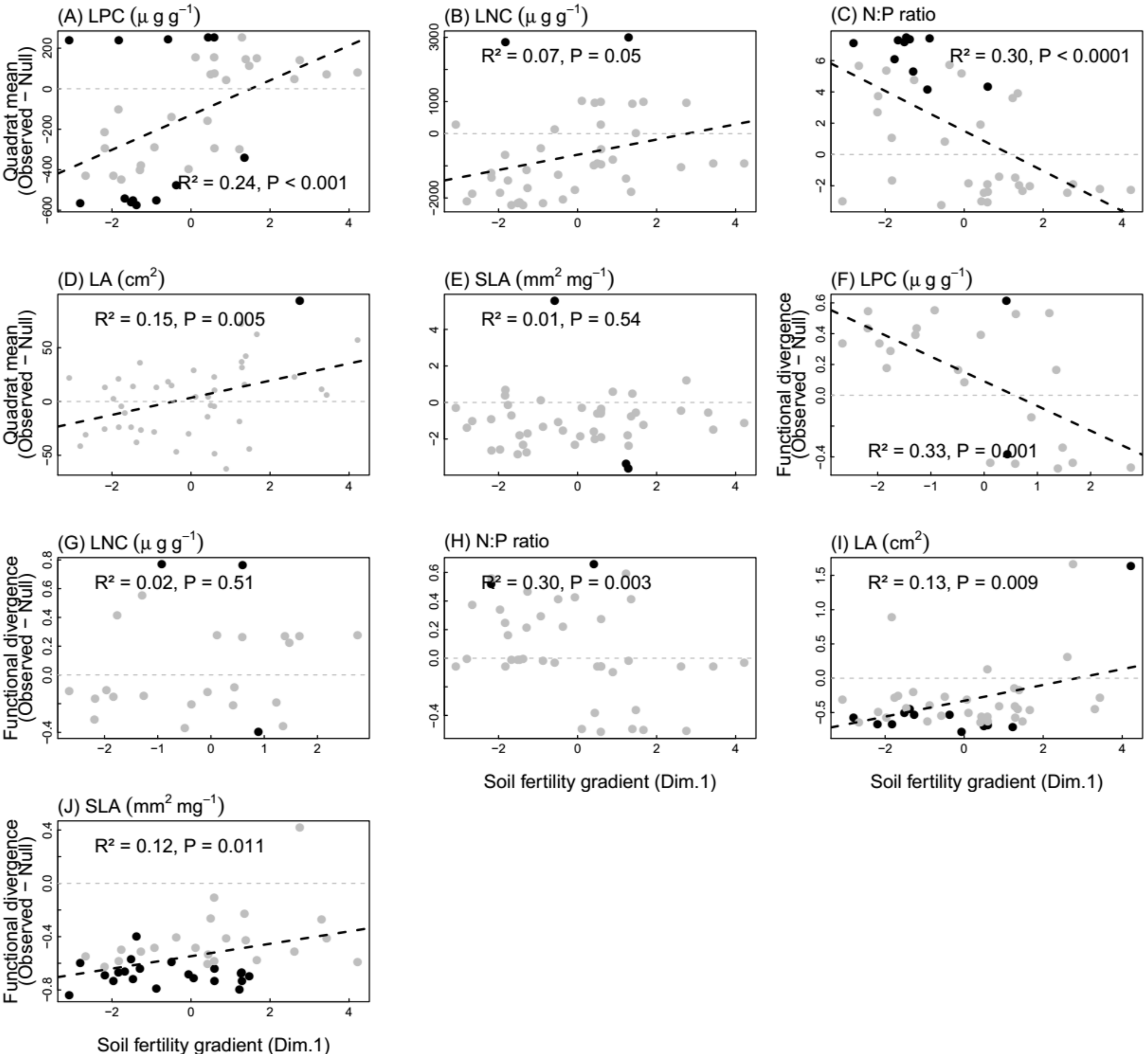


Fig. 41. Departures from non-random trait distribution for quadrat weighted mean and functional divergence.

Grey horizontal lines: null assumption of random assembly; Bold-faced dots: significantly different from null; Grey dots: non-significantly different different from null;

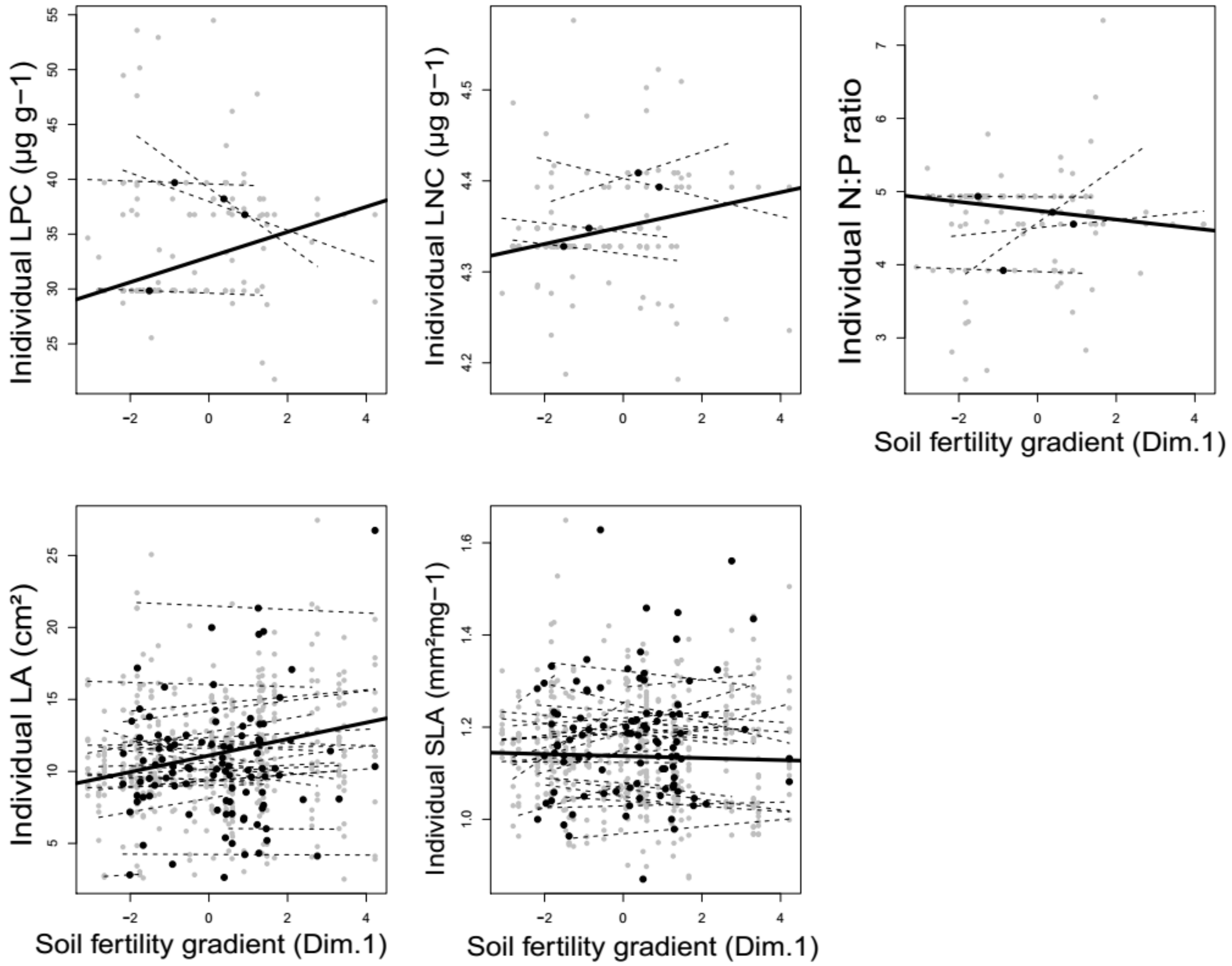


Fig. 42. Trends and directions of intraspecifc trait variation relative to quadrat weighted mean traits along soil fertility gradient.

Grey dots and grey dashed lines: species' individual trait and regression for intraspecifc trait variation; Black lines: quadrat weighted means and regression.

III.2. Discussion

III.2.1. Overview

Many factors are hypothesized to play a key role in tree community structure (i.e., tree height, species composition and functional traits distribution) of lowland African forests. Understanding the validity and role of each factor has captured the interests of community ecologists who have established different theories. However, the debate is on-going on whether patterns in species distribution can be explained by deterministic processes as postulated by the niche-based theory or stochastic forces as postulated by the neutral theory. The extent and limitations of these theories have been elaborated in section I.2.3.2. No one factor has singly explained the overall patterns of tree communities in lowland African forests (Zobel, 1992). At a holistic point of view, both deterministic and stochastic processes are at work in nature, although several studies have advocated for deterministic processes (Condit *et al.,* 2002; Duivenvoorden *et al.,* 2002; Tuomisto *et al.,* 2003).

This study takes particular interest to investigating the role of gradients in soil composition and bioclimatic variables on three components of tree community structure, particularly;

- floristic composition and distribution,
- tree height (vertical structure),
- functional traits composition.

III.2.2. Variation of species diversity between sites in Central African lowland forests

The analysis of species diversity in one ha plots across the Central African lowland forests between forest types permitted to understand variation in species diversity both in terms of the species number and Shannon index of diversity from the viewpoint of permanent sampling plots. The results revealed that significant but weak variation in species diversity occurred between sites and between forest types. This result does not contradict previous studies that have reported strong variations in species composition between tropical forests types (Condit *et al.,* 2005; Gonmadje, 2012; Kenfack *et al.,* 2007; Parmentier *et al.,* 2007) but rather exposes the limitation of the Shannon diversity index and species number used to evaluate species diversity. According to Barrantes and Sandoval (2009) & Losos and Miles (1994) these measures of species diversity do not account for the species “identity” and therefore their role in the community and biogeographical patterns are lost. However, multivariate analyses such as Canonical Correspondence Analysis provide very valuable information about the association between environmental variables and the presence/abundance of species in a community (Barrantes and Sandoval, 2009). Such multivariate analyses could therefore be used instead of diversity indices.

Another possible reason for the weak variation in species diversity between sites and forest types may be related to the sampling size. It could be presumed that sampling a surface area of 100 m x 100 m is sufficiently large to census an important number of species in a given area knowing that one ha plots in tropical forests can hosts about 254 tree species with diameter ≥ 10 cm (Condit *et al.,* 2005).

III.2.3. Role of regional soil and climate gradients on tree floristic patterns

III.2.3.1. Reliability of the data

The central aim of this section was to quantify the extent to which soil and bioclimatic gradients independently and jointly influenced species diversity and abundance over a large territory of ca. 110 000 km² mainly covering the eastern and part of centre Cameroon (Fig. 22). A similar study in the African lowland forests was limited to few sets of tree species; e.g. 73 tree species in Réjou-Méchain *et al.* (2008) because most studies that were able to consider climate or geology over a meso- or regional scales had to rely on forest inventories for which only a limited proportion of tree species can be considered as reliably identified by field prospectors from logging companies (Réjou-Méchain *et al.*, 2011).

The dataset collected for the present study is unique in that it features a fair sampling of the main rainfall gradient (climate PCA axis 1; Fig. 30) stretching over more than 250 km. More than 2 500 voucher specimens were collected to ensuring high standards of botanical determination for nearly 98 % of trees (resulting in 536 species found in 82 one ha permanent sampling plots). These vouchers are still being consulted at different herbaria and laboratories among which the National Herbarium in Yaoundé, Herbarium and Library of African Botany in Brussels, and Plant Systematic and Ecology Laboratory at the Higher Teachers' Training College in Yaoundé.

The sampling and analysis of soil composition variables within the 60 one ha plots permitted to study localised variation in classical soil textural and chemical properties and the influence on floristic patterns. Indeed, previous studies addressing soil-related (or geology) versus floristic variation employed coarse soil data such as chemical composition obtained from geological maps (e.g. alluvium, sandstone, schist, granite; Fayolle *et al.* (2012)), digital elevation geomorphological maps (e.g. Plain, Valley, Concave relief and Convex relief; Guitet *et al.* (2015)), and maps of soil types (e.g. Clay, Clay loam, Sand, Loamy coarse; Réjou-Méchain *et al.* (2008)).

Climatic variables obtained from recent remotely sensed satellite bioclimatic layers improved the detection of more precise species distribution at the regional scale. The major advantages of these bioclimatic layers rely on the very high resolution (3–30 arc-seconds or 90–900 m, respectively), free availability (http://chelsa-climate.org/) and designed to overcome the problems of less regular distribution of meteorological stations witnessed in some regions like the Congo Basin (Karger *et al.*, 2017). In addition, these remotely sensed bioclimatic variables has been reported to improve species distribution modelling in the tropics (Deblauwe *et al.*, 2016)

Studies of this magnitude that provide a balanced sampling of soils composition along climate gradients devoted to tropical forests are very rare in the literature (but see Swaine 1996; Réjou-

Méchain *et al.,* 2008; Condit *et al.,* 2013). One possible reason why most published works addressed either only soil at local scale (e.g. Clark, Palmer & Clark 1999; John *et al.,* 2007) or climate at regional scale (e.g. Pyke, 1999; Parmentier *et al.,* 2007; Fayolle *et al.,* 2014) could probably be linked to the high cost for analysing soil variables at a considerable scale. However, our plots were grouped in six localities and climate variables showed little variation within each locality due to limited resolution of climatic layers (Fig. 28), a fact that did not allow analysing potential effects linked to dispersal limitation and biogeography after factoring-out the effects of soil and climate (Table IX).

III.2.3.2. Influence of soil and climate gradients on species distribution

The analyses on the floristic data revealed that species distribution were characterized by abundant species that combined high frequencies and occurrences over the regional scale and by scarce species with densities of ≤ 1 tree ha^{-1}. The gradients in soil composition were principally dominated by soil texture (increasing clay and decreasing silt and sand contents) and by soil fertility dominated by increasing phosphorus concentration. The gradients in bioclimatic variables were characterized by specific elements of precipitation (e.g. increasing annual precipitation and precipitation seasonality) and temperature (e.g. increasing annual mean temperature and temperature of coldest and wettest quarter of the year). In the constrained analyses with the soil and climate gradients, it was found that the influence of the soil gradient was revealed mostly by scarce species while the climate gradient explained the distribution of species, most of which were abundant in the study area. In addition, the joint effects of soil and climate influenced the distribution of some other species, most of which were scarce in the entire study area.

For both CAIV and NSCAIV approaches employed in the apportioning of species variance by soil and/or climate gradients only a narrow difference was noticed between the proportion of variances explained by climate and soil gradients and both effects were nearly independent (section III.1.2.4). The proximity of the later results suggests that:

- one ha plots provide a sufficient sampling size of species for this type of forests as to make CA and NSCA results to converge;
- climate did not show hierarchical influence over soil as has been reported in other studies (Toledo *et al.,* 2012, 2011) and
- the high resolution CHELSA bioclimatic data explained variances approximately as soil composition. On the other hand, the absence of soils in the study area, that are physically constrained with the presence of highly concentrated ferruginous nodules and duricrust at the soil surface (shallow clay loam, Skeletic Acrisols, Petroplinthic Acrisols) (Gourlet-Fleury *et al.,* 2011) hosting climax forests is worthy of attention to support our results. Areas in the

> Central African forests comprising a section of the present study where such physically constrained soils occur, have rather reported contrasting results pointing to a strong explanatory power of edaphic factors over climatic conditions. For instance, soil types were more influential than climate on species distribution in the forests of the Central African Republic (Réjou-Méchain *et al.,* 2008), and geological substrates (such as sandy soils typical of sandstone and alluvium) shaped tree species more strongly than climate in the African moist forests (Fayolle *et al.*, 2012).

It was noticed in the present study that most variables of the climate gradients had narrow ranges: climate PCA axis 1 (e.g. annual precipitation was 1523–1970 mm; precipitation of wettest quarter 321–531 mm) and climate PCA axis 2 (e.g. annual mean temperature was 20.0–21.07 °C; mean temperature of driest quarter was 19.87–21.17 °C) and did not feature wet types of tropical forests. Nevertheless, the total variance explained on species distribution was remarkable (10.6–20.0 %). These variations are relatively small compared to those found in other tropical forests. For instance, annual rainfall across central Panama was found to range between 1500–3600 mm (Pyke *et al.,* 2001) while annual temperature range of 19–29 °C have been recorded in Western Ghats forests (Krishnadas *et al.,* 2016). These findings therefore highlight that small differences in climatic conditions in tropical African forests could have strong impacts on species distribution, and climate change (though still poorly documented and understood in central Africa) may have considerable influence on species distribution. Such small changes in temperature and precipitation may also influence species distribution via functional traits by decreasing seed mass in temperature and moisture stress areas and consequently species abundance (Moles *et al.*, 2007, 2014).

In terms of the proportion of species that were significantly influenced by the environmental predictors at P-value < 0.05, 130 species (26.37 %) revealed for the effects of climate, 76 species (15.42 %) revealed the effects of soil and only 35 species (7.1 %) were explained by the effects of both climate and soil. Although these figures are to some extent overestimated due to possible effects of autocorrelation (for climate), this indicates that most of the species were significantly explained by one of the assessed components of the environment (environmental specialists) rather than multiple components (environmental generalists). In contrast, Pitman *et al.*, (1999) had noted that 393 species (85 %) in the Upper Amazonian terre firme forests were habitat generalists, though this was based on coarse but contrasted classification of forest types (terre firme , floodplain, successional and swamp forests). Nevertheless, studies based on axes-summarizing species composition versus environmental properties have reported congruent results to our study: 29 common tree species (57 % of the studied species) were distributed following a rainfall and soil fertility gradients in the west African forest of Ghana (Swaine, 1996); 65 woody species (65 % of the studied species) responded to climate and soil gradients in the forests of lowland Bolivia (Toledo *et al.*, 2012). Recently, ter Steege *et al.* (2013) found that 227 tree species (1.4 %) of lower Amazonia were hyper-dominant and habitat specialists over large geographic ranges. This tendency therefore challenges the idea that most tropical forests species are habitat generalists rather than habitat specialists, although specialization may also correspond to broad habitat conditions. In the prospect of possible future climate change and their potential effect on tropical forests, it means that there may be a shift in species abundance along the climate gradients but the fact that it will primarily concern species displaying large populations, decreases the risks of extinction and shrinkage of the genetic pool. On the other hand, fairly scarce species that appeared as soil specialists did not show obvious dependence on climate and their exposition to climate change could be lower than expected from the sole consideration of scarcity. Species affected by the combined effects of soils and climates, which are mostly scarce, may observe faster and more severe extinction and shrinkage risks in the event of simultaneous manifestation of soil variation and climate change.

