Floristic composition, diversity and structure of the forest communities in the Kouilou Département, Republic of Congo

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Abstract:

The objectives of the study were to classify, describe and map the forest communities in the study area and to investigate possible gradients in plant diversity. The study area comprised approximately 166 000 ha in the Kouilou Département, Republic of Congo, a section of land targeted for extensive future development. In total 156 forest sample sites were surveyed using the Braun-Blanquet method of phytosociology. Diversity of each plant community was expressed in terms of species richness; Shannon-Wiener index; exponent of Shannon-Wiener index; evenness; Fisher's alpha; Simpson's index; and inverse Simpson index. Eleven plant communities were described and mapped at a much finer scale than has been done previously. The communities were arranged along two gradients: a degraded – relatively intact gradient and a wet – dry gradient. The least degraded communities, and consequently those with the highest conservation value, were the swamp forests and the okoumé forest. Overall, the values reported for the diversity parameters in the current study were within the range reported for other tropical forests in Central Africa. The study revealed a gradient between the coast (west) and the Mayombe mountain range (east) in plant diversity linked to topography and climate with plant diversity lowest at the coast. Furthermore, plant diversity was negatively related to the distance to human infrastructure. The forest communities appear to be fairly resilient to past anthropogenic disturbances, however, there is no historical analogue to the more severe types of forest destruction associated with some of the future developments anticipated, such as mechanized logging or mining.

Key words:
Diversity, Marantaceae forest; okoumé forest, phytosociology, plant communities, Shannon-Wiener index

Introduction

The deforestation rate in the Congo Basin has been notably slower than in the rest of the tropical world (Ernst *et al.* 2013; Malhi *et al.* 2013; Maniatis *et al.* 2013; Mayaux *et al.* 2013; Rudel 2013; Singh & Sharma 2009). This situation has been ascribed to various reasons such as political instability; inaccessibility of the region; lack of industrialized agriculture; and oil and mineral-based economies. This pattern is however changing, as many of the central African countries have in the past ten years become politically relatively stable enabling an upsurge in both public and private sector development projects (Megevand *et al.* 2013). These projects, accompanied by the creation of access roads into the vast and resource rich forest interior of the Congo Basin, bring their own range of ecological and environmental problems with local (Abernethy *et al.* 2013; Laurance *et al.* 2006; Petrozzi *et al.* 2016) as well as global consequences (Nogherotto *et al.* 2013). Environmental problems are further compounded by the fact that most of the knowledge on the ecology and diversity of the Congo Basin is descriptive and dated (De Wasseige *et al.* 2010), furthermore large areas remain unexplored (Corlett & Primack 2011; De Wasseige *et al.* 2010; Vande Weghe 2004). The lack of knowledge precludes proactive management, as it is impossible to predict the environmental imp-acts of development with any form of reliability (Willis *et al.* 2013). However, as most of the Congo Basin countries are signatories to international conventions on biodiversity, the challenge is to develop sustainable projects to bring economic growth with minimal negative environmental impacts. Consequently, research on the ecology and biodiversity of the Congo Basin is urgently needed (Cordeiro *et al.* 2007; Laurance *et al.* 2012; Parmentier *et al.* 2013; Willis *et al.* 2013).

In the Republic of Congo (ROC), a recent surge of private projects, spanning agriculture, commercial logging, afforestation, mining, urbanization and industrialization has been observed. This development surge is accompanied by active road-building programs to link the major cities within the country but also with neighbouring countries (Duveiller *et al.* 2008). These projects play a vital role in the growth and development of the country's economy and have significant political implications that may affect the outcome of both local and national elections. However, these activities will generally impact negatively on the environment and its biodiversity. Furthermore, when such activities are associated with deforestation, this poses a serious threat to the livelihoods of rural communities who rely directly on the natural resources provided by the forests (Brockington *et al.* 2006; Ickowitz 2006; Kameri-Mbote and Cullet 1997; Perrings and Lovett 1999). The challenge when exploiting an area for financial benefit is therefore to ensure that the impacts on biodiversity and ecosystem services have been adequately addressed and to that purpose the habitats and their diversity need to be assessed and understood (Laurance *et al.* 2012). Equipped with knowledge on habitat types and an understanding of their environmental determinants, dynamics and biodiversity, it becomes possible to evaluate impacts of development and plan for formal conservation of biodiversity and natural resources in such landscapes (Bhagwat *et al.* 2008; Cordeiro *et al.* 2007; Laurance *et al.* 2006).