III.2.3.3. Soil and climate complementarily explain floristic patterns at regional scale

Fig. 33 illustrates the dichotomy in the species distribution explained by each of the environmental predictors. Species explained by climate gradient happened to be abundant in the study area. For instance, *Greenwayodendron suaveolens* and *Anonidium mannii* are among the commonest mid-canopy tree species in the Central African lowland forests and are usually associated with wet areas (but not swampy) in forests of Cameroon and even Central Africa at least for *Greenwayodendron suaveolens*. On the other hand, species explained by soil were found to be scarce in the study area, e.g. *Monodora myristica* and *Tessmannia africana* are only locally abundant in the Mindourou I locality (though present in the other sites) and naturally not common in Central African lowland forests. *Sorindeia juglandifolia* and *Markhamia lutea* are small trees widely distributed but not abundant in tropical forests and are explained by both climate and soil. What is conspicuous is that not only climate and soils are complementary but that climate appeared as a good predictor of abundant species while soils are good predictors of a batch of scarce species. This is conspicuous because prediction of rare species distribution is notably difficult for simple statistical reasons.

Compensation between precipitation and soil texture has been reported by some studies in lowland tropical forests. Indeed, one interesting finding in our results is that the proportion of variance that remained after the effects of soil (10.3–11.8 % CAIV and NSCAIV, respectively) or climate (4.9–5.8 % CAIV and NSCAIV, respectively) were factored-out from the total explained variance was remarkable. This indicates clearly that both gradients were non-redundant. It is worthy to note that the absolute level of redundancy between soil and climate (1 – 1.5 variance shared) in this study is comparable to landscape vs. soil variables (Guitet *et al.,* 2016) or topography vs. forest structural variables (Couteron *et al.,* 2003; Ramesh *et al.,* 2010). These results reaffirm the reliability of applying soil and climate variables as determinants of tropical tree distribution. Considering the relative independent shares of variance, our study highlights the complementary power of soil and climate in explaining species distribution.

III.2.3.4. Sources and meaning of unexplained variance on species distribution

Despite the remarkable proportion of variance explained by the environmental predictors on species distribution, a considerable proportion (74–77 %) of the variance remained unexplained. The variances unexplained by the environmental predictors (soil and climate gradients) could have two major origins: unmeasured environmental and disturbance factors (e.g. light gaps, human, species interactions and natural disturbances) and stochastic processes (e.g. dispersal limitations). On large time-scales, past environmental variations and broad or recurrent disturbances are likely causes of biogeographic patterns of enduring legacy (Maley, 2001). Disturbances of both human and natural origins could have had significant influence on the current patterns in the species distribution. Pygmy dwellers are still common in most parts of our study area and have been reported to have arrived in the west Congo Basin wet forest since 5000 years ago (Oslisly *et al.,* 2013). It could be expected that their slash-and-burn farming method could have had an influence on the current patterns in species distribution and soil properties and structure. Though they failed to find statistical significance to support this hypothesis in the locality of Mindourou I (also one of the localities in this study), Vleminckx *et al.* (2014) attempted to explain the distribution of heliophile trees (e.g. *Petersianthus macrocarpus, Pentaclethra macrophylla, Hylodendron gabunense, Pycnanthus angolensis*) through the prevalence of soil charcoal as an evidence of ancient human settlement. Perhaps this non-significance was because of the natural catastrophes that occurred centuries ago (Maley, 2001), leading to the sinking of soil charcoal hence blurring the evidence of past human disturbance. On the other hand, the availability of sunlight to the forest floor (but also linked to disturbance) could have promoted the installation of some well-known forest species. During forest inventories, several light-demanding species (e.g. *Musanga cecropioides*, *Pycnanthus angolensis*, *Sterculia rhinopetala*, *Funtumia africana* and *Petersianthus macrocarpus*) were found especially in some areas where previous human activities such as commercial logging were noticed.

The contribution of stochastic processes to explaining species distribution cannot be assessed in this study because inter-site variation which is a sound basis for assessing neutral-like migration limitation (*sensu* Munoz *et al.,* 2008, 2007), cannot be disentangle from climate variation. In fact, Hardy & Sonké (2004) have noted that though a crude typology of habitats influenced species distribution in the Dja forests (a section of the Somalomo locality sampled in this study), limited dispersal appeared as the major factor affecting the pattern of spatial variation of tree community composition. The sampling of additional sites sufficiently distant albeit sharing main climatic features would be desirable as to allow measuring the relative influence of environmental constraints and migration limitation on observed variations of tree community composition.

III.2.4. Contribution of ecological factors in modelling tree height–diameter relationship

III.2.4.1. Tree height–diameter variation and allometry

Tree height is the third most important predictor of aboveground biomass (AGB) after tree diameter and wood density, respectively (Chave *et al.*, 2004; Holdaway *et al.*, 2014), and its geographical variation can guide on factors controlling tree vertical structure and forest communities (Banin *et al.*, 2012; Feldpausch *et al.*, 2011). Many studies have evoked the regional and continental variation of tree height but rarely have the contribution of ecological factors (soil, climate and parameters of forest structure) been analysed in the prediction of tree height and in the light of ABG estimation. This section of the present research was reserved to develop a model that predicts tree height from its diameter while integrating in the model, the ecological factors that influence the $H–D$ relationship. A first step was to analyse the simple (without integration ecological factors) tree height–diameter variation between sites of the central African lowland forests region, but noting that external factors could cause between-sites height–diameter variation. In this light, it was found that for a given diameter, trees were taller in sites belonging to semi-deciduous forests than evergreen forests and the latter were taller than in monodominant forests. In addition, trees were sometimes taller or shorter than the regional averaged tree height. These results are in agreement with the hypothesis that tree height–diameter allometry varies largely between forest plots as reported in French Guiana (Molto *et al.*, 2014) and within a forest type (Hunter *et al.*, 2013); between forest types as demonstrated in south-eastern Cameroon (Fayolle *et al.*, 2016) and that wet forest species are generally smaller in height than moist forest species from a pan-tropical study (Chave *et al.*, 2005). Such variations in tree height–diameter allometry may imply that environmental constraints determine the growth of tree heights and therefore more in-depth studies of the contribution of environmental factors in predicting tree height for biomass estimation are needed. Irrespective of the model form used, it has been shown that tree height–diameter allometry calibrated on local datasets yield improved performance over adapted regional or pan-tropical models (Kearsley *et al.*, 2017, 2013).

Thus, integrating the effects of local ecological factors in the height–diameter allometry can improve accuracy in tree height predictions and reduce uncertainties in biomass estimation. In this study, the variation of plots' coefficients suggests that abiotic and biotic factors likely cause the observed differences in height–diameter allometry. This result is obvious from inspection of height–diameter model coefficients (Fig. 36). While using tree height data obtained from laser altimeter footprints, Yang *et al.* (2016) found that height variation is controlled by edaphic and climatic factors across pan-tropical humid forests while climatic and forest structural characteristics have emerged as key drivers of variation in height–diameter relationships at the pan-tropical and regional scales (Banin *et al.*, 2012; Feldpausch *et al.*, 2011). Given the important role of ecological factors in the tree height–diameter relationships, tree height is expected to be moderated depending on ecological factors. Therefore, it is expected to obtain more accurate tree height prediction when environmental gradients are accounted for in the tree height prediction model. Indeed, integrating a combination of 1–12 ecological variables (including gradients in soil composition and bioclimatic variables, parameters of forest structure, bioclimatic stress variables, altitude and drainage) in the H–D model revealed that the best height prediction was obtained when the first axis of climate gradient (interpreted as precipitation gradient) was combined with the basal area of the forest stand. The integration of PCA climate axis 1 (CAxis1) combined with basal area (BA) results in an important improvement in the bias and error in the tree height prediction when compared to existing models. In fact, tree height predicted while integrating a combination of BA and CAxis1 in the model (equation 14b) resulted in a 5.0 % bias compared to 12.5 % and 21.5 % bias associated with the models by Chave *et al.*, (2014) and Feldpausch *et al.*, (2011), respectively (Fig. 38).

III.2.4.2. Improved aboveground biomass estimation

The reference AGB calculated using the field measured tree height yielded an average AGB of 375 Mg.ha^{-1} (range 157–664 Mg.ha^{-1} and s.d. of 92 Mg.ha^{-1}). Comparative to this value, inaccuracies in tree height prediction lead to overestimation of AGB of 25 Mg.ha^{-1} when the model integrating the bioclimatic stress variable was employed [$\mathrm{H_{ChE}}$: (Chave *et al.*, 2014)] while an overestimation of 55 Mg.ha^{-1} of AGB was recorded when the model based on regional average tree height was employed [$\mathrm{H_{Fel}}$: (Feldpausch *et al.*, 2011)]. The predicted tree heights for this study ($\mathrm{H_{Eco}}$) yielded an AGB of 175–658 Mg ha^{-1} which was only 6–18 Mg.ha^{-1} different from the reference AGB. While this study provides evidence that accuracy in height prediction can be attained by integrating biotic and abiotic factors in the H–D model, the present results and others (see Chave *et al.,* 2004; Feldpausch *et al.,* 2011; Banin *et al.,* 2012) also suggest that the uncertainties in AGB can be largely reduced when tree height is precisely predicted. However, despite the improvement in tree height prediction, a corresponding gain in stand-level biomass was not observed probably because of disproportionate allocation of tree height error. That is, greater error in tree height may be allocated to the largest trees that captured smaller biomass whereas most biomass being allocated to medium-statured trees (canopy stratum) but had smaller relative error in height measurements (Hunter *et al.,* 2013).

III.2.5. Influence of soil gradient on community functional traits

III.2.5.1. Community assembly and trait distribution along soil fertility gradient

Trait-gradient relationships are widely used to study community assembly processes operating along an abiotic gradient (Schwilk and Ackerly, 2005; Weiher and Keddy, 1995). These associations have increasingly been recognized as being important to gain insights on species and community strategies (Jager *et al.,* 2015; Spasojevic and Suding, 2012; Thuiller *et al.,* 2004; Wright *et al.,* 2005). It could be expected that leaf traits that are influenced by environmental stress (e.g. decrease in soil fertility) would change as the stress in the environment become more present. We found evidence to support this expectation for three of the five leaf traits examined. Quadrat-level mean trait for LPC, LNC and LA significantly decreased for quadrats on less fertile soils. This result is consistent with the notion of abiotic filtering for the considered traits (Diaz *et al.,* 1998). The non-significant association of quadrat-level mean trait for SLA to the soil fertility gradient and other soil-related variable (e.g. Topographic Wetness Index: Dilts (2015)) was surprising, given that LA (which showed significant association with the gradient) has been reported to be inversely correlated to SLA (Reich *et al.,* 1991). However, LA and SLA were not correlated in our dataset (r = -0.18). An initial analysis where the drainage effect was measured as Topographic Wetness Index, failed to explain the variation of SLA even though a gradient of annual drainage of the 50 ha FDP in Korup is observed (the fertile upper edge of the Korup plot is drier compared to the temporarily wet lower edge; M.B. Libalah, *pers. obs.*). This result could mean that SLA did not capture the dispensable filtering of soil fertility and drainage perhaps captured the blurring influence of light intensity. Light penetration through forest strata has been reported to influence the vertical variation of SLA at the upper and lower canopies (Petter *et al.,* 2015; Spasojevic *et al.,* 2014). Given the vertical stratification of tropical forests canopy, one can expect lower SLA values for quadrats with taller trees as an expression of competition for light, compared to SLA for quadrats with shorter trees. High values of LA (low SLA) have also been reported to be correlated to high investment in structural properties such as laminar thickness, high tissue density within the leaf (Reich *et al.,* 1999; Wilson *et al.,* 1999), characteristics that tend to relate to productive local environments.

Functional divergence of LA and SLA increased with the soil fertility gradient, implying the dominance of species with contrasting values for these traits in quadrats with higher fertility, for which less competition for soil nutrients can be assumed. Congruent with this interpretation is the fact that an increase in soil fertility among quadrats caused a decrease in functional divergence of LPC, pointing that possibly less competition for soil fertility occurred between species. Given that the soil fertility gradient was dominated by soil properties other than N and P (e.g. CEC and Clay) and was opposed to NIT, the results with LPC cannot be directly linked to P availability in the soil. Therefore the response of LPC could also mean that the advantage for some species having ectomycorrhizal association for P capture vanishes when P content increases for the whole community.

Soil fertility is also reported to influence leaf life span, as species on more fertile soils have short-lived leaves because of faster turnover in leaf tissues (Reich *et al.*, 1999). Consistent with previous studies, LPC displayed positive association with increase in soil fertility gradient (Ordoñez *et al.*, 2009; Webb *et al.*, 2000; Wright *et al.*, 2001). We presumed that increase in soil fertility might have increased leaf photosynthetic capacity and biomass allocation to the leaves. In an earlier study, Atwell *et al.*, (1999) noted that phosphorus and nitrogen in leaves are the main source of energy (ATP and NADPH) during metabolic processes and therefore can be related to photosynthetic capacity. Hence the average photosynthetic capacity for tree communities in most of the 50 ha FDP in Korup may be small for communities on low soil fertility gradient than those on the high soil fertility gradient.

III.2.5.2. Non-random community trait distribution along soil fertility gradient

A shift in community functional traits along an environmental gradient may represent either non-random (deterministic) and random (stochastic) processes that may simultaneously operating among communities (Schwilk and Ackerly, 2005; Weiher and Keddy, 1995). We found evidence for a shift in quadrat-level trait values along soil fertility gradient that partly supported our interpretations for random and non-random processes. Relative to the null expectation (traits are randomly distributed among communities); we noticed that up to 33% of the variance of among-quadrat traits along the soil fertility gradient was non-randomly distributed. Our results (Fig. 41) also showed that the partial non-random shift in quadrat-level mean trait and functional divergence, at least for some quadrats (i.e. between 1 and 22 quadrats), departed from the null expectation in both positive and negative directions. The above results suggest that in addition to non-random trait distribution, there was trait convergence (positive deviation) and trait divergence (negative deviation) as the gradient in soil fertility changes. Nevertheless, considering only abiotic filtering and competitive interaction to infer non-random assembly, may be far from perfect. Integrating assumptions about multiple assembly processes such as facilitation and equalizing fitness processes may improve the performance of testing non-random assembly (Spasojevic and Suding, 2012). Moreover, the set of traits we used is limited to leaf traits and extending the present analysis to wood and whole plant traits could provide more visibility in trait response to soil fertility and community assembly (Jager *et al.,* 2015). Interpretation of assembly processes should be cautious as cancelling out or counteracting assembly rules may be misinterpreted for random assembly.

III.2.5.3. Trends of intraspecific trait variation

Earlier studies on functional traits mostly used species mean trait values which largely ignore intraspecific variation. To account for total trait variation, recent studies have begun to include intraspecific trait variation, but have focused largely on the relative contribution vis-à-vis interspecific trait variation (de Bello *et al.,* 2011; Lepš *et al.,* 2011) and sometimes on the influence of intraspecific trait variation on community assembly (Jung *et al.,* 2014, 2010; Siefert, 2012). It could also be of importance to study the within species trends relative to mean trait along a gradient (Jiang and Ma, 2015; Pescador *et al.,* 2015). Considering that intraspecific trait variation could shift in the same direction as the species mean trait, the trends of intraspecific trait variation may be equal, lower or may show no trends with the gradient (Cornwell and Ackerly, 2009). In relation to these considerations, we recorded 43 species present in three or more quadrats in the 50 ha FDP in Korup and noticed that intraspecific trait variation were always smaller relative to variation in the quadrat-level trait variation. These trends supported that traits vary less within species than between species and intraspecific variation mirrored the quadrat-level trends. These results also suggest that mean trait values and intraspecific variation may both represent the response of genotype in a given environment (Ackerly, 2003).

Chapter IV

CONCLUSIONS AND PERSPECTIVES

Chapter IV: CONCLUSIONS AND PERSPECTIVES

IV.1. Conclusions

IV.1.1. Overview

Habitat heterogeneity governs forest structure and species response to environmental drivers is therefore crucial for both practical and scientific goals. The present study evaluated the influence of environmental drivers on three parameters of community structure (species composition and distribution, tree height and leaf functional traits) of Central African lowland forests. As concerns the scale of the study, it was realised at two spatial scales:

- regional scale > 10^4 km representing three countries of the Central African lowland forest namely Cameroon, Gabon and DR Congo and
- local scale focusing on the 50 ha Forest Dynamics Plot in the Korup forest.

The study specifically appraised how;

- floristic composition and distribution,
- tree height prediction and
- leaf functional traits, are governed by respective gradients in soil and bioclimatic variables at different spatial scales.

The conclusions to these specific subjects are arranged according to the questions mentioned in the introduction (see section I.1.4).

IV.1.2. Floristic patterns along pedo-climatic gradients

The rich diversity in species composition of CALF followed two main floristic patterns characterised by few species that are common and widely distributed (abundant species) and by many scarce species that are more restricted in their occurrences (scarce species). The environmental determinants of this type of floristic pattern also identified as oligarchy by Pitman *et al.* (2001) was revealed in this study.

Climate appeared as a good predictor of a large proportion of abundant species while soils are good predictors of a batch of scarce species, and both climate and soils complementarily explained a large share of the variance of tree community composition. These results, therefore highlight that in the prospect of possible climate change, there may be a shift in species dominance while relative independence of scarce species with respect to soil may limit the risks of extinction.

IV.1.3. Improved model of tree height–diameter relationship

An improved tree height prediction model (4b & here below) was developed in this study. From the selection of a combination of twelve ecological variables, Tree basal area (BA) and interannual temperature variation (CAxis1 or first PCA axis) were the most important ecological variables to improve the prediction of tree height from diameter. The improved model also out-performed (less bias and error) two major pre-existing pantropical height–diameter models currently used for Central African forests. Also, the estimated aboveground biomass that used predicted tree heights from the improved height–diameter model propagated lower uncertainty compared to the estimated biomass that used predicted tree heights from the two major pre-existing pantropical models.

$$H_{Eco} = \exp(a + b \times \ln(D) + \mathrm{c} \times \ln(D)^2 + x_i + BA + CAxis1 + \varepsilon) \text{ …………Equation 14b}$$

IV.1.4. Leaf functional traits along soil fertility gradient

The main gradient at the local scale was driven by soil fertility which was predominated by cation exchange capacity and Clay content and to a lesser extent of total nitrogen (Table XIII). Most of the five leaf functional traits evaluated (leaf area, specific leaf area, leaf nitrogen and phosphorus contents, nitrogen to phosphorus ratio) were correlated with the soil fertility gradient. These traits were either over-dispersed or under-dispersed with respect to the null model (i.e. random trait distribution), accounting for of non-random trait distribution along the soil fertility gradient. In addition, trends in intraspecific traits variation were consistently lower than the community mean traits along the soil fertility gradient.

These results support the notion that functional traits, particularly leaf traits mediate the influence soil fertility on species distribution via abiotic filtering and competitive interaction (niche theory). This study also highlights that tree communities, as reflected by leaf traits are non-randomly distributed. However, not all the proportion of tree community leaf traits were explained by the soil fertility gradient implying that other factors not investigated in this study (e.g. natural disturbance) could interplay to structure the FDP in Korup.