The Kouilou Département spans the Atlantic coastal plain of the ROC and provides a low altitude savanna and forest continuum between the rain forests of the Gabon and those of the Democratic Republic of the Congo. A section of this coastal plain has been earmarked for intensive development within the next 10 years and critical biodiversity knowledge gaps have been identified between the Conkouati Douli National Park and the city of Pointe Noire (WCS 2010). Forest resources on this coastal plain are poorly known and existing inventories are dated (dating from 1985–1991). Moreover, almost all of the area has been logged (at least once, but in most areas more) since the inventories were undertaken (Bayol & Atyi 2009). Overall, there is a dearth of detailed phytosociological studies in the ROC and the available vegetation maps at a regional scale are not sufficient for understanding the pattern and process governing vegetation occurrence and subsequently for developing environmental management plans, which recent studies highlight as an important design feature (Murthy *et al.* 2016).

The present study was part of a multidisciplinary effort to provide an up-to-date overview of the biodiversity and its key determinants in the northern section of the Kouilou Département. The vegetation was chosen as the basis for the classification of the ecosystems because it integrates the ecological processes acting on a site or landscape more measurably than any other factor or set of factors (Kent 2012). The vegetation displays patterns that reflect the influence of environmental factors such as soil, geology and climate and provides information on the habitats for animals and rare plant species. It also reflects the degree of man's influence, degradation and temporal aspects operating on it.

The vegetation in the study area comprises both forests and savanna/grasslands. The current paper will focus specifically on the forest communities. The aims of this investigation were to

i) classify the vegetation in order to identify, describe and map plant communities, ii) quantify plantdiversity of the plant communities and place it in context to other studies conducted in tropical Africa, iii) investigate a west to east gradient between the coast and the Mayombe mountain range in biodiversity linked to topography and climate (Vande Weghe 2004), iv) investigate an anthropogenic and utilization gradient on biodiversity, and v) investigate a northwest–southeast gradient (parallel to coast) in biodiversity within selected communities.

Study Area

The study area comprised approximately 165 906 ha in the Kouilou Département in the south-western corner of the ROC. The study area lies between two conservation areas (Conkouati-Douli National Park and Tchimpounga Natural Reserve) that will be affected by development in this sector. The study's exploration area falls within an 'economic development zone', which has been ear-marked for commercial activities such as mining, logging and agriculture.

Topographically the study area is quite varied, consisting of beaches and low dunes along the Atlantic Ocean, and low undulating terrain on the coastal plains intersected by numerous drainage channels forming small lagoons and lakes. To the east the study area is bounded by the Mayombe Mountains. Most of the area belongs to the Tertiary and Quaternary coastal sedimentary basin comprising heavily leached sandy to sandy-clay soils. Cirque series sand sheets of the Pliocene epoch also occur on the coastline (Dowsett and Dowsett-Lemaire 1991; Vande Weghe 2004).

Rainfall is restricted to the wet season, which runs from October until May with a mean of 1200 mm per annum. The mean temperature in the region is 25°C with variations of 5°C from the mean during the wet and dry seasons. Mean relative humidity is 85% with variations of 2% between the seasons (Laclau *et al.* 2003).

Methodology

Field survey

Homogeneous areas were delineated on satellite imagery based on vegetation cover and density, topography, colour and texture as well from information gathered during a reconnaissance visit. These homogeneous units provided a first level of stratification for selecting sample sites. In order to establish major gradients between the coast (west) and the Mayombe mountain range (east) and northwest–southeast along the coast, a second level of stratification was applied by sampling at 5 km intervals along these gradients.