IV.2. Perspectives

Given the relevance of tropical forests to human wellbeing and nature, variation in environmental factors, particularly climate change scenarios, play a central role in forest structure and its existence. This study has only shown how gradients in climate and soil shape three important aspects of forest structure. In-depth or further studies oriented in the following subjects indicated below will probably contribute towards the sustainable management of tropical lowland forests.

Monitoring forest dynamics in Central African lowland forests is imperative. It would be desirable to continue data collection following a unique protocol such as permanent sampling plots, conducting measurements over a longer period and respecting measurement intervals. These data will increase the reliability of the results on growth, recruitment and mortality rates, and also long-term carbon dynamics of tropical lowland forests.

Factors influencing forest structure are not limited to climate and soil rather future research should address the impact of dispersal limitations, species interactions, geographical barriers and human activities.

Collection and analysis of other functional traits such as wood- and root-related traits have direct impact on forest structure. Prospects on these traits are also relevant for carbon sequestration.

Also, studying community structure via novel phylogenetic approach is encouraged to enrich the understanding of forest diversity beyond species. A combination of functional traits and phylogenetic signals might reveal ecological differences between species and communities.

The analysis of floristic patterns on the bases of individual species (abundant vs. scarce) are sometimes difficult to apprehend whereas determination of a group of species responding to a given descriptors (indicator species) would be more interesting capture phytosociogical assemblage linked to environmental factors.

REFERENCES

REFERENCES

Ackerly D.D., 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences*, 164: S165–S184.

Ackerly D.D., Cornwell W.K., 2007. A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters*, 10: 135–145.

Adler P.B., HilleRislambers J., Levine J.M., 2007. A niche for neutrality. *Ecology Letters*, 10: 95–104.

Alder D., Synnott T.J., 1992. Permanent sample plot techniques for mixed tropical forest, Tropical Forest Papers, pp 30.

Anderson, J. M. & Ingram J.S.I., 1998. *Tropical Soil Biology and Fertility: A Handbook of Methods.*, Second. ed. CAB International, Aberstwyth, pp. 221.

Anonymous 1, 2006. Les forets du Bassin du Congo - Etat des forêts 2006, pp. 257.

Anonymous 2, 2006. World reference base for soil resources 2006: a framework for international classification, correlation and communication, World Soil Resources Reports. Rome, pp. 145.

Anonymous, 2011. State of the world’s forests: 2011, State of the world’s forests, pp. 164.

Anonymous, 2013. *Soil Atlas of Africa*, Soil Atlas of Africa, pp. 176.

APG IV., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181: 1–20.

Arellano G., Jørgensen P.M., Fuentes A.F., Loza M.I., Torrez V., Macía M.J., 2016. Oligarchic patterns in tropical forests: Role of the spatial extent, environmental heterogeneity and diversity. *Journal of Biogeography*, 43: 616–626.

Asner G.P., Mascaro J., 2014. Mapping tropical forest carbon: Calibrating plot estimates to a simple LiDAR metric. *Remote Sensing of Environment*, 140: 614–624.

Atwell B.J., Kriedemann P.E., Turnbull C.G.N., 1999. *Plants in action: adaptation in nature, performance in cultivation*. MacMillan Education Australia, Melbourne, pp. 664.

Auger S., Shipley B., 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science*, 24: 419–428.

Banin L., Feldpausch T.R., Phillips O.L., Baker T.R., Lloyd J., Affum-Baffoe K., Arets E.J.M.M., Berry N.J., Bradford M., Brienen R.J.W., Davies S., Drescher M., Higuchi N., Hilbert D.W., Hladik A., Iida Y., Salim K.A., Kassim A.R., King D.A., Lopez-Gonzalez G., Metcalfe D., Nilus R., Peh K.S.H., Reitsma J.M., Sonké B., Taedoumg H., Tan S., White L., Wöll H., Lewis S.L., 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography*, 21: 1179–1190.

Barrantes G., Sandoval L., 2009. Conceptual and statistical problems associated with the use of diversity indices in ecology. *International Journal of Tropical Biology,* 57: 451–60.

Baskerville G., 1972. Use of Logarithmic Regression in the Estimation of Plant Biomass. *Canadian Journal of Forestry*, 2: 49–53.

Becker P., Meinzer F.C., Wullschleger S.D., 2000. Hydraulic limitation of tree height : a critique 4–11.

Borcard D., Gillet F., Legendre P., 2011. *Numerical ecology with R*. Springer New York Dordrecht London Heidelberg, pp. 319.

Borianne P., Brunel G., 2012. Automated valuation of leaves area for large-scale analysis needing data coupling or petioles deletion, *In*: *Proceedings - 2012 IEEE 4th International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications, PMA 2012*. IEEE, pp. 50–57.

Botta-Dukat Z., 2005. Rao' s quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16: 533–540.

Bouyoucos G.J., 1951. A recalibration of the hydrometer method for making mechanical analysis of Soils. *Agronomy Journal,* 43: 434.

Brown A.M., Warton D.I., Andrew N.R., Binns M., Cassis G., Gibb H., 2014. The fourth-corner solution - using predictive models to understand how species traits interact with the environment. *Methods in Ecology and Evolution,* 5: 344–352.

Buondonno A., Rashad A.A., Coppola E., 1995. Comparing tests for soil fertility. II. The hydrogen peroxide/sulfuric acid treatment as an alternative to the copper/selenium catalyzed digestion process for routine determination of soil nitrogen kjeldahl. *Communications in Soil Science and Plant Analysis*, 26: 1607–1619.

Cayuela L., Granzow-de la Cerda Í., Albuquerque F.S., Golicher D.J., 2012. Taxonstand: An r package for species names standardisation in vegetation databases. *Methods in Ecology and Evolution*, 3: 1078–1083.

Chapin J.P., 1923. Ecological Aspects of Bird Distribution in Tropical Africa. *The American Naturalist,* 57: 106–125.

Chase J.M., Myers J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366: 2351–2363.

Chave J., 2004. Neutral theory and community ecology. *Ecology Letters*, 7: 241–253.

Chave J., Andalo C., Brown S., Cairns M. a., Chambers J.Q., Eamus D., Fölster H., Fromard F., Higuchi N., Kira T., Lescure J.P., Nelson B.W., Ogawa H., Puig H., Riéra B., Yamakura T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145: 87–99.

Chave J., Condit R., Aguilar S., Hernandez A., Lao S., Perez R., 2004. Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 359: 409–420.

Chave J., Coomes D., Jansen S., Lewis S.L., Swenson N.G., Zanne A.E., 2009. Towards a worldwide wood economics spectrum. *Ecology letters*, 12: 351–66.

Chave J., Olivier J., Bongers F., Châtelet P., Forget P.-M., van der Meer P., Norden N., Riéra B., Charles-Dominique P., 2008. Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology*, 24: 355–366.

Chave J., Réjou-Méchain M., Búrquez A., Chidumayo E., Colgan M.S., Delitti W.B.C., Duque A., Eid T., Fearnside P.M., Goodman R.C., Henry M., Martínez-Yrízar A., Mugasha W.A., Muller-Landau H.C., Mencuccini M., Nelson B.W., Ngomanda A., Nogueira E.M., Ortiz-Malavassi E., Pélissier R., Ploton P., Ryan C.M., Saldarriaga J.G., Vieilledent G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20: 3177–3190.

Chuyong G.B., Condit R., Kenfack D., Losos E.C., Moses S.N., Songwe N.C., Thomas D.W., 2004. Korup Forest Dynamics Plot, Cameroon, *In*: *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. pp. 505–516.

Chuyong G.B., Kenfack D., Condit R., Comita L.S., 2011. Habitat specificity and diversity of tree species in an African wet tropical forest. *Plant Ecology*, 212: 1363–1374.

Clark D.B., Palmer M.W., Clark D. a., 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology*, 80: 2662–2675.

Condit R., Ashton P., Balslev H., Brokaw N., Bunyavejchewin S., Chuyong G., Co L., Dattaraja H.S., Davies S., Esufali S., Ewango C.E.N., Foster R., Gunatilleke N., Gunatilleke S., Hernandez C., Hubbell S., John R., Kenfack D., Kiratiprayoon S., Hall P., Hart T., Itoh A., LaFrankie J. V, Liengola I., Lagunzad D., De Lao S.L., Losos E., Magard E., Makana J.-R., Manokaran N., Navarrete H., Nur S.M., Okhubo T., Perez R., Samper C., Seng L.H., Sukumar R., Svenning J.-C., Tan S., Thomas D., Thompson J., Vallejo M.I., Munoz G.V., Valencia R., Yamakura T., Zimmerman J.K., 2005. Tropical tree a-diversity: Results from a worldwide network of large plots. *Biologiske Skrifter*, 55: 565–582.

Condit R., Engelbrecht B.M.J., Pino D., Perez R., Turner B.L., 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, 110: 5064–5068.

Condit R., Pitman N.C.A., Egbert L.J., Chave J., Terborgh J., Foster R.B., Nunez P., Aguilar S., Valencia R., Villa G., Muller-landau H.C., Hubbell, Villa G., Muller-landau H.C., Losos E., 2002. Beta-Diversity in Tropical Forest Trees. *Science*, 295: 1066854.

Coomes D.A., Allen R.B., 2007. Effects of size, competition and altitude on tree growth. *Journal of Ecology*, 95: 1084–1097.

Cornelissen J., Lavorel S., Garnier E., Diaz S., Buchmann N.D., Gurvich D.E., Reich P.B., ter Steege H., Morgan H.D.G., Van Der Heijden M.G.A., Pausas J.G., Poorter H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51: 335–380.

Cornwell W.K., Ackerly D.D., 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79: 109–126.

Couteron P., Pélissier R., 2004. Additive apportioning of species diversity: towards more sophisticated models and analyses. *Oikos*, 107: 215–221.

Couteron P., Pélissier R., Mapaga D., Molino J.F., Teillier L., 2003. Drawing ecological insights from a management-oriented forest inventory in French Guiana. *Forest Ecology and Management*, 172: 89–108.

Dallmmeier F., Kabel M., Mayne C.J., Rice R., Taylor M.C., 1992. *Long-term monitoring of biological diversity in tropical forest areas: methods for establishment and inventory of permanent plots*. MAB Digest 11. UNESCO, Paris, pp. 92.

Day P.R., 1953. Experimental confirmation of hydrometer theory. *Soil Science*, 75: 181–186.

de Bello F., Lavorel S., Albert C.H., Thuiller W., Grigulis K., Dolezal J., Janeček Š., Lepš J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution*, 2: 163–174.

de Wasseige C., Flynn J., Louppe D., Hiol F., Mayaux., 2014. *The Forests of the Congo Basin - State of the Forest 2013*, Publications Office of the European Union. Luxembourg, pp. 328.

De Wit M.J., Linol B., 2015. Precambrian basement of the Congo Basin and its flanking terrains, *In*: *Geology and Resource Potential of the Congo Basin*. pp. 19–37.

Deblauwe V., Droissart V., Bose R., Sonké B., Blach-Overgaard A., Svenning J.C., Wieringa J.J., Ramesh B.R., Stévart T., Couvreur T.L.P., 2016. Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. *Global Ecology and Biogeography*, 25: 443–454.

Dexter K.G., Smart B., Baldauf C., Baker T.R., Balinga M.P.B., Brienen R.J.W., Fauset S., Feldpausch T.R., Silva L.F.-D., Muledi J.I., Lewis S.L., Lopez-Gonzalez G., Marimon-Junior B.H., Marimon B.S., Meerts P., Page N., Parthasarathy N., Phillips O.L., Sunderland T.C.H., Theilade I., Weintritt J., Affum-Baffoe K., Araujo A., Arroyo L., Begne S.K., Neves E.C.-D., Collins M., Cuni-Sanchez A., Djuikouo M.N.K., Elias F., Foli E.G., Jeffery K.J., Killeen T.J., Malhi Y., Maracahipes L., Mendoza C., Monteagudo-Mendoza A., Morandi P., Santos C.O.-D., Parada A.G., Pardo G., Peh K.S.-H., Salomão R.P., Silveira M., Sinatora–Miranda H., Slik J.W.F., Sonke B., Taedoumg H.E., Toledo M., Umetsu R.K., Villaroel R.G., Vos V.A., White L.J.T., Pennington R.T., 2015. Floristics and biogeography of vegetation in seasonally dry tropical regions. *International Forestry Review*, 17: 10–32.

Dezfuli A., 2017. Climate of Western and Central Equatorial Africa. *[online]*, 1: 1–46.

Díaz S., Cabido M., 1997. Plant functional types and ecosystem function in relation to global change. *Journal of vegetation science*, 8: 463–474.

Diaz S., Cabido M., Casanoves F., 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, 9: 113–122.

Dilts T.E., 2015. Topography Tools for ArcGIS 10.1. University of Nevada Reno. Available at: http://www.arcgis.com/home/item.html?id=b13b3b40fa3c43d4a23a1a09c5fe96b9.

Djuikouo M.N.K., Doucet J.-L., Nguembou C.K., Lewis S.L., Sonké B., 2010. Diversity and above ground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. *African Journal of Ecology*, 48: 1053–1063.

Dray S., Dufour A.B., 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*, 22: 1–20.

Dray S., Pélissier R., Couteron P., Fortin M.J., Legendre P., Peres-Neto P.R., Bellier E., Bivand R., Blanchet F.G., De Cáceres M., Dufour a. B., Heegaard E., Jombart T., Munoz F., Oksanen J., Thioulouse J., Wagner H.H., 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs,* 82: 257–275.

Duivenvoorden J.F., Svenning J., Wright S.J., 2002. Beta Diversity in Tropical Forests. *Science*, 295: 636–637.

Dunn O.J., 1961. Multiple Comparisons among Means. *Journal of the American Statistical Association*, 56: 52–64.

Dwass M., 1957. Modified Randomization Tests for Nonparametric Hypotheses. *The Annals of Mathematical Statistics*, 28: 181–187.

Efron B., Stein C., 1981. The Jackknife Estimate of Variance. *The Annals of Statistics*, 9: 586–596.

Ehrlen J., Eriksson O., 2000. Dispersal limitation and patch occumpancy in forest herbs. *Ecology*, 81: 1667–1674.

Elton C., 1927. *Animal Ecology,* Animal Ecology, pp. 207.

Ewango C.E.N., Kenfack D., Sainge M.N., Thomas D.W., van der Burgt X.M., 2016. Gambeya korupensis (Sapotaceae: Chrysophylloideae), a new rain forest tree species from the Southwest Region in Cameroon. *Kew Bulletin*, 71: 28.

Farr T., Rosen P., Caro E., Crippen R., Duren R., Hensley S., Kobrick M., Paller M., Rodriguez E., Roth L., Seal D., Shaffer S., Shimada J., Umland J., Werner M., Oskin M., Burbank D., Alsdorf D., 2007. The shuttle radar topography mission. *Reviews of Geophysics*, 45: 1–33.

Fayolle A., Doucet J.L., Gillet J.F., Bourland N., Lejeune P., 2013. Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. *Forest Ecology and Management,* 305: 29–37.

Fayolle A., Engelbrecht B., Freycon V., Mortier F., Swaine M., Réjou-Méchain M., Doucet J.L., Fauvet N., Cornu G., Gourlet-Fleury S., 2012. Geological substrates shape tree species and trait distributions in African moist forests. *Plos One,* 7: 12–14.

Fayolle A., Loubota Panzou G.J., Drouet T., Swaine M.D., Bauwens S., Vleminckx J., Biwole A., Lejeune P., Doucet J.-L., 2016. Taller trees, denser stands and greater biomass in semi-deciduous than in evergreen lowland central African forests. *Forest Ecology and Management*, 374: 42–50.

Fayolle A., Swaine M.D., Bastin J.-F., Bourland N., Comiskey J. a., Dauby G., Doucet J.-L., Gillet J.-F., Gourlet-Fleury S., Hardy O.J., Kirunda B., Kouamé F.N., Plumptre A.J., 2014. Patterns of tree species composition across tropical African forests. *Journal of Biogeography*, 41: 2320–2331.

Feldpausch T.R., Banin L., Phillips O.L., Baker T.R., Lewis S.L., Quesada C.A., Affum-Baffoe K., Arets E.J.M.M., Berry N.J., Bird M., Brondizio E.S., de Camargo P., Chave J., Djagbletey G., Domingues T.F., Drescher M., Fearnside P.M., França M.B., Fyllas N.M., Lopez-Gonzalez G., Hladik A., Higuchi N., Hunter M.O., Iida Y., Salim K., Kassim R., Keller M., Kemp J., King D., Lovett J.C., Marimon B.S., Marimon-Junior B.H., Lenza E., Marshall R., Metcalfe D.J., Mitchard E.T., Moran E.F., Nelson B.W., Nilus R., Nogueira E.M., Palace M., Patiño S., Peh K.S.-H., Raventos M.T., Reitsma J.M., Saiz G., Schrodt F., Sonké B., Taedoumg H.E., Tan S., White L., Wöll H., Lloyd J., 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences,* 8: 1081–1106.

Feldpausch T.R., Lloyd J., Lewis S.L., Brienen R.J.W., Gloor M., Monteagudo Mendoza A., Lopez-Gonzalez G., Banin L., Abu Salim K., Affum-Baffoe K., Alexiades M., Almeida S., Amaral I., Andrade A., Aragão L.E.O.C., Araujo Murakami A., Arets E.J.M., Arroyo L., Aymard C. G.A., Baker T.R., Bánki O.S., Berry N.J., Cardozo N., Chave J., Comiskey J.A., Alvarez E., De Oliveira A., Di Fiore A., Djagbletey G., Domingues T.F., Erwin T.L., Fearnside P.M., França M.B., Freitas M.A., Higuchi N., Honorio C. E., Iida Y., Jiménez E., Kassim A.R., Killeen T.J., Laurance W.F., Lovett J.C., Malhi Y., Marimon B.S., Marimon-Junior B.H., Lenza E., Marshall A.R., Mendoza C., Metcalfe D.J., Mitchard E.T.A., Neill D.A., Nelson B.W., Nilus R., Nogueira E.M., Parada A., S.-H. Peh K., Pena Cruz A., Peñuela M.C., Pitman N.C.A., Prieto A., Quesada C.A., Ramírez F., Ramírez-Angulo H., Reitsma J.M., Rudas A., Saiz G., Salomão R.P., Schwarz M., Silva N., Silva-Espejo J.E., Silveira M., Sonké B., Stropp J., Taedoumg H.E., Tan S., Ter Steege H., Terborgh J., Torello-Raventos M., Van Der Heijden G.M.F., Vásquez R., Vilanova E., Vos V.A., White L., Willcock S., Woell H., Phillips O.L., 2012. Tree height integrated into pantropical forest biomass estimates. *Biogeosciences,* 9: 3381–3403.