Vegetation surveys were conducted over two seasons (May 2012 and July/August 2012) following the Zurich-Montpellier (Braun-Blanquet) School of total floristic composition (Mueller-Dombois & Ellenberg 1974). In total 243 sample plots were surveyed with 156 of these plots in forest communities. An assessment of habitat features (topography, aspect, slope, degree of erosion, stone/rock cover, clay content of the soil, drainage) was made at each 25 m x 25 m sample plot delineated. Square sample plots were used for operational simplicity, although Newton (2007) lists the limitations of such square plots. Nevertheless, these plots are commonly used in tropical forest sampling (see Davidar *et al.* 2007). All identifiable plant species within the delineated area were identified and a percentage cover value allocated to each species according to the Domin Krajina-scale (Mueller-Dombois & Ellenberg 1974). Furthermore, representative percentage estimates of the vegetation cover and crown height were made for the tree, shrub and herbaceous strata at four/two levels *viz.* lower, intermediate, upper and very tall/emergent levels.

Data analysis

Floristic data classification was done with the TURBOVEG and JUICE computer programs (Hennekens & Schaminee, 2001; Tichy, 2002). TURBOVEG software was used to capture the data and a TWINSPAN was run in JUICE as a first step in the classification of the data. Furthermore, To further assist the separation of the floristic data into groups an Incremental Sum of Squares (ISS) cluster analysis was run in SYNTAX 2000 (Podani, 2001). For the ISS the cover/abundance values were converted to percentages (Van der Maarel 2007) and the percentage values standardised using a natural logarithmic ($\log_e$) standardisation. The Bray-Curtis measure (Podani 2001) was applied for the analysis. The ISS of the floristic data of all 243 relevés clearly indicated the separation between the forest (156 relevés) and savanna/grassland (87 relevés) plant communities. A second ISS cluster analysis was performed on only the forest relevés. The resulting table of sample plots against species was further refined using Braun-Blanquet tabulation procedures (Werger 1974) to produce a hierarchical classification.

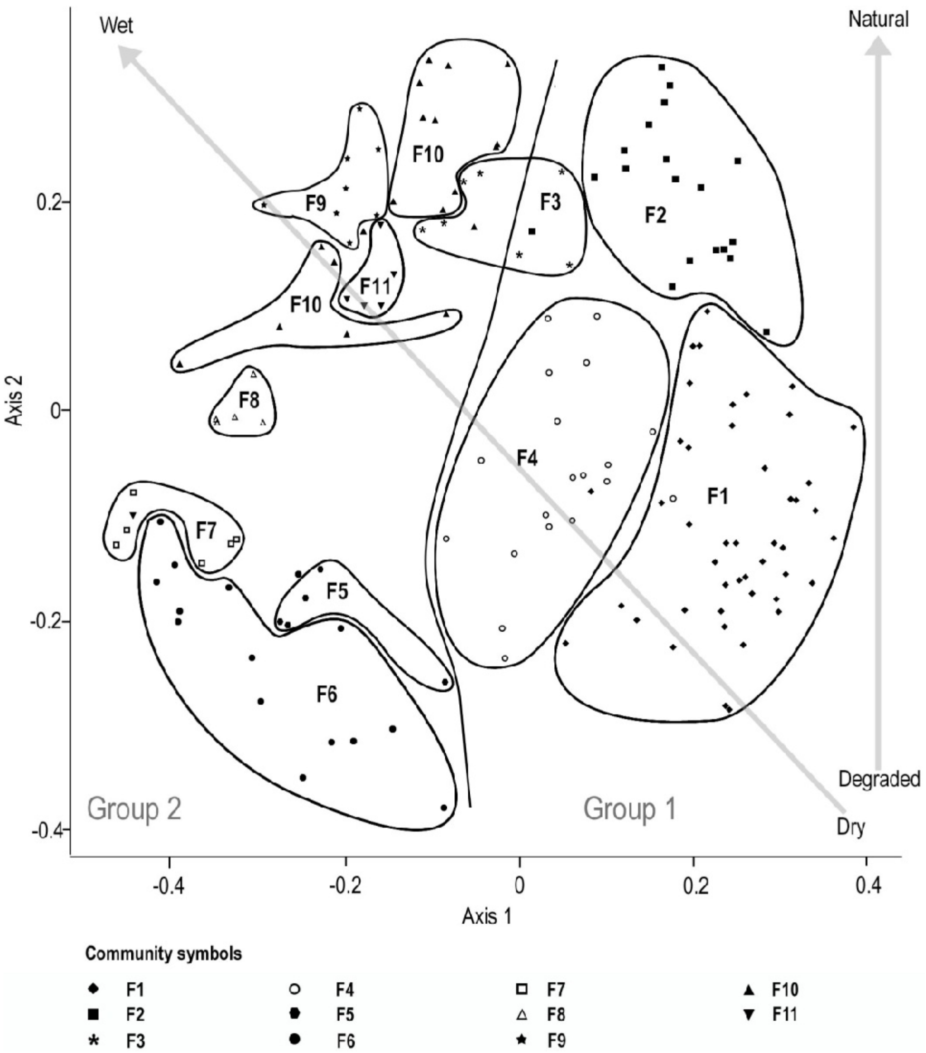

Fig. 1.A principal coordinate analysis of all the plots within the forest communities indicating the presence of two groups (black line) and 11 communities. Wet–dry and degraded–natural gradients are indicated by arrows.

To visualise the relationship between the communities the floristic data were ordinated using principal coordinate's analysis (PCoA) (McCune & Grace 2002) in SYN-TAX 2000 (Podani 2001). To indicate the vegetation succession on fallow land of different ages, an ordination was then run within the group of communities in which fallows occurred.

The following diversity parameters were calculated across all forest plots (EstimateS version 9; Colwell, 2013) as well as for each community (PAST, version 3.02; Hammer 2014):

i. Species richness (S), expressed as the mean number of species per sample plot;
ii. Shannon-Wiener index (H´), H´= $-\sum_i \frac{n_i}{n} ln \frac{n_i}{n}$ where n is number of individuals;
iii. Exponent H´ was calculated to convert H´ to the effective number of species. This conversion provides a true diversity indicating the number of equally-common species required to give the particular value of H´ (Jost 2006);
iv. Evenness (E); calculated as the Shannon-Wiener index divided by the logarithm of the number of taxa (S);
v. Fisher's alpha (a), S =a ln (1+n/a) where a is Fisher's alpha;
vi. The complement of Simpson's index of dominance, Diversity = 1 - $\sum_i^S p_i^2$ where p_i = proportion of individuals belonging to species I; and
vii. Inverse Simpson calculated as 1/(1 – D).

Table 1. Summary of the hierarchical classification of the forest communities/subcommunities of the coastal plains in the Kouilou Département, Republic of Congo.