Gartlan J.S., Newbery D.M., Thomas D.W., Waterman P.G., 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroun. *Vegetatio,* 65: 131–148.

Gaston K.J., 1996. The multiple forms of the interspecific abundance-distribution relationship. *Oikos*, 76: 211–220.

Gaston K.J., Blackburn T.M., Greenwood J.J.D., Gregory R.D., Quinn R.M., Lawton J.H., 2000. Abundance-occupancy relationships. *Journal of Applied Ecology*, 37: 39–59.

Gauch H.G., 1982. *Multivariate analysis in community ecology*, Cambridge Studies in Ecology, pp. 307.

Geisser S., 1993. Predictive Inference. *Philosophy of Science*, 24: 180.

Gentry A.H., 1992. Tropical Forest Biodiversity: Distributional Patterns and Their Conservational Significance. *Oikos*, 63: 19.

Gond V., Fayolle A., Pennec A., Cornu G., Mayaux P., Camberlin P., Doumenge C., Fauvet N., Gourlet-Fleury S., 2013. Vegetation structure and greenness in Central Africa from Modis multi-temporal data. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368: 20120309.

Gonmadje C., 2012. Analyse phytogéographique des forêts d'Afrique Centrale: le cas du massif de Ngovayang (Cameroun). *Plant Ecology and Evolution*, 145: 152–164.

Gourlet-Fleury S., Rossi V., Rejou-Mechain M., Freycon V., Fayolle A., Saint-Andre L., Cornu G., Gerard J., Sarrailh J.M., Flores O., Baya F., Billand A., Fauvet N., Gally M., Henry M., Hubert D., Pasquier A., Picard N., 2011. Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. *Journal of Ecology,* 99: 981–990.

Gravel D., Canham C.D., Beaudet M., Messier C., 2006. Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters*, 9: 399–409.

Grime P.J., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Evolutionary Theory*, 3: 1169–1194.

Grinnell J., 1917. The Niche-Relationships of the California Thrasher. *American Ornithologists' Union*, 34: 427–433.

Guitet S., Freycon V., Brunaux O., Pélissier R., Sabatier D., Couteron P., 2016. Geomorphic control of rain-forest floristic composition in French Guiana: more than a soil filtering effect? *Journal of Tropical Ecology*, 32: 22–40.

Guitet S., Pélissier R., Brunaux O., Jaouen G., Sabatier D., 2015. Geomorphological landscape features explain floristic patterns in French Guiana rainforest. *Biodiversity and Conservation*, 24: 1215–1237.

Hardy O., Sonké B., 2004. Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation. *Forest ecology and management*, 197: 191–202.

Hart T., Hart J., Murphy P., 1989. Monodominant and Species-Rich Forests of the Humid Tropics: Causes for Their Co-Occurrence. *American Naturalist*, 133: 613–633.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965–1978.

HilleRisLambers J., Adler P.B., Harpole W.S., Levine J.M., Mayfield M.M., 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics*, 43: 227–248.

Holdaway R.J., McNeill S.J., Mason N.W.H., Carswell F.E., 2014. Propagating Uncertainty in Plot-based Estimates of Forest Carbon Stock and Carbon Stock Change. *Ecosystems*, 17: 627–640.

Hubbell S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press, Princeton, NJ. Princeton University Press, Princeton, pp. 375.

Hulshof C.M., Violle C., Spasojevic M.J., Mcgill B., Damschen E., Harrison S., Enquist B.J., 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science*, 24: 921–931.

Hunter M.O., Keller M., Victoria D., Morton D.C., 2013. Tree height and tropical forest biomass estimation. *Biogeosciences*, 10: 8385–8399.

Hutchinson G.E., 1957. Population studies – animal ecology and demography – concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22: 415–427.

Jager M.M., Richardson S.J., Bellingham P.J., Clearwater M.J., Laughlin D.C., 2015. Soil fertility induces coordinated responses of multiple independent functional traits. *Journal of Ecology*, 103: 374–385.

Jiang Z., Ma K., 2015. Environmental filtering drives herb community composition and functional trait changes across an elevational gradient. *Plant Ecology and Evolution*, 148: 301–310.

John M.K., 1970. Colorimetric determination of phosphorus in soil and plant materials with ascorbic acid. *Soil Science*, 109: 214–220.

John R., Dalling J.W., Harms K.E., Yavitt J.B., Stallard R.F., Mirabello M., Hubbell S.P., Valencia R., Navarrete H., Vallejo M., Foster R.B., 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 104: 864–9.

Jung V., Albert C.H., Violle C., Kunstler G., Loucougaray G., Spiegelberger T., 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, 102: 45–53.

Jung V., Violle C., Mondy C., Hoffmann L., Muller S., 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology*, 98: 1134–1140.

Karger D.N., Conrad O., Böhner J., Kawohl T., Kreft H., Soria-Auza R.W., Zimmermann N.E., Linder H.P., Kessler M., 2017. Climatologies at high resolution for the earth’s land surface areas. *Scientific Data*, 4: 170122.

Kearsley E., de Haulleville T., Hufkens K., Kidimbu A., Toirambe B., Baert G., Huygens D., Kebede Y., Defourny P., Bogaert J., Beeckman H., Steppe K., Boeckx P., Verbeeck H., 2013. Conventional tree height-diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. *Nature communications*, 4: 86–94.

Kearsley E., Hufkens K., Doetterl S., Lisingo J., Bosela F.B., Boeckx P., Beeckman H., Verbeeck H., 2017. Model performance of tree height-diameter relationships in central Congo Basin. *Annals of Forest Science*, 74: 1–13.

Keddy P.A., 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3: 157–164.

Kenfack D., Gereau R.E., Thomas D.W., Sainge M.N., 2015. The Tropical African Genus *Crotonogynopsis* (Euphorbiaceae), with Two New Species. *Novon: A Journal for Botanical Nomenclature*, 24: 246–255.

Kenfack D., Thomas D.W., Chuyong G., Condit R., 2007. Rarity and abundance in a diverse African forest. *Biodiversity and Conservation*, 16: 2045–2074.

King D.A., 1990. The Adaptive Significance of Tree Height. *The American naturalist*, 135: 809–828.

Köppen W., 1900. Versuch einer Klassifikation der Klimate, vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. *Geographische Zeitschrift*,. 11: 593–611

Kraft N.J.B., Ackerly D.D., 2014. Assembly of Plant Communities, *In*: *Ecology and the Environment*. Springer New York, pp. 67–88.

Kraft N.J.B., Comita L.S., Chase J.M., Sanders N.J., Swenson N.G., Crist T.O., Stegen J.C., Vellend M., Boyle B., Anderson M.J., Cornell H. V, Davies K.F., Freestone A.L., Inouye B.D., Harrison S.P., Myers J.A., Hillebrand H., Rahbek C., Ricklefs R.E., Dyer L.A., Schemske D.W., Mittelbach G.G., Cornell H. V., Sobel J.M., Roy K., Ricklefs R.E., Cornell H. V., Karlson R.H., Hughes T.P., Qian H., Ricklefs R.E., Soininen J., Lennon J.J., Hillebrand H., Dahl C., Novotny V., Moravec J., Richards S.J., Rodríguez P., Arita H.T., Gentry A.H., Anderson M.J., Whittaker R.H., Tuomisto H., Kraft N.J.B., Valencia R., Ackerly D.D., Canham C.D., LePage P.T., Coates K.D., Comita L.S., Muller-Landau H.C., Aguilar S., Hubbell S.P., Currie D.J., Caley M.J., Schluter D., Koleff P., Gaston K.J., Lennon J.J., Jost L., Ricotta C., Crist T.O., Veech J.A., Crist T.O., Veech J.A., Gering J.C., Summerville K.S., Condit R., Svenning J.C., Valencia R., Chase J.M., RisLambers J.H., Clark J.S., Beckage B., Kraft N.J.B., Ackerly D.D., Wills C., 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, 333: 1755–8.

Krishnadas M., Kumar A., Comita L.S., 2016. Environmental gradients structure tropical tree assemblages at the regional scale. *Journal of Vegetation Science*, 27: 1117–1128.

Laliberté A.E., Legendre P., Shipley B., Laliberté M.E., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. *R package*, 0–12.

Lavorel S., Garnier E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits : revisiting the Holy Grail. *Funcitional Ecology*, 16: 545–556.

Lavorel S., Grigulis K., McIntyre S., Williams N.S.G., Garden D., Dorrough J., Berman S., Quétier F., Thébault A., Bonis A., 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology*, 22: 134–147.

Lê S., Josse J., Husson F., 2008. FactoMineR : An R package for multivariate analysis. *Journal of Statistical Software*, 25: 1–18.

Leal M.E., 2004. The African rain forest during the Last Glacial Maximum, an archipelago of forests in a sea of grass, pp. 110.

Lebrun J., Gilbert G., 1954. *Une classification écologique des forêts du Congo*. Institut national pour l'étude agronomique du Congo Belge, pp. 89.

Legendre P., Borcard D., Couteron P., Peres-Neto P.R., Tuomisto H., Ruokolainen K., Pelissier R., Dray S., Laliberté E., 2005. The discussion "Analyzing beta diversity" contains the following papers: *Ecological Monographs*, 75: 435–450.

Legendre P., Legendre L., 1998. *Numerical ecology*, Numerical Ecology Second English Edition.

Leibold M.A., McPeek M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87: 1399–1410.

Leonard J., 1965. Contribution à la subdivision phytogéographique de la région guinéo-congolaise d'après la répartition géographique d'Euphorbiacées d'Afrique tropicale. Laboratoire de botanique systématique.

Lepš J., de Bello F., Šmilauer P., Doležal J., 2011. Community trait response to environment: Disentangling species turnover vs intraspecific trait variability effects. *Ecography*, 34: 856–863.

Letouzey R., 1968. *Etude phytogéographique du Cameroun*, Paul Cheva. ed. Paris, pp. 511.

Letouzey R., 1985. *Notice de la carte phytogéographique du Cameroun au 1:500.000*, 1st–5th ed. Institut de la carte Internationale de la Végétation, Toulouse, France, pp. 95-142.

Lewis S.L., Sonke B., Sunderland T., Begne S.K., Lopez-Gonzalez G., van der Heijden G.M.F., Phillips O.L., Affum-Baffoe K., Baker T.R., Banin L., Bastin J.-F., Beeckman H., Boeckx P., Bogaert J., De Canniere C., Chezeaux E., Clark C.J., Collins M., Djagbletey G., Djuikouo

M.N.K., Droissart V., Doucet J.-L., Ewango C.E.N., Fauset S., Feldpausch T.R., Foli E.G., Gillet J.-F., Hamilton A.C., Harris D.J., Hart T.B., de Haulleville T., Hladik A., Hufkens K., Huygens D., Jeanmart P., Jeffery K.J., Kearsley E., Leal M.E., Lloyd J., Lovett J.C., Makana J.-R., Malhi Y., Marshall A.R., Ojo L., Peh K.S.-H., Pickavance G., Poulsen J.R., Reitsma J.M., Sheil D., Simo M., Steppe K., Taedoumg H.E., Talbot J., Taplin J.R.D., Taylor D., Thomas S.C., Toirambe B., Verbeeck H., Vleminckx J., White L.J.T., Willcock S., Woell H., Zemagho L., 2013. Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368: 20120295.

Libalah M.B., 2017. Manuel pour l'installation des parcelles permanentes dans la forêt tropical humide. Yaounde, pp. 13.

Libalah M.B., Fongod A.G.N., Veranso M.C., Kenfack D., 2014. Field and morphometric studies of Phyllobotryon Müell.Arg. (Salicaceae) in the Korup Forest Area of Cameroon. *Adansonia*, 36: 303–313.

Linder H.P., de Klerk H.M., Born J., Burgess N.D., Fjeldså J., Rahbek C., 2012. The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, 39: 1189–1205.

Linder P.H., Lovett J., Mutke J.M., Barthlott W., Jürgens N., Rebelo T., Küper Linder W., Mutke J., Küper W., 2005. A numerical re-evaluation of the sub-Saharan phytochoria of mainland Africa. *Biologiske Skrifter,* 55: 229–252.

Losos E.C., Leigh E.G., 2004. *Tropical forest diversity and dynamism : findings from a large-scale plot network*. University of Chicago Press, pp. 645.

Losos J.B., Miles D.B., 1994. Adaptation, Constraint, and the Comparative Method: Phylogenetic Issues and Methods. *Ecological morphology integrative organismal biology*, , pp. 60:98.

Lutz J.A., 2015. The Evolution of Long-Term Data for Forestry: Large Temperate Research Plots in an Era of Global Change. *Northwest Science*, 89: 255–269.

Macarthur R., Levins R., 1967. The limiting similarity, convegence and divergence of coexisting species. *The American Naturalist*, 101: 377–385.

MacArthur R.H., 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America,* 43: 293–295.

MacArthur R.H., Wilson E.O., 1967. *The theory of island biogeography*, Monographs in Population Biology.

Mäkelä A., Valentine H.T., 2006. Crown ratio influences allometric scaling in trees. *Ecology*, 87: 2967–2972.

Maley J., 1998. La Forêt Dense Humide Africaine : principales caractéristiques des changements de végétation et de climat du Crétacé supérieur au Quaternaire, *In*: Watline, R., Swaine, M. D., Alexander, I. J. (eds.): *West African Forests : Studies in the Guineo-Congolian Domain*. The Royal Society of Edinburg, pp. 1–29.

Maley J., 2001. La destruction catastrophique des forêts d'Afrique centrale survenue il y a environ 2500 ans exerce encore une influence majeure sur la répartition actuelle des formations végétales. *Systematics and Geography of Plants*, 71: 777–796.

Malhi Y., Adu-bredu S., Asare R.A., Lewis S.L., Mayaux P., 2013. African rainforests : past, present and future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368: 20120312.

Mascaro J., Litton C.M., Hughes R.F., Uowolo A., Schnitzer S.A., 2011. Minimizing Bias in Biomass Allometry: Model Selection and Log-Transformation of Data. *Biotropica*, 43: 649–653.

Mayaux P., Pekel J.-F., Desclee B., Donnay F., Lupi A., Achard F., Clerici M., Bodart C., Brink A., Nasi R., Belward A., 2013. State and evolution of the African rainforests between 1990 and 2010. *Philosophical Transactions of the Royal Society B*, 368: 20120300–20120300.

Mayaux P., Richards T., Janodet E., 1999. A vegetation map of Central Africa derived from satellite imagery. *Journal of Biogeography*, 26: 353–366.

McGill B.J., Enquist B.J., Weiher E., Westoby M., 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21: 178–185.

McMahon T., 1973. Size and shape in biology: elastic criteria impose limits on biological proportions, and consequently on metabolic rates. *Science*, 179: 1201–1204.

McPeek M.A., 2017. *Evolutionary community ecology*. Princeton University Press, Princeton, pp. 313.

Mehtatalo L., 2017. lmfor: Functions for Forest Biometrics [WWW Document]. *CRAN - An R software for statistical analysis*,. URL https://cran.r-project.org/web/packages/lmfor/index.html (accessed 7.22.17).

Milesi J.P., Toteu S.F., Deschamps Y., Feybesse J.L., Lerouge C., Cocherie A., Penaye J., Tchameni R., Moloto-A-Kenguemba G., Kampunzu H.A.B., Nicol N., Duguey E., Leistel J.M., Saint-Martin M., Ralay F., Heinry C., Bouchot V., Doumnang Mbaigane J.C., Kanda Kula V., Chene F., Monthel J., Boutin P., Cailteux J., 2006. An overview of the geology and major ore deposits of Central Africa: Explanatory note for the 1:4,000,000 map "Geology and major ore deposits of Central Africa." *Journal of African Earth Sciences*, 44: 571–595.

Moles A., Ackerly D., Tweddle J., Dickie J., Smith R., Leishman M., Mayfield M., Pitman A., Wood J., Westoby M., 2007. Global patterns in seed size. *Global Ecology and Biogeography*, 16: 109–116.

Moles A.T., Perkins S.E., Laffan S.W., Flores-Moreno H., Awasthy M., Tindall M.L., Sack L., Pitman A., Kattge J., Aarssen L.W., Anand M., Bahn M., Blonder B., Cavender-Bares J., Cornelissen J.H.C., Cornwell W.K., Díaz S., Dickie J.B., Freschet G.T., Griffiths J.G., Gutierrez A.G., Hemmings F.A., Hickler T., Hitchcock T.D., Keighery M., Kleyer M., Kurokawa H., Leishman M.R., Liu K., Niinemets Ü., Onipchenko V., Onoda Y., Penuelas J., Pillar V.D., Reich P.B., Shiodera S., Siefert A., Sosinski E.E., Soudzilovskaia N.A., Swaine E.K., Swenson N.G., van Bodegom P.M., Warman L., Weiher E., Wright I.J., Zhang H., Zobel M., Bonser S.P., 2014. Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, 25: 1167–1180.

Moles A.T., Warton D.I., Warman L., Swenson N.G., Laffan S.W., Zanne A.E., Pitman A., Hemmings F.A., Leishman M.R., 2009. Global patterns in plant height. *Journal of Ecology*, 97: 923–932.

Molto Q., Hérault B., Boreux J.J., Daullet M., Rousteau A., Rossi V., 2014. Predicting tree heights for biomass estimates in tropical forests -A test from French Guiana. *Biogeosciences*, 11: 3121–3130.

Molto Q., Rossi V., Blanc L., 2013. Error propagation in biomass estimation in tropical forests. *Methods in Ecology and Evolution*, 4: 175–183.

Mouchet M.A., Villéger S., Mason N.W.H., Mouillot D., 2010. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24: 867–876.

Muller-Landau H.C., Condit R.S., Chave J., Thomas S.C., Bohlman S.A., Bunyavejchewin S., Davies S., Foster R., Gunatilleke S., Gunatilleke N., Harms K.E., Hart T., Hubbell S.P., Itoh A., Kassim A.R., LaFrankie J. V., Lee H.S., Losos E., Makana J.R., Ohkubo T., Sukumar R., Sun I.F., Nur Supardi M.N., Tan S., Thompson J., Valencia R., Muñoz G.V., Wills C., Yamakura T., Chuyong G., Dattaraja H.S., Esufali S., Hall P., Hernandez C., Kenfack D., Kiratiprayoon S., Suresh H.S., Thomas D., Vallejo M.I., Ashton P., 2006a. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters*, 9: 575–588.

Muller-Landau H.C., Condit R.S., Harms K.E., Marks C.O., Thomas S.C., Bunyavejchewin S., Chuyong G., Co L., Davies S., Foster R., Gunatilleke S., Gunatilleke N., Hart T., Hubbell S.P., Itoh A., Kassim A.R., Kenfack D., LaFrankie J. V., Lagunzad D., Lee H.S., Losos E., Makana J.R., Ohkubo T., Samper C., Sukumar R., Sun I.F., Nur Supardi M.N., Tan S., Thomas D., Thompson J., Valencia R., Vallejo M.I., Muñoz G.V., Yamakura T., Zimmerman J.K., Dattaraja H.S., Esufali S., Hall P., He F., Hernandez C., Kiratiprayoon S., Suresh H.S., Wills C., Ashton P., 2006b. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecology Letters*, 9: 589–602.

Munoz F., Couteron P., Ramesh B.R., 2008. Beta diversity in spatially implicit neutral models: a new way to assess species migration. *The American naturalist*, 172: 116–127.

Munoz F., Couteron P., Ramesh B.R., Etienne R.S., 2007. Estimating parameters of neutral communities: From one single large to several small samples. *Ecology*, 88: 2482–2488.

Murphy J., Riley J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, 27: 31–36.

Nascimento H.E.M., Laurance W.F., 2002. Total aboveground biomass in central Amazonian rainforests: A landscape-scale study. *Forest Ecology and Management*, 168: 311–321.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H., 2012. vegan: Community Ecology Package. *R package version* R package version 2.0-4

Ordoñez J.C., van Bodegom P.M., Witte J.-P.M., Wright I.J., Reich P.B., Aerts R., 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, 18: 137–149.

Oslisly R., White L., Bentaleb I., Favier C., Fontugne M., Gillet J.-F., Sebag D., 2013. Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 368: 20120304.

Parmentier I., Malhi Y., Senterre B., Whittaker R.J., Alonso A., Balinga M.P.B., Bakayoko A., Bongers F., Chatelain C., Comiskey J. a., Cortay R., Kamdem M.-N.D., Doucet J.-L., Gautier

L., Hawthorne W.D., Issembe Y. a., Kouamé F.N., Kouka L. a., Leal M.E., Lejoly J., Lewis S.L., Nusbaumer L., Parren M.P.E., Peh K.S.-H., Phillips O.L., Sheil D., Sonké B., Sosef M.S.M., Sunderland T.C.H., Stropp J., Ter Steege H., Swaine M.D., Tchouto M.G.P., Gemerden B.S. Van, Van Valkenburg J.L.C.H., Wöll H., 2007. The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology*, 95: 1058–1071.

Pélissier R., 2013. diversity.R: Diversity analysis (v.1.5-13). R package version 1.5-13.

Pélissier R., Couteron P., Dray S., Sabatier D., 2003. Consistency between ordination techniques and diversity measurements: Two strategies for species occurrence data. *Ecology*, 84: 242–251.

Pélissier R., Dray S., Sabatier D., 2001. Within-plot relationships between tree species occurrences and hydrological soil constraints: an example in French Guiana investigated\rthrough canonical correlation analysis. *Plant Ecology*, 162: 143–156.

Pescador D.S., de Bello F., Valladares F., Escudero A., 2015. Plant Trait variation along an Altitudinal Gradient in Mediterranean High Mountain Grasslands: Controlling the Species Turnover Effect. *PloS ONE*, 10: e0118876.

Petter G., Wagner K., Wanek W., Sánchez Delgado E.J., Zotz G., Cabral J.S., Kreft H., 2015. Functional leaf traits of vascular epiphytes:vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. *Functional Ecology*, 30: 188–198.

Phillips O.L., Vasquez Marti-nez R., Nunez Vargas P., Monteagudo A.L., Chuspe Zans M., Galiano Sanchez W., Pena Cruz A., Timana M., Yli-Halla M., Rose S., 2003. Efficient plot-based floristic assessment of tropical forests. *Journal of Tropical Ecology*, 19: 629–645.

Picard N., 2007. Dispositifs permanents pour le suivi des forêts en Afrique Centrale : un état des lieux. Yaounde, pp. 38.

Picard N., Magnussen S., Ngok L., Namkosserena S., Yalibanda Y., 2010. Permanent sample plots for natural tropical forests : A rationale with special emphasis on Central Africa. *Environmental Monitoring and Assessment*, 164: *279-295*.

Pitman N.C.A., Silman M.R., Terborgh J.W., 2013. Oligarchies in Amazonian tree communities: A ten-year review. *Ecography*, 36: 114–123.

Pitman N.C.A., Terborgh J., Silman M.R., Nuñez V P., David A N., Carlos E C., Walter A P., Aulestia M., 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology*, 82: 2101–2117.

Pitman N.C., Terborgh J., Silman M.R., Nunez P. V., 1999. Tree Species Distributions in an Upper Amazonian Forest. *Ecology*, 80: 2651–2661.

Purves D.W., Turnbull L.A., 2010. Different but equal: The implausible assumption at the heart of neutral theory. *Journal of Animal Ecology*, 79: 1215–1225.

Pyke C.R., Condit R., Aguilar S., Lao S., 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, 12: 553–566.

Pyke G.H., 1999. Floristic composition across a climatic gradient in a neotropical forest.

University of California, Santa Barbara, pp. 84.

Ramesh B.R., Venugopal P.D., Pélissier R., Patil S. V., Swaminath M.H., Couteron P., 2010. Mesoscale patterns in the floristic composition of forests in the Central Western Ghats of Karnataka, India. *Biotropica*, 42: 435–443.

Reich P.B., 1995. Phenology of tropical forests: Patterns, causes, and consequences. *Canadian Journal of Botany*, 73: 164–174.

Reich P.B., 2014. The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102: 275–301.

Reich P.B., Ellsworth D.S., Walters M.B., Vose J.M., Gresham C., Volin J.C., Bowman W.D., 1999. Generality of leaf trair relationships: a test across six biomes. *Ecology*, 80: 1955–1969.

Reich P.B., Tjoelker M.G., Machado J.L., Oleksyn J., 2006. Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature*, 439: 457–461.

Réjou-Méchain M., Fayolle A., Nasi R., Gourlet-Fleury S., Doucet J.L., Gally M., Hubert D., Pasquier A., Billand A., 2011. Detecting large-scale diversity patterns in tropical trees: Can we trust commercial forest inventories? *Forest Ecology and Management*, 261: 187–194.

Réjou-Méchain M., Flores O., Pélissier R., Fayolle A., Fauvet N., Gourlet-Fleury S., 2014. Tropical tree assembly depends on the interactions between successional and soil filtering processes. *Global Ecology and Biogeography*, 23: 1440–1449.

Réjou-Méchain M., Pélissier R., Gourlet-Fleury S., Couteron P., Nasi R., Thompson J.D., 2008. Regional variation in tropical forest tree species composition in the Central African Republic: an assessment based on inventories by forest companies. *Journal of Tropical Ecology*, 24: 663–674.

Réjou-méchain M., Tanguy A., Piponiot C., Chave J., Hérault B., 2017. BIOMASS: an R Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical Forests. *Methods in Ecology and Evolution*, 8: 1163-1167.

Réjou-Méchain M., Tymen B., Blanc L., Fauset S., Feldpausch T.R., Monteagudo A., Phillips O.L., Richard H., Chave J., 2015. Using repeated small-footprint LiDAR acquisitions to infer spatial and temporal variations of a high-biomass Neotropical forest. *Remote Sensing of Environment*, 169: 93–101.

Rennó C.D., Nobre A.D., Cuartas L.A., Soares J.V., Hodnett M.G., Tomasella J., Waterloo M.J., 2008. HAND, a new terrain descriptor using SRTM-DEM: Mapping terra-firme rainforest environments in Amazonia. *Remote Sensing of Environment*, 112: 3469–3481.

Ricklefs R.E., 1987. Community diversity relative roles of local and regional processes. *Science*, 235: 167–171.

Ricklefs R.E., Ricklefs R.E., 2003. Genetics, evolution, and ecological communities. *Ecology*, 84: 588–591.

Robbrecht E., 1996. Geography of African Rubiaceae with reference to glacial rain forest refuges, *In*: *The Biodiversity of African Plants*. Springer Netherlands, Dordrecht, pp. 564–581.

Ryan M.G., Phillips N., Bond B.J., 2006. The hydraulic limitation hypothesis revisited. *Plant, Cell* *and Environment*, 29: 367–381.

Ryan M.G., Yoder B.J., 1997. Hydraulic limits to tree height and tree growth. *BioScience*, 47: 235–242.

Saatchi S., Marlier M., Chazdon R.L., Clark D.B., Russell A.E., 2011. Impact of spatial variability of tropical forest structure on radar estimation of aboveground biomass. *Remote Sensing of Environment*, 115: 2836–2849.

Schietti J., Emilio T., Rennó C.D., Drucker D.P., Costa F.R.C., Nogueira A., Baccaro F.B., Figueiredo F., Castilho C. V, Kinupp V., Guillaumet J.-L., Garcia A.R.M., Lima A.P., Magnusson W.E., 2013. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecology & Diversity*, 7: 1–13.

Schwilk D.W., Ackerly D.D., 2005. Limiting similarity and functional diversity along environmental gradients. *Ecology Letters*, 8: 272–281.

Shipley B., Lechowicz M.J., Wright I., Reich P.B., 2006. Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, 87: 535–541.

Siefert A., 2012. Incorporating intraspecific variation in tests of trait-based community assembly. *Oecologia*, 170: 767–75.

Siefert A., Violle C., Albert C.H., Taudiere A., Fajardo A., Aarssen L.W., Baraloto C., Carlucci M.B., Cianciaruso M. V, de L. Dantas V., de Bello F., Duarte L.D.S., Fonseca C.R., Freschet G.T., Gaucherand S., Gross N., Hikosaka K., Jackson B., Jung V., Kamiyama C., Katabuchi M., Kembel S.W., Kichenin E., Kraft N.J.B., Largerstrom A., Bagousse-Pinguet Y. Le, Li Y., Mason N., Messier J., Nakashizuka T., McC M Overton J., Peltzer D.A., Perez-Ramos I.M., Pillar V.D., Prentice H.C., Richardson S.J., Sasaki T., Schamp B.S., Schob C., Shipley B., Sundqvist M., Sykes M.T., Vandewalle M., Wardle D.A., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18: 1406–1419.

Slik J.W.F., Arroyo-Rodríguez V., Aiba S.-I., Alvarez-Loayza P., Alves L.F., Ashton P., Balvanera P., Bastian M.L., Bellingham P.J., van den Berg E., Bernacci L., da Conceição Bispo P., Blanc L., Böhning-Gaese K., Boeckx P., Bongers F., Boyle B., Bradford M., Brearley F.Q., Breuer-Ndoundou Hockemba M., Bunyavejchewin S., Calderado Leal Matos D., Castillo-Santiago M., Catharino E.L.M., Chai S.-L., Chen Y., Colwell R.K., Chazdon R.L., Robin C.L., Clark C., Clark D.B., Clark D.A., Culmsee H., Damas K., Dattaraja H.S., Dauby G., Davidar P., DeWalt S.J., Doucet J.-L., Duque A., Durigan G., Eichhorn K.A.O., Eisenlohr P. V., Eler E., Ewango C., Farwig N., Feeley K.J., Ferreira L., Field R., de Oliveira Filho A.T., Fletcher C., Forshed O., Franco G., Fredriksson G., Gillespie T., Gillet J.-F., Amarnath G., Griffith D.M., Grogan J., Gunatilleke N., Harris D., Harrison R., Hector A., Homeier J., Imai N., Itoh A., Jansen P.A., Joly C.A., de Jong B.H.J., Kartawinata K., Kearsley E., Kelly D.L., Kenfack D., Kessler M., Kitayama K., Kooyman R., Larney E., Laumonier Y., Laurance S., Laurance W.F., Lawes M.J., Amaral I.L. do, Letcher S.G., Lindsell J., Lu X., Mansor A., Marjokorpi A., Martin E.H., Meilby H., Melo F.P.L., Metcalfe D.J., Medjibe V.P., Metzger J.P., Millet J., Mohandass D., Montero J.C., de Morisson Valeriano M., Mugerwa B., Nagamasu H., Nilus R., Ochoa-Gaona S., Onrizal, Page N., Parolin P., Parren M., Parthasarathy N., Paudel E., Permana A., Piedade M.T.F., Pitman N.C.A., Poorter L., Poulsen A.D., Poulsen J., Powers J., Prasad R.C., Puyravaud J.-P., Razafimahaimodison J.-C., Reitsma J., Dos Santos J.R., Roberto Spironello W., Romero-Saltos H., Rovero F., Rozak A.H., Ruokolainen K., Rutishauser E., Saiter F., Saner P., Santos

B.A., Santos F., Sarker S.K., Satdichanh M., Schmitt C.B., Schöngart J., Schulze M., Suganuma M.S., Sheil D., da Silva Pinheiro E., Sist P., Stevart T., Sukumar R., Sun I.-F., Sunderland T., Sunderand T., Suresh H.S., Suzuki E., Tabarelli M., Tang J., Targhetta N., Theilade I., Thomas D.W., Tchouto P., Hurtado J., Valencia R., van Valkenburg J.L.C.H., Van Do T., Vasquez R., Verbeeck H., Adekunle V., Vieira S.A., Webb C.O., Whitfeld T., Wich S.A., Williams J., Wittmann F., Wöll H., Yang X., Adou Yao C.Y., Yap S.L., Yoneda T., Zahawi R.A., Zakaria R., Zang R., de Assis R.L., Garcia Luize B., Venticinque E.M., 2015. An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 112: 7472–7.

Sosef M.S.M., Dauby G., Blach-Overgaard A., van der Burgt X., Catarino L., Damen T., Deblauwe V., Dessein S., Dransfield J., Droissart V., Duarte M.C., Engledow H., Fadeur G., Figueira R., Gereau R.E., Hardy O.J., Harris D.J., de Heij J., Janssens S., Klomberg Y., Ley A.C., Mackinder B.A., Meerts P., van de Poel J.L., Sonké B., Stévart T., Stoffelen P., Svenning J.-C., Sepulchre P., Zaiss R., Wieringa J.J., Couvreur T.L.P., 2017. Exploring the floristic diversity of tropical Africa. *BMC Biology*, 15: 1–23.

Spasojevic M.J., Suding K.N., 2012. Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, 100: 652–661.

Spasojevic M.J., Yablon E.A., Oberle B., Myers J.A., 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere*, 5: art129.

Stegen J.C., Lin X., Konopka A.E., Fredrickson J.K., 2012. Stochastic and deterministic assembly processes in subsurface microbial communities. *The ISME Journal*, 6: 1653–1664.

Swaine M.D., 1996. Rainfall and soil fertility as factors forest limiting species distributions in Ghana. *Journal of Ecology*, 84: 419–428.

Taudiere A., Violle C., 2015. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. *Ecography*, 38: 1–10.

Ter Braak C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67: 1167-1179.

Ter Braak C.J.F., Prentice I.C., 1988. A Theory of Gradient Analysis. *Advances in Ecological Research*, 18: 271–317.

ter Steege H., Pitman N.C. a, Sabatier D., Baraloto C., Salomão R.P., Guevara J.E., Phillips O.L., Castilho C. V, Magnusson W.E., Molino J.-F., Monteagudo A., Núñez Vargas P., Montero J.C., Feldpausch T.R., Coronado E.N.H., Killeen T.J., Mostacedo B., Vasquez R., Assis R.L., Terborgh J., Wittmann F., Andrade A., Laurance W.F., Laurance S.G.W., Marimon B.S., Marimon B.-H., Guimarães Vieira I.C., Amaral I.L., Brienen R., Castellanos H., Cárdenas López D., Duivenvoorden J.F., Mogollón H.F., Matos F.D.D.A., Dávila N., García-Villacorta R., Stevenson Diaz P.R., Costa F., Emilio T., Levis C., Schietti J., Souza P., Alonso A., Dallmeier F., Montoya A.J.D., Fernandez Piedade M.T., Araujo-Murakami A., Arroyo L., Gribel R., Fine P.V. a, Peres C. a, Toledo M., Aymard C G. a, Baker T.R., Cerón C., Engel J., Henkel T.W., Maas P., Petronelli P., Stropp J., Zartman C.E., Daly D., Neill D., Silveira M., Paredes M.R., Chave J., Lima Filho D.D.A., Jørgensen P.M., Fuentes A., Schöngart J., Cornejo Valverde F., Di Fiore A., Jimenez E.M., Peñuela Mora M.C., Phillips J.F., Rivas G., van Andel T.R., von Hildebrand P., Hoffman B., Zent E.L., Malhi Y., Prieto A., Rudas A., Ruschell A.R., Silva N., Vos V., Zent S., Oliveira A. a, Schutz A.C., Gonzales T., Trindade Nascimento M., Ramirez-Angulo H., Sierra R., Tirado M., Umaña Medina M.N., van der

Heijden G., Vela C.I. a, Vilanova Torre E., Vriesendorp C., Wang O., Young K.R., Baider C., Balslev H., Ferreira C., Mesones I., Torres-Lezama A., Urrego Giraldo L.E., Zagt R., Alexiades M.N., Hernandez L., Huamantupa-Chuquimaco I., Milliken W., Palacios Cuenca W., Pauletto D., Valderrama Sandoval E., Valenzuela Gamarra L., Dexter K.G., Feeley K., Lopez-Gonzalez G., Silman M.R., 2013. Hyperdominance in the Amazonian tree flora. *Science*, 342: 1243092.

Thiers M.B., 2012. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium [WWW Document]. *New York Botanical Garden's Virtual Herbarium,*. URL http://sweetgum.nybg.org/science/ih/

Thomas D.W., Kenfack D., Chuyong G.B., Moses S.N., Losos E.C., Condit R.S., Songwe N.C., 2003. *Tree species of Southwestern Cameroon: Tree Distribution Maps, Diameter Tables, and Species Documentation of the 50-Hectare Korup Forest Dynamics Plot*. Center for Tropical Forest Science of the Smithsonian Tropical Research Institute and Bioresources Development and Conservation Programme - Cameroon, Washington, D.C, pp. 254.

Thuiller W., Lavorel S., Midgley G.F., Lavergne S., Rebe., 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 Leucadendron Taxa. *Ecology,* 85: 1688–1699.

Tilman D., 1980. Resources: a graphical-mechanistic approach to competition and predation. *The American Naturalist,* 116: 1–32.

Toledo M., Peña-Claros M., Bongers F., Alarcón A., Balcázar J., Chuviña J., Leaño C., Licona J.C., Poorter L., 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology,* 100: 253–263.

Toledo M., Poorter L., Peña-Claros M., Alarcón A., Balcázar J., Chuviña J., Leaño C., Licona J.C., Ter Steege H., Bongers F., 2011. Patterns and Determinants of Floristic Variation across Lowland Forests of Bolivia. *Biotropica*, 43: 405–413.

Tuomisto H., Poulsen A.D., Ruokolainen K., Moran C.R., Quintaana C., Celi J., Gustavo C., 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological applications*, 13: 352–371.

Tuomisto H., Ruokolainen K., Yli-Halla M., 2010. Dispersal, Environment, and Floristic Variation of Western Amazonian Forests. *Science*, 241: 241–4.

Van Wambeke., 1989. Tropical Soils and Soil Classification Updates, *In*: *Advances in Soil Science*. New York, pp. 171–12.