Community No.		Basic description, including sub communities if applicable
F1.		*Megastachya mucronata* Degraded Forest
	1a.	*Sherbournia bignoniiflora - Argocoffeopsis eketensis* Degraded Forest
	1b.	*Megastachya mucronata- Ancistrocarpus densispinosus* Degraded Forest
	1c.	*Megastachya mucronata - Ipomoea involucrata* Degraded Forest
	1d.	*Megastachya mucronata - Afromomum longipetiolatum – Tetrorchidium didymostemon* Degraded Forest
	1e.	*Megastachya mucronata - Haumania liebrechtsiana – Musanga cecropioides* Degraded Forest
	1f.	*Megastachya mucronata - Mussaenada chippii – Argocoffeopsis eketensis* Degraded Forest
	1g.	*Megastachya mucronata - Ricinodendron heudelotii – Trema orientalis* Degraded Forest
	1h.	*Megastachya mucronata - Pteridium aquilinum – Manihot esculenta* Degraded Forest
	1i.	*Megastachya mucronata - Croton haumanianus – Macaranga barteri* Degraded Forest
F2.		*Haumania liebrechtsiana - Cynometra lujae* Marantaceae Forest
	2a.	*Haumania liebrechtsiana - Chazaliella letouzeyi* Marantaceae Forest
	2b.	*Haumania liebrechtsiana - Tabernaemontana crassa* Marantaceae Forest
	2c.	*Haumania liebrechtsiana - Cynometra lujae* Marantaceae Forest
	2d.	*Haumania liebrechtsiana - Pentaclethra eetveldeana* Marantaceae Forest
F3.		*Aucoumea klaineana - Klainedoxa gabonensis - Chrysobalanus icaco* Okoumé Forest
	3a.	*Aucoumea klaineana - Sacoglottis gabonensis* OkouméForest
	3b.	*Aucoumea klaineana - Geophila afzelii* Okoumé Forest
F4.		*Hymenocardia ulmoides - Milletia comosa* Secondary Forest
	4a.	*Sorindeia juglandifolia - Chaetocarpus africanus* Secondary Forest
	4b.	*Pentaclethra macrophylla - Hymenocardia ulmoides* Secondary Forest
	4c.	*Carapa procera - Pentaclethra eetveldeana* Secondary Forest
	4d.	*Millettia comosa - Thomandersia butayei* Secondary Forest
F5.		*Manilkara obovata - Manotes expensa - Symphonia globulifera* Cirque Forest
F6.		*Mangifera indica - Chrysobalanus icaco* Anthropogenic Forest
F7.		*Manilkara obovata - Borassus aethiopica - Chrysobalanus icaco* Coastal Thicket
F8.		*Manikara obovata - Syzygium guineense* Ecotonal Forest
F9.		*Lasimorpha senegalensis* Coastal Swamp Forest
F10.		*Anthostema aubryanum - Xylopia rubescens* Lowland Swamp Forest
	10a	*Symphonia globulifera - Raphia hookeri* Lowland Swamp Forest
	10b	*Elaeis guineensis - Hallea stipulosa* Lowland Swamp Forest
	10c	*Uapaca guineensis - Gilbertiodendron dewevrei* Lowland Swamp Forest
	10d	*Anthostema aubryanum - Piper guineensis* Lowland Swamp Forest
F11.		*Rhizophora racemosa* Mangrove Forest

Map preparation

Once the data analysis was complete, the preliminary map from the reconnaissance study was amended to its final version as appear in Fig. 2. The mapping process used a combination of the following: i) representation of each vegetation type by using verified information from the sample sites; ii) handmapping of different vegetation types based on vegetation types highlighted, vegetation cover and density, topography, colour and texture of the satelite pictures used (2.5 - 5.0 m resolution sourced from Google Earth ©), iii) for areas where definition of different habitat types by visual obser-