Vellend M., 2010. Conceptual synthesis in community ecology. *The Quarterly review of biology*, 85: 183–206.

Viennois G., Barbier N., Fabre I., Couteron P., 2013. Multiresolution quantification of deciduousness in West-Central African forests. *Biogeosciences,* 10: 6957–6967.

Violle C., Navas M.L., Vile D., Kazakou E., Fortunel C., Hummel I., Garnier E., 2007. Let the concept of trait be functional! *Oikos*, 116: 882–892.

Vleminckx J., Morin-Rivat J., Biwolé A.B., Daïnou K., Gillet J.-F., Doucet J., Drouet T., Hardy O.J., 2014. Soil Charcoal to Assess the Impacts of Past Human Disturbances on Tropical Forests. *Plos One,* 9: e108121.

Washington R., James R., Pearce H., Pokam W.M., Moufouma-Okia W., 2013. Congo Basin rainfall climatology: can we believe the climate models? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368: 20120296.

Webb C.T., Hoeting J. a, Ames G.M., Pyne M.I., LeRoy Poff N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters*, 13: 267–83.

Webb M.J., Reddell P., Hambleton A., Robson K., 2000. Growth response of four tropical plantation timber species to increasing phosphorus supply and assessment of phosphorus requirements using foliar analysis. *New Forests*, 20: 193–211.

Weiher E., Keddy P.A., 1995. The assembly of experimental wetland plant communities. *Oikos*, 73: 323–335.

Westoby M., Falster D.S., Moles A.T., Vesk P.A., Wright I.J., 2002. PLANT ECOLOGICAL STRATEGIES: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33: 125–159.

Westoby M., Wright I.J., 2006. Land-plant ecology on the basis of functional traits. *Trends in ecology & evolution*, 21: 261–268.

White F., 1979. The Guineo-Congolian region and its relationships to other phytochoria. *Bulletin du Jardin botanique national de Belgique/Bulletin van de Nationale Plantentuin van Belgie*, 49: 11–55.

White F., 1983. *The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*, UNESCO, pp. 391.

Wilson A.M., Jetz W., 2016. Remotely Sensed High-Resolution Global Cloud Dynamics for Predicting Ecosystem and Biodiversity Distributions. *PLoS Biology*, 14: 1–20.

Wilson P.J., Thompson K., Hodgson J.G., 1999. Specific leaf area and dry leaf matter content as alternative predictors of plant strategies. *New Phytologist*, 143: 155–162.

Wright I.J., Reich P.B., Cornelissen J.H.C., Falster D.S., Hikosaka K., Lamont B.B., Lee W., Oleksyn J., Osada N., Poorter H., Villar R., Warton D.I., Westoby M., Garnier E., 2005. Assessing the generality of leaf trait of global relationships. *New Phytologist*, 166: 485–496.

Wright I.J., Reich P.B., Westoby M., 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, 15: 423–434.

Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H.C., Diemer M., Flexas J., Garnier E., Groom P.K., Gulias J., Hikosaka K., Lamont B.B., Lee T., Lee W., Lusk C., Midgley J.J., Navas M.-L., Niinemets U., Oleksyn J., Osada N., Poorter H., Poot P., Prior L., Pyankov V.I., Roumet C., Thomas S.C., Tjoelker M.G., Veneklaas E.J., Villar R., 2004. The worldwide leaf economics spectrum. *Nature*, 428: 821–7.

Yang Y., Saatchi S., Xu L., Yu Y., Lefsky M., White L., Knyazikhin Y., Myneni R., 2016. Abiotic controls on macroscale variations of Humid Tropical Forest height. *Remote Sensing*, 8: 1–18.

Yeomans K., Golder P., 1982. The Guttman-Kaiser criterion as a predictor of the number of common factors. *The Statistician*, 31: 221–229.

Zanne A.E., Lopez-Gonzalez G., Coomes D.A.A., Ilic J., Jansen S., Lewis S.L.S.L., Miller R.B.B., Swenson N.G.G., Wiemann M.C.C., Chave J., 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository [WWW Document]. *[Online],*. URL http://hdl.handle.net/10255/dryad.235.

Zobel M., 1992. Plant species coexistence- the role of historical, evolutionary and ecological factors. *Oikos*, 65: 314–320.

APPENDICES

APPENDICES

Appendix 1. Detailed protocol for laboratory analysis of soil composition.

The soil samples collected in the field were air-dried for three days to exclude moisture and prevent fungi infestation. The samples were using a motorized – Retch RM200® – grinder and sieved using a 2 mm and 0.5 mm stainless steel sieve. The samples were stored in polythene bags and used for chemical assays.

To measure the soil moisture content by gravimetry:

- Weigh empty aluminium dishes;
- Add approximately 50 g of moist soil into each aluminium dish and reweigh the dishes. Hence, the moist weight of the soil sample is now known;
- Dry the soil overnight at 105 °C in the oven;
- Reweigh the dishes plus the oven dry soil after cooling. Now the weight of the dry soil is known.
- Calculate the soil moisture content for each sample using the following equation:
- Moisture content = [(weight of moist soil – weight of dry soil) ÷ weight of dry soil]*100.

To measure the soil pH in water:

- Weigh 20 g of soil into a 50 ml beaker;
- Add distill water increasingly while stirring with glass rod to mix. Let stand for 30 minutes and stir occasionally until a suspension is formed;
- Add 0.25 ml of 2 M $CaCl_2$ to the 1:2.5 soil: water suspension to make a 0.01 M solution. Mix, and let stand the suspension;
- Swirl the suspension and carefully insert the combination pH electrode into it. Record pH of supernatant when the reading settles down.

To measure the soil total nitrogen by wet acid digest and colorimetery:

- Weigh 1 g of soil into digestion tube;
- Add onto the sample 10 ml of concentrated sulphuric acid and 5 g of catalyst mixture (mixture of 250 g potassium sulphate, 50 g cupric sulphate and 5 g metallic selenium powder);
- Heat the digestion tube initially with 100 ℃ until after frothing then increase temperature to 400 ℃ for 24 hours or until sample turns green or colourless;
- After cooling, place the digestion tubes in distillation unit and add 40 ml of boric acid. Heat the digested samples at steady rate until colour change;

- Titrate the coloured sample with 0.02 N sulphuric acid and the colour changes to pinkish;
- Determine the concentration of nitrogen using colorimeter.

<u>To measure the soil total phosphorus wet acid digest and colorimetery</u>:

- Weigh 2.5 g of soil in 150 ml conical flask and add 0.5 g activated charcoal (Darco G-60);
- Add 50 ml of 0.5 M sodium bicarbonate and shake the solution for 30 minutes;
- Prepare the blank (control) by repeating the step above but without soil sample;
- Filter the solution using a Whatman paper no. 40;
- Transfer 5 ml of the filtrate into a 25 ml volumetric flask, add 5 N of sulphuric acid;
- Add small quantity of distilled water and 4 ml of reagent B;
- Observe colour change and measure colour concentration using a colorimeter.

<u>To measure the soil organic carbon chromic acid digestion</u>:

- Weigh 1 g soil in 500 ml conical flask and add 10 ml of 1 N $K_2Cr_2O_7$ and 20 ml of conc. H_2SO_4. Mix and allow reaction for 30 minutes.
- Dilute mixture with 200 ml water and 10 H_3PO_4, add 10 ml of NaF and 2 ml of diphenylamine;
- Titrate the solution to a brilliant green colour and measure colour concentration using a colorimeter.

<u>To measure the soil cation exchange capacity by ammonium acetate</u>:

- Add 25.0 g of soil to a 500 ml Erlenmeyer flask.
- Add 125 ml of the 1 M ammonium acetate shake thoroughly and allow standing 16 hours (or overnighting).
- Fit a 5.5 cm Buchner funnel with retentive filter paper, moisten the paper, apply light suction, and transfer the soil.
- Gently wash the soil four times with 25 ml additions of the ammonium acetate, allowing each addition to filter through but not allowing the soil to crack or dry.
- Apply suction only as needed to ensure slow filtering.
- Wash the soil with eight separate additions of 95 % ethanol to remove excess saturating solution. Only add enough to cover the soil surface, and allow each addition to filter through before adding more.
- Extract the adsorbed NH4 by leaching the soil with eight separate 25 ml additions of 1 M KCl, leaching slowly and completely as above.
- Determine the concentration of NH4-N in the KCl extract by colorimetry.

<u>To measure the soil particle size by hydrometry</u>:

- Prepare a dispersing solution by dissolving 50 g of sodium hexametaphosphate, $Na_6(PO_3)_6$ in deionized water and dilute to 1 litter.

- Prepare the black solution by mixing 100 ml of the 5% dispersing solution and add 880 ml of deionized water in a 1000 ml cylinder.
- Weigh 25-50 g of soil and transfer to a dispersing cup.
- Add 100 ml of 5 % dispersing solution and mix the sample for 30 – 60 sec.
- Fill to the 1000 ml mark with deionized water equilibrated to room temperature, or allow standing overnight to equilibrate.
- Insert plunger into suspension, and carefully mix for 30 seconds until a uniform suspension is obtained.
- Gently insert the hydrometer into the suspension and record the hydrometer reading at 40 sec. to obtain the amount of silt plus clay suspended. The sand has settled to the bottom of the cylinder by this time.
- (Repeat step 6 and7 for each sample)
- Record the hydrometer reading again after 6 hours, 52 minutes.
- <u>Calculations</u>
  - Percent clay = % clay = corrected hydrometer reading at 6 hrs, 52 min. x 100/ wt. of sample;
  - Percent silt = corrected hydrometer reading at 40 sec. x 100/ wt. of sample - % clay
  - Percent sand =% sand = 100% - % silt - % clay

Appendix 2. Species list and total number of inviduals sampled from 82 one ha permanent sampling plots from eastern Cameroon.

Species are ordered in descending order of number of inviduals. Family nomenclature: APG IV, (2016); Species nomenclature: the African Plant Database (version 3.4.0) (http://www.ville-ge.ch/musinfo/bd/cjb/africa/)

Scientific names	**Family**	**Total individuals**
Tabernaemontana crassa	Apocynaceae	1561
Greenwayodendron suaveolens	Annonaceae	1508
Anonidium mannii	Annonaceae	1442
Petersianthus macrocarpus	Lecythidaceae	871
Strombosia grandifolia	Olacaceae	826
Desbordesia insignis	Irvingiaceae	806
Funtumia africana	Apocynaceae	788
Plagiostyles africana	Euphorbiaceae	582
Trichilia welwitschii	Meliaceae	560
Baphia leptobotrys	Fabaceae	540
Santiria trimera	Burseraceae	540
Uapaca guineensis	Phyllanthaceae	517
Musanga cecropioides	Urticaceae	464
Hylodendron gabunense	Fabaceae	432
Coelocaryon preussii	Myristicaceae	423
Celtis adolfi-friderici	Cannabaceae	415
Trichilia prieuriana	Meliaceae	413

Scientific names	**Family**	**Total individuals**
Garcinia epunctata	Clusiaceae	15
Maesobotrya griffoniana	Phyllanthaceae	15
Maesobotrya spp.	Phyllanthaceae	15
Ochna afzelii	Ochnaceae	15
Oncoba welwitschii	Salicaceae	15
Pterygota macrocarpa	Malvaceae	15
Aulacocalyx jasminiflora	Rubiaceae	14
Chrysophyllum beguei	Sapotaceae	14
Chrysophyllum pruniforme	Sapotaceae	14
Dialium angolense	Fabaceae	14
Erismadelphus exsul	Vochysiaceae	14
Hymenocardia lyrata	Phyllanthaceae	14
Klaineanthus spp.	Euphorbiaceae	14
Laccodiscus pseudostipularis	Sapindaceae	14
Psychotria spp.	Rubiaceae	14
Zanthoxylum heitzii	Rutaceae	14
Zanthoxylum spp.	Rutaceae	14

Staudtia kamerunensis	Myristicaceae	393
Corynanthe pachyceras	Rubiaceae	390
Celtis mildbraedii	Cannabaceae	373
Heisteria parvifolia	Olacaceae	355
Strombosiopsis tetrandra	Olacaceae	344
Duboscia macrocarpa	Malvaceae	337
Chrysophyllum boukokoense	Sapotaceae	331
Drypetes spp.	Putranjivaceae	330
Millettia sanagana	Fabaceae	330
Sorindeia grandifolia	Anacardiaceae	317
Pentaclethra macrophylla	Fabaceae	315
Trilepisium madagascariense	Moraceae	311
Pausinystalia macroceras	Rubiaceae	310
Celtis zenkeri	Cannabaceae	307
Cola lateritia	Malvaceae	306
Carapa procera	Meliaceae	297
Pancovia laurentii	Sapindaceae	293
Pycnanthus angolensis	Myristicaceae	279
Anthonotha macrophylla	Fabaceae	266
Aidia micrantha	Rubiaceae	264
Sterculia rhinopetala	Malvaceae	257

Anthonotha ferruginea	Fabaceae	13
Dacryodes spp.	Burseraceae	13
Ficus mucuso	Moraceae	13
Irvingia spp.	Irvingiaceae	13
Meiocarpidium lepidotum	Annonaceae	13
Poga oleosa	Anisophylleaceae	13
Syzygium rowlandii	Myrtaceae	13
Diospyros preussii	Ebenaceae	12
Entandrophragma congoense	Meliaceae	12
Macaranga monandra	Euphorbiaceae	12
Quassia spp.	Simaroubaceae	12
Strephonema pseudocola	Combretaceae	12
Anthonotha spp.	Fabaceae	11
Chrysophyllum perpulchrum	Sapotaceae	11
Desplatsia chrysochlamys	Malvaceae	11
Diospyros cinnabarina	Ebenaceae	11
Erythrina excelsa	Fabaceae	11
Ficus spp.	Moraceae	11
Homalium spp.	Salicaceae	11
Maranthes spp.	Chrysobalanaceae	11
Monodora myristica	Annonaceae	11

Pterocarpus soyauxii	Fabaceae	253
Phyllocosmus africanus	Ixonanthaceae	249
Terminalia superba	Combretaceae	242
Annickia affinis	Annonaceae	238
Tricalysia spp.	Rubiaceae	238
Macaranga spinosa	Euphorbiaceae	235
Klainedoxa gabonensis	Irvingiaceae	217
Desplatsia dewevrei	Malvaceae	216
Myrianthus arboreus	Urticaceae	216
Mansonia altissima	Malvaceae	214
Trichilia tessmannii	Meliaceae	209
Chrysophyllum lacourtianum	Sapotaceae	207
Uapaca paludosa	Phyllanthaceae	203
Lecaniodiscus cupanioides	Sapindaceae	202
Angylocalyx pynaertii	Fabaceae	201
Barteria fistulosa	Passifloraceae	199
Centroplacus glaucinus	Centroplacaceae	197
Triplochiton scleroxylon	Malvaceae	191
Celtis tessmannii	Cannabaceae	186
Oncoba glauca	Salicaceae	185
Piptadeniastrum africanum	Fabaceae	185

Pachyelasma tessmannii	Fabaceae	11
Parkia bicolor	Fabaceae	11
Bombax buonopozense	Malvaceae	10
Dialium dinklagei	Fabaceae	10
Heisteria zimmereri	Olacaceae	10
Khaya ivorensis	Meliaceae	10
Omphalocarpum procerum	Sapotaceae	10
Xylopia parviflora	Annonaceae	10
Cola cordifolia	Malvaceae	9
Corynanthe mayumbensis	Rubiaceae	9
Dacryodes klaineana	Burseraceae	9
Dracaena arborea	Asparagaceae	9
Rothmannia spp.	Rubiaceae	9
Strombosia scheffleri	Olacaceae	9
Aidia spp.	Rubiaceae	8
Antiaris toxicaria	Moraceae	8
Canthium rheedei	Rubiaceae	8
Canthium spp.	Rubiaceae	8
Chrysophyllum spp.	Sapotaceae	8
Khaya grandifoliola	Meliaceae	8
Millettia saga	Fabaceae	8

Leplaea thompsonii	Meliaceae	180
Irvingia excelsa	Irvingiaceae	178
Baphia pubescens	Fabaceae	177
Macaranga barteri	Euphorbiaceae	177
Blighia spp.	Sapindaceae	174
Panda oleosa	Pandaceae	174
Trichoscypha acuminata	Anacardiaceae	173
Drypetes leonensis	Putranjivaceae	172
Maesobotrya klaineana	Phyllanthaceae	171
Keayodendron bridelioides	Phyllanthaceae	166
Annickia chlorantha	Annonaceae	160
Drypetes preussii	Putranjivaceae	157
Albizia adianthifolia	Fabaceae	156
Rothmannia lujae	Rubiaceae	156
Alstonia boonei	Apocynaceae	154
Antidesma membranaceum	Phyllanthaceae	152
Antidesma laciniatum	Phyllanthaceae	149
Sterculia tragacantha	Malvaceae	149
Trichilia rubescens	Meliaceae	149
Lepidobotrys staudtii	Lepidobotryaceae	148
Blighia welwitschii	Sapindaceae	146
Rinorea oblongifolia	Violaceae	142

Olax spp.	Olacaceae	8
Parinari hypochrysea	Chrysobalanaceae	8
Pauridiantha floribunda	Rubiaceae	8
Combretum spp.	Combretaceae	7
Diospyros mannii	Ebenaceae	7
Diospyros sanza-minika	Ebenaceae	7
Dovyalis zenkeri	Salicaceae	7
Emblica spp.	Phyllanthaceae	7
Entandrophragma utile	Meliaceae	7
Fernandoa ferdinandi	Bignoniaceae	7
Millettia laurentii	Fabaceae	7
Myrianthus preussii	Urticaceae	7
Rothmannia hispida	Rubiaceae	7
Rothmannia longiflora	Rubiaceae	7
Rothmannia talbotii	Rubiaceae	7
Amphimas ferrugineus	Fabaceae	6
Baikiaea insignis	Fabaceae	6
Bridelia grandis	Phyllanthaceae	6
Croton oligandrus	Euphorbiaceae	6
Diospyros dendo	Ebenaceae	6
Drypetes laciniata	Putranjivaceae	6
Eugenia spp.	Myrtaceae	6

Markhamia lutea	Bignoniaceae	140
Leplaea cedrata	Meliaceae	136
Treculia africana	Moraceae	135
Entandrophragma cylindricum	Meliaceae	134
Parkia biglobosa	Fabaceae	129
Xylopia quintasii	Annonaceae	128
Treculia obovoidea	Moraceae	123
Albizia glaberrima	Fabaceae	121
Duguetia staudtii	Annonaceae	121
Zanthoxylum gilletii	Rutaceae	120
Markhamia tomentosa	Bignoniaceae	115
Xylopia aethiopica	Annonaceae	115
Olax subscorpioidea	Olacaceae	112
Xylopia spp.	Annonaceae	110
Nesogordonia kabingaensis	Malvaceae	109
Mareyopsis longifolia	Euphorbiaceae	108
Rinorea cuspa	Violaceae	108
Sloetiopsis usambarensis	Moraceae	108
Hexalobus crispiflorus	Annonaceae	107
Diospyros bipindensis	Ebenaceae	103
Tricalysia pangolina	Rubiaceae	98

Grewia coriacea	Malvaceae	6
Hexalobus spp.	Annonaceae	6
Homalium longistylum	Salicaceae	6
Isolona hexaloba	Annonaceae	6
Memecylon aberrans	Melastomataceae	6
Ochna calodendron	Ochnaceae	6
Phyllocosmus calothyrsus	Ixonanthaceae	6
Pterygota bequaertii	Malvaceae	6
Vitex spp.	Lamiaceae	6
Antrocaryon micraster	Anacardiaceae	5
Croton sylvaticus	Euphorbiaceae	5
Drypetes molunduana	Putranjivaceae	5
Euphorbia drupifera	Euphorbiaceae	5
Garcinia kola	Clusiaceae	5
Maranthes chrysophylla	Chrysobalanaceae	5
Nesogordonia papaverifera	Malvaceae	5
Ochna spp.	Ochnaceae	5
Psydrax arnoldiana	Rubiaceae	5
Sacoglottis gabonensis	Humiriaceae	5
Strombosia zenkeri	Olacaceae	5
Uapaca spp.	Phyllanthaceae	5

Dacryodes igaganga	Burseraceae	97
Celtis philippensis	Cannabaceae	96
Ongokea gore	Olacaceae	96
Lovoa trichilioides	Meliaceae	93
Coffea spp.	Rubiaceae	92
Dialium bipindense	Fabaceae	91
Synsepalum dulcificum	Sapotaceae	91
Vitex rivularis	Lamiaceae	91
Erythrophleum suaveolens	Fabaceae	90
Tetrapleura tetraptera	Fabaceae	90
Xylopia hypolampra	Annonaceae	90
Eribroma oblongum	Malvaceae	86
Millettia mannii	Fabaceae	86
Picralima nitida	Apocynaceae	86
Homalium le-testui	Salicaceae	82
Lasiodiscus mannii	Rhamnaceae	80
Maranthes glabra	Chrysobalanaceae	79
Ricinodendron heudelotii	Euphorbiaceae	78
Drypetes klainei	Putranjivaceae	77
Afrostyrax kamerunensis	Huaceae	75
Amphimas pterocarpoides	Fabaceae	75
Fernandoa adolfi-friderici	Bignoniaceae	73

Xylopia rubescens	Annonaceae	5
Allanblackia gabonensis	Clusiaceae	4
Balanites wilsoniana	Zygophyllaceae	4
Breviea sericea	Sapotaceae	4
Carapa grandiflora	Meliaceae	4
Chrysophyllum giganteum	Sapotaceae	4
Corynanthe spp.	Rubiaceae	4
Diospyros iturensis	Ebenaceae	4
Fillaeopsis discophora	Fabaceae	4
Klainedoxa spp.	Irvingiaceae	4
Morinda lucida	Rubiaceae	4
Octolobus spectabilis	Malvaceae	4
Olax subscorpioides	Olacaceae	4
Oncoba mannii	Salicaceae	4
Parinari spp.	Chrysobalanaceae	4
Pittosporum viridiflorum	Pittosporaceae	4
Synsepalum spp.	Sapotaceae	4
Zanthoxylum rubescens	Rutaceae	4
Afzelia africana	Fabaceae	3
Afzelia pachyloba	Fabaceae	3
Angylocalyx spp.	Fabaceae	3
Aulacocalyx talbotii	Rubiaceae	3

Lannea welwitschii	Anacardiaceae	73
Strombosia pustulata	Olacaceae	71
Cleistopholis patens	Annonaceae	70
Oricia spp.	Rutaceae	70
Margaritaria discoidea	Phyllanthaceae	69
Cleistanthus itsoghensis	Phyllanthaceae	67
Lasiodiscus marmoratus	Rhamnaceae	67
Pseudospondias microcarpa	Anacardiaceae	67
Sorindeia juglandifolia	Anacardiaceae	66
Uvariastrum pierreanum	Annonaceae	66
Beilschmiedia obscura	Lauraceae	65
Pteleopsis hylodendron	Combretaceae	62
Baphia spp.	Fabaceae	61
Cola acuminata	Malvaceae	61
Diospyros spp.	Ebenaceae	61
Discoglypremna caloneura	Euphorbiaceae	61
Oncoba spp.	Salicaceae	60
Allanblackia floribunda	Clusiaceae	59
Diospyros suaveolens	Ebenaceae	58
Irvingia grandifolia	Irvingiaceae	58
Irvingia robur	Irvingiaceae	57
Quassia gabonensis	Simaroubaceae	57

Beilschmiedia anacardioides	Lauraceae	3
Cavacoa quintasii	Euphorbiaceae	3
Cola ficifolia	Malvaceae	3
Cordia africana	Boraginaceae	3
Dactyladenia spp.	Chrysobalanaceae	3
Diospyros monbuttensis	Ebenaceae	3
Drypetes chevalieri	Putranjivaceae	3
Endodesmia calophylloides	Calophyllaceae	3
Eriocoelum spp.	Sapindaceae	3
Hymenocardia heudelotii	Phyllanthaceae	3
Kigelia africana	Bignoniaceae	3
Leptonychia spp.	Malvaceae	3
Macaranga hurifolia	Euphorbiaceae	3
Morus mesozygia	Moraceae	3
Nauclea spp.	Rubiaceae	3
Newtonia griffoniana	Fabaceae	3
Paropsia grewioides	Passifloraceae	3
Persea americana	Lauraceae	3
Pierreodendron africanum	Simaroubaceae	3
Pouteria spp.	Sapotaceae	3
Sibangea spp.	Putranjivaceae	3
Trema orientalis	Cannabaceae	3

Trichilia spp.	Meliaceae	57
Garcinia mannii	Clusiaceae	56
Trichilia dregeana	Meliaceae	56
Vepris louisii	Rutaceae	56
Milicia excelsa	Moraceae	55
Xylopia aurantiiodora	Annonaceae	55
Cola nitida	Malvaceae	54
Campylospermum spp.	Ochnaceae	53
Anopyxis klaineana	Rhizophoraceae	52
Rauvolfia vomitoria	Apocynaceae	51
Diospyros crassiflora	Ebenaceae	50
Entandrophragma candollei	Meliaceae	50
Scottellia klaineana	Achariaceae	50
Calpocalyx dinklagei	Fabaceae	49
Cleistopholis glauca	Annonaceae	49
Drypetes gossweileri	Putranjivaceae	49
Pouteria altissima	Sapotaceae	49
Distemonanthus benthamianus	Fabaceae	48
Pouteria alnifolia	Sapotaceae	48
Turraeanthus africana	Meliaceae	48
Afrostyrax lepidophyllus	Huaceae	47

Voacanga spp.	Apocynaceae	3
Zanthoxylum tessmannii	Rutaceae	3
Beilschmiedia congolana	Lauraceae	2
Berlinia spp.	Fabaceae	2
Bombax spp.	Malvaceae	2
Borassus aethiopum	Arecaceae	2
Celtis gomphophylla	Cannabaceae	2
Cola ballayi	Malvaceae	2
Cuviera longiflora	Rubiaceae	2
Cyrtogonone argentea	Euphorbiaceae	2
Dacryodes buettneri	Burseraceae	2
Dacryodes macrophylla	Burseraceae	2
Dichrostachys cinerea	Fabaceae	2
Diospyros conocarpa	Ebenaceae	2
Drypetes principum	Putranjivaceae	2
Garcinia spp.	Clusiaceae	2
Grewia spp.	Malvaceae	2
Guibourtia spp.	Fabaceae	2
Hymenocardia spp.	Phyllanthaceae	2
Isolona thonneri	Annonaceae	2
Lecaniodiscus spp.	Sapindaceae	2

Chytranthus spp.	Sapindaceae	47
Macaranga spp.	Euphorbiaceae	47
Millettia barteri	Fabaceae	46
Majidea forsteri	Sapindaceae	45
Parinari excelsa	Chrysobalanaceae	45
Glyphaea brevis	Malvaceae	44
Monodora tenuifolia	Annonaceae	44
Pancovia spp.	Sapindaceae	43
Symphonia globulifera	Clusiaceae	43
Cylicodiscus gabunensis	Fabaceae	42
Maprounea membranacea	Euphorbiaceae	42
Grossera macrantha	Euphorbiaceae	41
Rinorea leiophylla	Violaceae	41
Cola spp.	Malvaceae	40
Cordia platythyrsa	Boraginaceae	40
Mallotus oppositifolius	Euphorbiaceae	40
Manilkara obovata	Sapotaceae	40
Albizia ferruginea	Fabaceae	39
Cola verticillata	Malvaceae	39
Berlinia grandiflora	Fabaceae	38
Detarium macrocarpum	Fabaceae	38
Erythroxylum mannii	Erythroxylaceae	38

Leptonychia echinocarpa	Malvaceae	2
Monodora spp.	Annonaceae	2
Oubanguia spp.	Lecythidaceae	2
Pentadesma butyracea	Clusiaceae	2
Premna angolensis	Lamiaceae	2
Prioria oxyphylla	Fabaceae	2
Rinorea grandifolia	Violaceae	2
Sericanthe spp.	Rubiaceae	2
Spathodea campanulata	Bignoniaceae	2
Spondias spp.	Anacardiaceae	2
Strychnos staudtii	Loganiaceae	2
Thomandersia hensii	Schlegeliaceae	2
Tricalysia spp.	Rubiaceae	2
Tricalysia discolor	Rubiaceae	2
Tridesmostemon spp.	Sapotaceae	2
Vitex dentata	Lamiaceae	2
Alchornea cordifolia	Euphorbiaceae	1
Angylocalyx oligophyllus	Fabaceae	1
Angylocalyx talbotii	Fabaceae	1
Anthocleista schweinfurthii	Gentianaceae	1
Anthonotha lamprophylla	Fabaceae	1
Antidesma vogelianum	Phyllanthaceae	1

Psydrax subcordata	Rubiaceae	38
Allanblackia kisonghi	Clusiaceae	37
Beilschmiedia spp.	Lauraceae	37
Manilkara spp.	Sapotaceae	37
Nauclea diderrichii	Rubiaceae	37
Rhabdophyllum spp.	Ochnaceae	37
Uapaca staudtii	Phyllanthaceae	37
Aoranthe cladantha	Rubiaceae	36
Dialium guineense	Fabaceae	36
Dictyandra arborescens	Rubiaceae	36
Heisteria trillesiana	Olacaceae	36
Rinorea dentata	Violaceae	35
Syzygium spp.	Myrtaceae	35
Celtis africana	Cannabaceae	34
Diospyros hoyleana	Ebenaceae	34
Shirakiopsis elliptica	Euphorbiaceae	34
Tessmannia anomala	Fabaceae	34
Antrocaryon klaineanum	Anacardiaceae	32
Maesopsis eminii	Rhamnaceae	32
Oncoba dentata	Salicaceae	32
Voacanga africana	Apocynaceae	32
Bombax brevicuspe	Malvaceae	31

Baphia nitida	Fabaceae	1
Barteria spp.	Passifloraceae	1
Buchholzia coriacea	Capparaceae	1
Calpocalyx heitzii	Fabaceae	1
Calycosiphonia macrochlamys	Rubiaceae	1
Celtis conferta	Cannabaceae	1
Chrysophyllum ubanguiense	Sapotaceae	1
Chytranthus talbotii	Sapindaceae	1
Cola flavovelutina	Malvaceae	1
Cola heterophylla	Malvaceae	1
Cola reticulata	Malvaceae	1
Cola rostrata	Malvaceae	1
Copaifera religiosa	Fabaceae	1
Cordia aurantiaca	Boraginaceae	1
Coula edulis	Olacaceae	1
Craterispermum cerinanthum	Rubiaceae	1
Daniellia ogea	Fabaceae	1
Diospyros cinbari	Ebenaceae	1
Diospyros heudelotii	Ebenaceae	1
Diospyros zenkeri	Ebenaceae	1
Empogona crepiniana	Rubiaceae	1
Ficus variifolia	Moraceae	1

Gomphia mannii	Ochnaceae	31
Tridesmostemon omphalocarpoides	Sapotaceae	31
Uapaca heudelotii	Phyllanthaceae	31
Vepris spp.	Rutaceae	31
Xylopia staudtii	Annonaceae	31
Antidesma venosum	Phyllanthaceae	30
Canarium schweinfurtii	Burseraceae	30
Eriocoelum macrocarpum	Sapindaceae	30
Funtumia elastica	Apocynaceae	30
Mammea africana	Calophyllaceae	30
Sapium spp.	Euphorbiaceae	30
Tessmannia africana	Fabaceae	30
Brenania brieyi	Rubiaceae	29
Mareyopsis spp.	Euphorbiaceae	29
Bridelia micrantha	Phyllanthaceae	28
Casearia spp.	Salicaceae	28
Ceiba pentandra	Malvaceae	28
Phoenix reclinata	Arecaceae	28
Spondias mombin	Anacardiaceae	28
Trichoscypha oddonii	Anacardiaceae	28

Fleroya ledermannii	Rubiaceae	1
Garcinia ovalifolia	Clusiaceae	1
Garcinia staudtii	Clusiaceae	1
Gilbertiodendron brachystegioides	Fabaceae	1
Harungana madagascariensis	Hypericaceae	1
Homalium laurentii	Salicaceae	1
Irvingia smithii	Irvingiaceae	1
Lasiodiscus fasciculiflorus	Rhamnaceae	1
Leonardoxa africana	Fabaceae	1
Leptactina involucrata	Rubiaceae	1
Letestua durissima	Sapotaceae	1
Maesobotrya staudtii	Phyllanthaceae	1
Memecylon amshoffae	Melastomataceae	1
Memecylon spp.	Melastomataceae	1
Mildbraediodendron excelsum	Fabaceae	1
Neoboutonia mannii	Euphorbiaceae	1
Newtonia duparquetiana	Fabaceae	1
Newtonia glandulifera	Fabaceae	1
Newtonia leucocarpa	Fabaceae	1
Oncoba gilgiana	Salicaceae	1

Uapaca acuminata	Phyllanthaceae	28
Citropsis articulata	Rutaceae	27
Bobgunnia fistuloides	Fabaceae	26
Vitex grandifolia	Lamiaceae	26
Afzelia bipindensis	Fabaceae	25
Cola chlamydantha	Malvaceae	25
Klaineanthus gabonii	Euphorbiaceae	25
Massularia acuminata	Rubiaceae	25
Microdesmis puberula	Pandaceae	25
Sterculia micrantha	Malvaceae	25
Trichoscypha spp.	Anacardiaceae	25
Blighia sapida	Sapindaceae	24
Carapa spp.	Meliaceae	24
Omphalocarpum elatum	Sapotaceae	24
Sorindeia spp.	Anacardiaceae	24
Albizia zygia	Fabaceae	23
Dichostemma glaucescens	Euphorbiaceae	23
Khaya anthotheca	Meliaceae	23
Trichoscypha arborea	Anacardiaceae	23
Uapaca vanhouttei	Phyllanthaceae	23
Dacryodes edulis	Burseraceae	22
Parkia filicoidea	Fabaceae	22
Oubanguia africana	Lecythidaceae	1
Pancovia pedicellaris	Sapindaceae	1
Pausinystalia johimbe	Rubiaceae	1
Pentaclethra eetveldeana	Fabaceae	1
Pericopsis elata	Fabaceae	1
Pinacopodium congolense	Erythroxylaceae	1
Piptocarpha riedelii	Asteraceae	1
Polyceratocarpus parviflorus	Annonaceae	1
Pouteria pierrei	Sapotaceae	1
Psydrax palma	Rubiaceae	1
Quassia undulata	Simaroubaceae	1
Radlkofera calodendron	Sapindaceae	1
Rhodognaphalon brevicuspe	Malvaceae	1
Schumanniophyton magnificum	Rubiaceae	1
Sorindeia africana	Anacardiaceae	1
Spondias cytherea	Anacardiaceae	1
Strephonema sericeum	Combretaceae	1
Tabernaemontana pachysiphon	Apocynaceae	1
Tessmannia spp.	Fabaceae	1
Tetrorchidium oppositifolium	Euphorbiaceae	1
Usteria guineensis	Loganiaceae	1
Uvariodendron molundense	Annonaceae	1

Rauvolfia caffra	Apocynaceae	22
Vitex doniana	Lamiaceae	22
Anthonotha cladantha	Fabaceae	21
Anthonotha fragrans	Fabaceae	21
Holoptelea grandis	Ulmaceae	21
Celtis spp.	Cannabaceae	20
Syzygium guineense	Myrtaceae	20
Zanthoxylum leprieurii	Rutaceae	20
Casearia aculeata	Salicaceae	19
Cola altissima	Malvaceae	19
Tetrorchidium didymostemon	Euphorbiaceae	19
Baillonella toxisperma	Sapotaceae	18
Entandrophragma angolense	Meliaceae	18
Ficus exasperata	Moraceae	18
Gilletiodendron pierreanum	Fabaceae	18
Hunteria umbellata	Apocynaceae	18
Uvariastrum zenkeri	Annonaceae	18
Irvingia gabonensis	Irvingiaceae	17
Pterocarpus mildbraedii	Fabaceae	17
Albizia gummifera	Fabaceae	16
Cassia javanica	Fabaceae	16

Uvariopsis bakeriana	Annonaceae	1

Chrysophyllum africanum	Sapotaceae	16
Erythrophleum ivorense	Fabaceae	16
Strombosia spp.	Olacaceae	16
Allophylus africanus	Sapindaceae	15
Dialium spp.	Fabaceae	15
Diospyros canaliculata	Ebenaceae	15
Eriocoelum oblongum	Sapindaceae	15

Appendix 3. Summary statistics of the topography and soil-related variables used in the analysis of edaphic gradient. For each variable, the minimum, maximum, mean and standard deviation and codes are provided.

Variable (unit)	Total nitrogen (g kg^{-1})	Total phosphorus (g kg^{-1})	Sand content (%)	Silt Content (%)	Cation exchange capacity (cmol kg-1)	Organic matter (%)	Clay content (%)	Moisture content (%)	pH	Elevation (m)	Slope (°)
Min.	0.17	22.51	27.75	2.94	1.88	10.95	10.99	0.81	4.30	278.82	2.55
Max.	2.30	2375.59	51.08	9.07	9.39	42.96	32.07	11.86	5.97	373.74	30.96
Mean	1.31	432.18	38.17	5.12	5.45	27.67	20.68	4.08	5.10	313.10	11.74
SD	0.39	506.26	5.48	1.25	1.98	7.73	4.29	2.52	0.31	33.49	7.75

Appendix 4. List of studied species in the 50-hectare Forest Dynamics Plot in Korup ordered alphabetically.

A: Four abundant species and the four traits sampled; B: Other species studied; LA: Leaf area; SLA: Specific leaf area; LPC: Leaf phosphorus content; LNC: Leaf nitrogen content; N:P ratios.