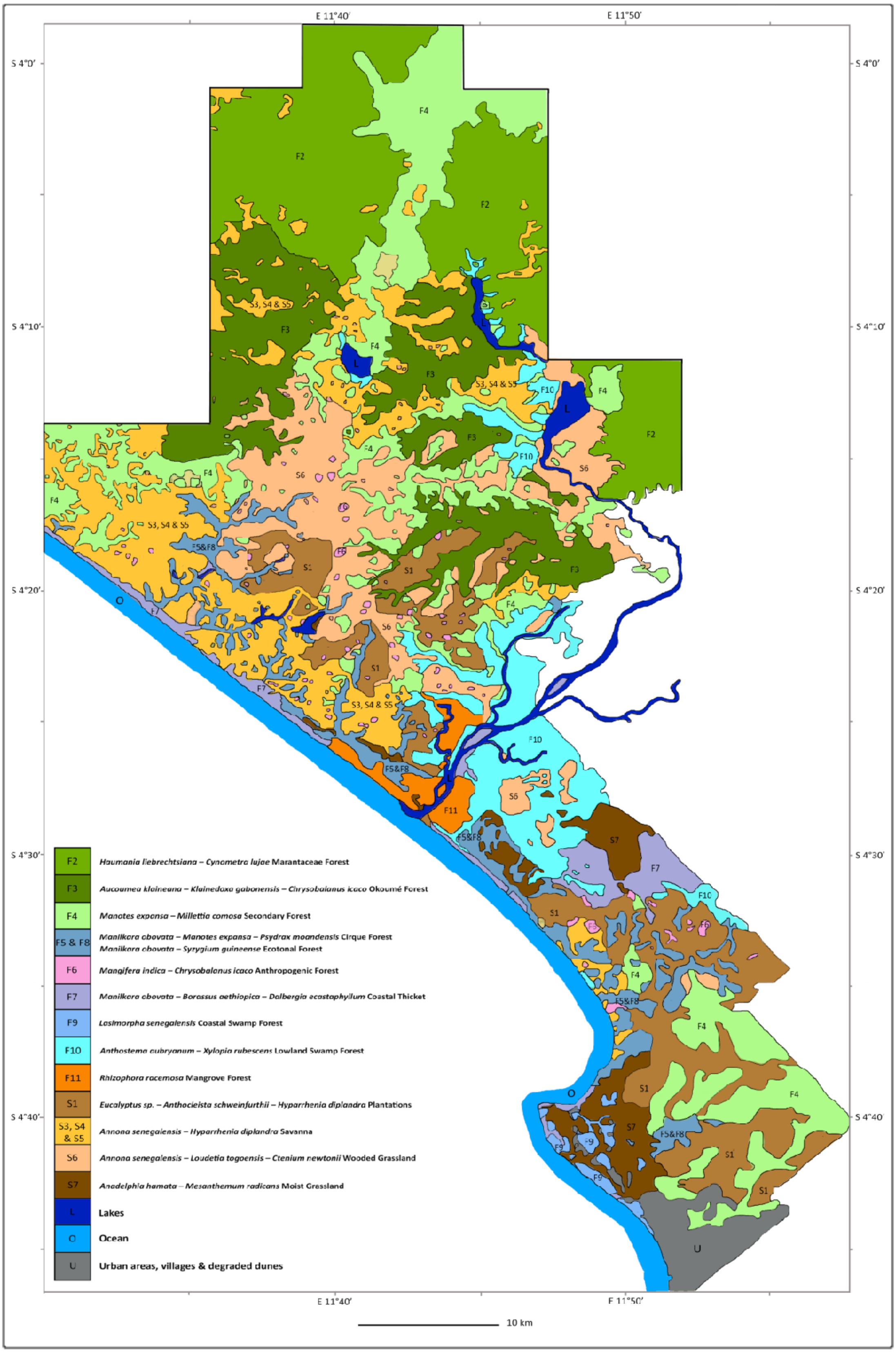

Fig. 2. Vegetation map of the study area in the Kouilou Département, Republic of Congo.

Table 3. Summary of species richness and Shannon-Wiener index of diversity for the different plant communities of Sintoukola, Republic of Congo.

Community no	For entire community			Mean values per plot						Total for community		
	Number of sample plots	Total area covered (ha)	Total number of species	Species richness	Shannon-Wiener	Exponent Shannon-Wiener	Simpson (1 - D)	Inverse Simpson	Even-ness	Fisher's Alpha	Shannon-Wiener	Inverse Simpson
F1	44	2.75	222	23	2.6	14.84	0.86	9.95	0.84	31.93	4.10	60.11
F2	19	1.19	202	28	2.6	16.63	0.84	10.16	0.83	44.96	3.95	52.12
F3	9	0.56	110	28	2.5	13.35	0.82	6.16	0.76	23.50	3.49	32.66
F4	21	1.31	138	21	2.4	12.20	0.83	7.65	0.82	19.83	4.00	54.75
F5	6	0.38	56	20	2.2	9.75	0.77	4.58	0.76	18.92	3.10	22.15
F6	17	1.06	101	19	2.1	8.98	0.75	4.73	0.72	16.28	3.12	22.74
F7	5	0.31	50	20	2.1	8.00	0.78	4.59	0.69	10.07	2.70	14.92
F8	5	0.31	14	4	0.8	3.08	0.39	2.96	0.74	0.64	1.23	3.41
F9	8	0.50	55	14	1.8	6.47	0.71	3.90	0.71	8.72	3.11	22.37
F10	17	1.06	152	22	2.5	13.19	0.83	8.72	0.81	20.65	3.77	43.52
F11	5	0.31	23	7	1.0	2.91	0.44	1.92	0.53	2.97	1.70	5.45
All plots	156		466			132.8				112.6	4.9	61.14

vation was not possible a categorisation procedure was performed in ArcView 9.2 over the whole area using 15 classes: expert opinion was then used to define whether the classes obtained in this manner were relevant or not, iv) a land use and land use change analysis performed for the study area was also used to guide the differentiation between secondary forest and mature forest.