A.	Abundance								
Species	50 ha FDP	44 sampled quadrats	individuals sampled	Incidence	LA (cm^2)	SLA (mm^{2}mg^{-1})	LPC (µg g^{-1})	LNC (µg g^{-1})	N:P ratio
Cola rostrata K.Schum	922	27	23	14	145.35	13.76	1,653.18	23,100	13.97
Hymenostegia afzelii (Oliv.) Harms	691	28	24	17	19.8	18.8	1,475.38	22,000	14.91
Oubanguia alata Baker f.	4,103	106	74	23	91.31	13.6	845.43	20,700	24.48
Strombosiopsis tetrandra Engl.	317	18	15	14	136.79	15.27	1,647.38	25,800	15.66
B.									
Anisophyllea purpurascens Hutch. & Dalziel	16	1	1	1	24.94	17	663.979		
Annickia affinis (Exell) Versteegh & Sosef	133	3	2	2	98.3	20.99	602.263		
Anthonotha macrophylla P.Beauv.	31	3	3	2	99.72	13.22	1482.625		
Antidesma vogelianum Müll.Arg.	70	3	3	3	64.5	20.1	1100.354		
Aoranthe cladantha (K.Schum.) Somers	21	1	1	1	715.07	13.55	180.576		
Aulacocalyx talbotii (Wernham) Keay	44	1	1	1	83.25	19.21	735.338		
Baphia capparidifolia Baker	273	3	3	3	49.64	17.56	917.766		
Baphia laurifolia Bail.	126	4	4	3	78.03	20.95	422.009		
Barteria fistulosa Mast.	18	1	1	1	190.32	9.73	1293.861		
Beilschmiedia sp1	15	1	1	1	205.63	17.09	917.766		
Beilschmiedia sp2	79	3	2	2	165.25	11.88	773.082		

Berlinia auriculata Benth.	159	5	3	3	130.52	11.68	1001.570
Bridelia micrantha (Hochst.) Baill.	9	1	1	1	68.75	13.75	481.189
Calpocalyx dinklagei Harms	NA	5	3	3	54.29	14.04	789.046
Carapa procera DC.	196	5	5	5	121.07	12	760.875
Casearia barteri Mast.	NA	3	3	2	124.54	20.31	1145.475
Chytranthus talbotii (Baker f.) Keay	11	2	1	1	107.79	7.42	730.224
Cola flavovelutina K.Schum.	8	1	1	1	81.56	9.2	842.243
Cola lateritia K.Schum.	119	3	2	2	269.35	10.74	686.602
Cola lepidota K.Schum.	44	2	1	1	181.99	10.83	537.464
Cola acuminata (P.Beauv.) Schott & Endl.	79	5	4	3	94.54	11.63	829.622
Cola praeacuta Brenan & Keay	457	19	13	9	151.78	14.3	1015.783
Craterispermum aristatum Wernham	22	2	2	2	138.91	15.83	692.013
Dacryodes klaineana (Pierre) H.J.Lam	34	5	3	1	151.39	12.26	742.542
Dasylepis thomasii Obama & Breteler	286	7	7	7	145.64	9.63	664.003
Dialium pachyphyllum Harms	71	2	2	2	44.24	14.84	52.938
Dichostemma glaucescens Pierre	2,274.00	28	13	8	80.98	15.79	658.882
Diogoa zenkeri (Engl.) Exell & Mendonça	423	18	15	11	158.08	15.25	1026.970
Diospyros hoyleana F.White	22	2	2	2	6.96	14.37	1629.255
Diospyros gabunensis Gürke	855	18	12	8	206.16	10.73	721.372
Diospyros iturensis (Gürke) Letouzey & F.White	509	18	18	14	97.36	11.24	1838.960
Diospyros sp1	7	1	1	1	69.16	10.98	786.037

Diospyros zenkeri (Gürke) F.White	181	7	7	7	36.71	15.45	508.879
Discoglypremna caloneura (Pax) Prain	69	1	1	1	177.01	28.1	836.297
Drypetes principum (Müll.Arg.) Hutch.	5	1	1	1	140.77	15.88	752.451
Drypetes staudtii (Pax) Hutch.	1,085.00	50	42	17	229.12	11.29	680.996
Erythrophleum ivorense A.Chev.	35	2	1	1	12.59	22.22	436.539
Erythroxylum mannii Oliv.	7	1	1	1	16.97	36.37	863.702
Garcinia kola Heckel	3	1	1	1	78.18	15.74	1258.558
Garcinia mannii Oliv.	23	1	1	1	58.54	17.74	2040.059
Garcinia conrauana Engl.	344	4	3	1	102.96	11.11	1034.271
Gilbertiodendron demonstrans (Baill.) J.Leonard	53	1	1	1	152.15	11.44	632.586
Grewia coriacea Mast.	47	2	2	2	148	16.99	560.967
Homalium le-testui Pellegr.	51	2	1	1	156.98	10.24	712.775
Homalium longistylum Mast.	74	2	1	1	72.97	24.6	759.711
Hunteria umbellata (K.Schum.) Hallier f.	224	11	10	8	93.36	16.87	1041.523
Hymenostegia bakeriana Hutch. & Dalziel	45	1	1	1	18.59	14.3	1201.140
Hypodaphnis zenkeri (Engl.) Stapf	153	5	5	5	112.67	16.99	651.028
Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill.	44	1	1	1	45.69	13.71	952.260
Klaineanthus gabonii Pierre	485	13	10	9	152.73	15.16	1295.185
Lecomtedoxa klaineana (Pierre ex Engl.) Pierre ex Dubard	208	1	1	1	126.33	10	861.241

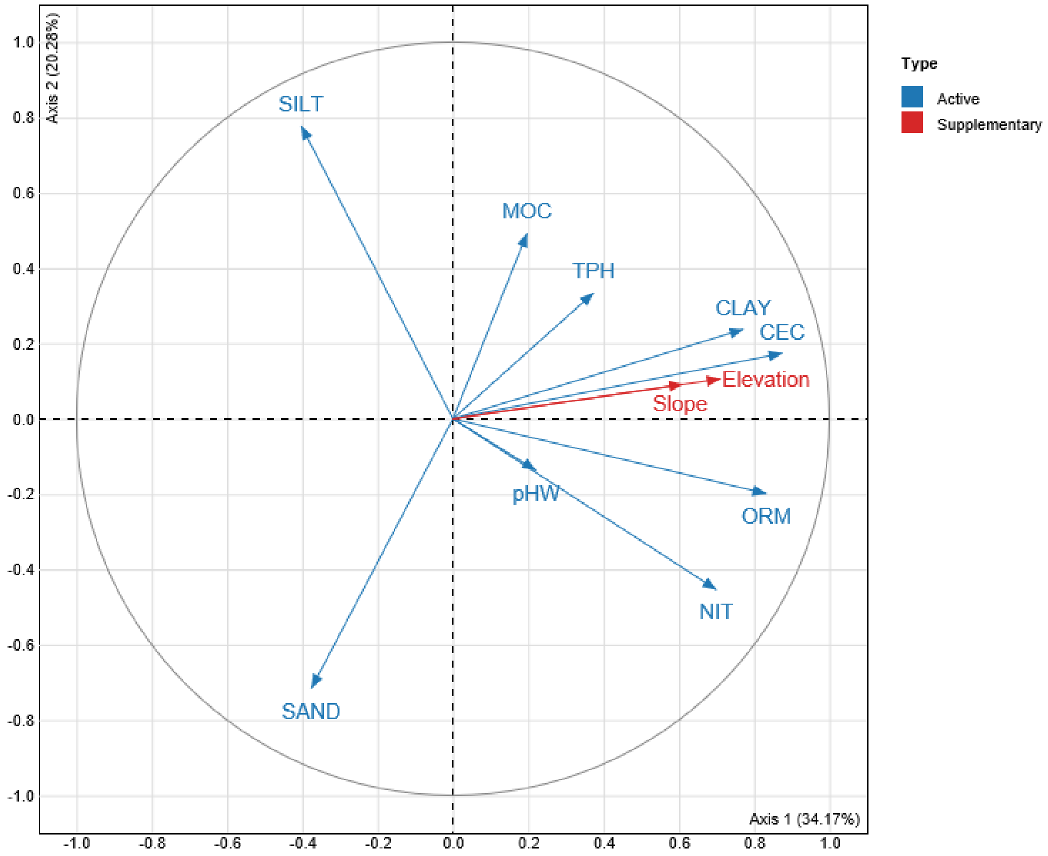
Leptaulus daphnoides Benth.	108	1	1	1	94.74	21.21	749.547
Lophira alata Banks ex C.F.Gaertn.	28	1	1	1	388.78	11.49	511.986
Maesobotrya klaineana (Pierre) J.Léonard	158	5	5	5	110.82	16.05	553.415
Maranthes sp1	2	1	1	1	104.11	14.73	257.569
Mareyopsis longifolia (Pax) Pax & K.Hoffm.	18	1	1	1	106.89	12.07	942.149
Musanga cecropioides R.Br. ex Tedlie	91	1	1	1	65.35	27.23	873.463
Octoknema affinis Pierre	47	1	1	1	381.32	13.01	738.886
Oubanguia laurifolia (Pierre) Pierre	8	1	1	1	23.66	16.9	801.484
Panda oleosa Pierre	4	1	1	1	98.03	19.1	1065.150
Pauridiantha floribunda (K.Schum. & K.Krause) Bremek.	78	2	1	1	157.01	19.3	486.877
Pausinystalia macroceras (K.Schum.) Pierre ex Beille	68	1	1	1	49.25	23.08	665.299
Piptostigma oyemense Pellegr.	118	3	3	3	173.67	16.38	1488.618
Placodiscus sp1	34	3	3	3	146.77	11.51	467.323
Protomegabaria stapfiana (Beille) Hutch.	936	30	20	12	254.87	15.67	530.653
Psydrax sp1	NA	1	1	1	126.69	10	1335.193
Ptychopetalum petiolatum Oliv.	35	1	1	1	55.32	13.71	1583.244
Rauvolfia vomitoria Afzel.	10	1	1	1	62.33	21.49	633.058
Rinorea sp1	NA	1	1	1	63.59	13.25	257.482
Rinorea lepidobotrys Mildbr.	95	2	2	1	29.03	20.26	1127.298
Rinorea cauliflora Kuntze	11	1	1	1	399.69	10.16	605.154

Rinorea oblongifolia (C.H.Wright) C.Marquand ex Chipp	282	7	5	4	140.75	20.54	2713.887
Santiria trimera (Oliv.) Aubré	61	3	3	3	55.51	16.81	852.369
Scottellia klaineana Pierre	186	2	2	2	74.55	11.34	773.088
Scytopetalum klaineanum Pierre ex Engl.	53	1	1	1	39.64	13.67	734.138
Sorindeia juglandifolia (A.Rich.) Planch. ex Oliv.	47	2	1	1	176.61	12.32	862.659
Soyauxia gabonensis Olíiv.	498	5	5	5	91.17	16.62	213.380
Strombosia pustulata Oliv.	787	17	12	8	99.64	15.42	831.444
Strombosia scheffleri Engl.	201	8	7	6	104.43	20.32	740.776
Strombosia sp1	489	17	12	8	128.74	16.15	1027.949
Tabernaemontana crassa Benth.	83	2	2	2	295.54	16.29	572.875
Tabernaemontana brachyantha Stapf	471	10	7	5	465.9	16.95	550.385
Talbotiella korupensis Mackinder & Wieringa	194	6	4	3	7.63	22.14	849.921
Tapura africana Oliv.	81	3	3	3	96.18	16.61	617.034
Treculia africana Decne. ex Trécul	10	2	1	1	148.97	11.76	2852.229
Trichilia prieuriana A.Juss.	46	3	2	2	88.85	13.5	2619.363
Trichoscypha sp4	7	1	1	1	115.36	14.42	1159.845
Uapaca staudtii Pax	151	3	3	2	281.99	13.5	582.351
Uvariastrum pynaertii De Wild.	52	1	1	1	67.28	14.52	943.979
Uvariodendron connivens (Benth.) R.E. Fr.	NA	3	3	3	190.25	13.42	612.950

Vitex grandifolia Gürke	97	2	2	2	113.59	13.07	615.789
Vitex sp1	56	1	1	1	49.81	28.74	969.363
Warneckea jasminoides (Gilg) Jacq.-Fél.	20	1	1	1	27.06	13.53	770.486
Zanthoxylum gilletii (De Wild.) P.G.Waterman	153	2	1	1	83.53	42.47	1015.352

Appendix 5. Correlation circle to illustrate spatial distribution of topography and soil-related variables.

pHW: pH in water; NIT: total nitrogen; TPH: total phosphorus; CEC: Cation exchange capacity; MOC: Moisture content; ORM: Soil organic matter.



Appendix 6. Species and intraspecific trait slope trends from Jackknife analysis.

SE slope: standard error of slope; *P*: significance of intraspecific slope from 0; Bold-faced values: significantly different species at P ≤ 0.05; LA: Leaf area; SLA: Specific leaf area; LPC: Leaf phosphorus content; LNC: Leaf nitrogen content; N:P ratios

Species	Traits	Intraspecific slope	SE slope	*P*
Annickia affinis (Exell) Versteegh & Sosef	LA	-0.57	0.25	0.27
	SLA	-8.33	3.72	0.27
Anthonotha macrophylla P.Beauv.	LA	-0.31	0.2	0.37
	SLA	-7.9	30.1	0.84
Antidesma vogelianum Müll.Arg.	SLA	-0.32	0.06	0.12
	LA	-0.24	0.95	0.84
Baphia laurifolia Bail.	SLA	0.31	0.22	0.3
	LA	1.12	2.24	0.67
Baphia capparidifolia Baker	LA	-0.14	0.64	0.86
	SLA	3.31	40.73	0.95
Berlinia auriculata Benth.	SLA	-1.64	0.77	0.12
	LA	-0.51	0.67	0.5
Beilschmiedia sp2	LA	3.89	1.74	0.27
	SLA	-1.03	0.46	0.27
Calpocalyx dinklagei Harms	LA	0.56	0.34	0.19
	SLA	0.5	0.48	0.37
Carapa procera DC.	SLA	0.46	0.68	0.55
	LA	0	0.31	0.99
*Casearia barter*i Mast.	LA	**0.65**	**0**	**0**
	SLA	**3.94**	**0**	**0**
Cola flavovelutina K.Schum.	SLA	-2.1	1.07	0.07
	LA	0.6	0.51	0.25
Cola lateritia K.Schum.	LA	-5.12	2.29	0.27
	SLA	0.23	0.1	0.27
Cola acuminata (P.Beauv.) Schott & Endl.	SLA	-1.39	1.07	0.28
	LA	-0.12	0.37	0.76
Cola rostrata K.Schum	SLA	0.41	0.15	0.01
	LNC	-0.51	0.38	0.2
	LPC	-0.18	0.14	0.21
	LA	0.13	0.19	0.51
*Dasylepis thomas*ii Obama & Breteler	LA	0.32	0.22	0.2
	SLA	1.19	0.75	0.17
Diospyros gabunensis Gürke	SLA	-0.08	0.27	0.76
	LA	0.04	0.36	0.91
Dichostemma glaucescens Pierre	LA	0.21	0.2	0.31
	SLA	-0.3	0.29	0.31
Diospyros iturensis (Gürke) Letouzey & F.White	SLA	**0.85**	**0.39**	**0.04**
	LA	-0.04	0.13	0.75
Diogoa zenkeri (Engl.) Exell & Mendonça	LA	-0.22	0.33	0.5
	SLA	-0.12	1.17	0.92
Diospyros zenkeri (Gürke) F.White	SLA	0.61	0.38	0.17

	LA	-0.16	0.2	0.46
Drypetes staudtii (Pax) Hutch.	SLA	-0.14	0.13	0.29
	LA	0.03	0.14	0.84
Hunteria umbellata (K.Schum.) Hallier f.	LA	0.3	0.22	0.21
	SLA	-0.19	0.25	0.47
Hymenostegia afzelii (Oliv.) Harms	LA	0.09	0.1	0.36
	SLA	0.59	0.56	0.3
	LNC	-0.13	0.14	0.38
	LPC	0	0.22	1
Hypodaphnis zenkeri (Engl.) Stapf	LA	-0.43	0.15	0.06
	SLA	0.19	2.21	0.94
Klaineanthus gabonii Pierre	SLA	-0.21	0.45	0.65
	LA	-0.01	0.28	0.97
Maesobotrya klaineana (Pierre) J.Léonard	SLA	1.4	1.57	0.44
	LA	0.43	0.53	0.48
Oubanguia alata Baker f.	SLA	**0.28**	**0.09**	**0**
	LA	0.1	0.06	0.09
	LNC	0.03	0.03	0.32
	LPC	0.01	0.01	0.63
Piptostigma oyemense Pellegr.	LA	**-0.62**	**0.05**	**0.05**
	SLA	-0.91	0.82	0.47
Placodiscus sp1	LA	-0.67	0.13	0.12
	SLA	0.03	0.6	0.97
Protomegabaria stapfiana (Beille) Hutch.	SLA	0.39	0.18	0.04
	LA	-0.08	0.13	0.57
Rinorea oblongifolia (C.H.Wright) C.Marquand ex Chipp	LA	0.22	0.51	0.69
	SLA	-0.09	0.31	0.79
Santiria trimera (Oliv.) Aubré	LA	1.24	0.8	0.36
	SLA	3.06	4.96	0.65
Soyauxia gabonensis Oliv.	LA	-0.05	0.06	0.51
	SLA	-0.15	0.31	0.66
Strombosia pustulata Oliv.	LA	0.16	0.2	0.43
	SLA	-0.02	0.45	0.96
Strombosia sp1	SLA	-0.14	0.22	0.53
	LA	0.05	0.51	0.93
Strombosia scheffleri Engl.	LA	0.25	0.22	0.3
	SLA	-0.08	0.95	0.94
Strombosiopsis tetrandra Engl.	SLA	-0.31	0.49	0.53
	LA	0.08	0.14	0.57
	LPC	-0.19	0.37	0.61
	LNC	0.26	0.36	0.49
Tapura africana Oliv.	SLA	-6.24	2.31	0.23
	LA	-1.93	2.2	0.54
Tabernaemontana brachyantha Stapf	LA	-0.38	1.54	0.81
	SLA	0.28	2.42	0.91
Talbotiella korupensis Mackinder & Wieringa	LA	0.2	0.1	0.13
	SLA	1.03	3.47	0.78
Trichilia prieuriana A.Juss.	LA	0.6	0.27	0.27

	SLA	-1.54	0.69	0.27
Uapaca staudtii Pax	LA	-2.43	1.36	0.33
	SLA	2.02	4.41	0.73
Uvariodendron connivens (Benth.) R.E. Fr.	LA	0.73	0.8	0.53
	SLA	0.29	4.53	0.96