Results

Eleven forest communities (F1 - F11), of which five were further subdivided into subcommunities, were identified (Table 1, Fig. 1 and 2). The full differential table of the forest communities is available from the corresponding author (jeromeg-augris@florafaunaman.com). Overall, the hierarchical classification of the floristic data was supported by the ISS cluster analysis and the PCoA ordination (Fig. 1). The cluster analysis of the forest communities indicated a separation between communities F1 - F4 and communities F5 - F11 (indicated in Fig. 1) with the two subcommunities of F3 divided between the two groups. Subcommunity 11a was separated from the rest of the subcommunities of F11, possibly as a result of differences in permanent *versus* seasonal inundation.

The following descriptions provide a brief assessment of the salient habitat features, the species composition of the tree, shrub and herbaceous strata as well as the structure in terms of mean crown height and mean crown cover (Table 2). For the differences in species composition between the subcommunities the reader is referred to a full differential table summarising species in each of the communities based on cover abundance values (copy to be requested from the corresponding author).

F1. *Megastachya mucronata* Degraded Forest

These degraded or secondary forests were associated with exploration tracks or with abandoned fallows. In general these forests were considered as degraded as they had been recently (within the past 7 years) disturbed by people, however, in some instances these forests were already in a process of recovery and were then considered as secondary forests. These forests occurred in valleys at a mean distance of 28.0 km from the coast at a mean altitude of 52 m above sea level. Because these degraded forests were either narrow bands following tracks or small, previously cultivated patches, they could not be mapped separately (Fig. 2). The community was found on sandy soil and erosion was low or non-existent. The mean distance to human infrastructure was 96 m (calculated as distance from plot centre to nearest man made item such as track, road or house).

The community as a whole was differentiated by species group N (full differential table - source from corresponding author) including *Megastachya mucronata*, *Camoensia brevicalyx* and *Vernonia brazza-*

Table 2. Mean crown cover (± standard error) and crown height (± standard error) of the tree, shrub and herbaceous stratum at four different levels in the forest communities.

	Tree stratum		Shrub stratum		Herbaceous stratum	
	Cover (%)	Height (m)	Cover (%)	Height (m)	Cover (%)	Height (m)
F1: *Megastachya mucronata* Degraded Forest						
Emergent/very high level	38.8±4.7	26.0±1.1	50.0±0.0	15±0.0	-	-
Upper level	49.0±5.0	20.5±1.1	-	-	90.0±0.0	4.0±0.0
Intermediate level	46.0±13.3	20.0±10.4	26.3±3.0	4.6±3.5	65.6±5.9	4.0±0.4
Lower level	24.4±7.5	0.7±0.1	32.5±7.8	1.6±0.1	58.3±5.8	1.3±0.1
F2: *Haumania liebrechtsiana - Cynometra lujae* Marantaceae Forest						
Emergent/very high level	31.9±5.9	30.9±2.1	56.4±3.2	15.0±0.0	44.3±6.9	14.3±1.3
Upper level	56.4±3.2	24.7±11.5	39.2±4.0	13.3±1.1	31.8±8.0	8.3±0.0
Intermediate level	44.5±5.3	21.4±1.4	36.5±3.8	7.8±0.5	31.1±7.7	5.3±1.1
Lower level	49.4±5.8	0.5±0.0	46.4±5.9	1.3±0.2	46.2±5.0	1.4±0.2
F3: *Aucoumea klaineana - Klainedoxa gabonensis - Chrysobalanus icaco* Okoumé Forest						
Emergent/very high level	45.7±8.4	28.9±1.6	25.0±17.6	18.3±1.7	-	-
Upper level	45.7±5.7	22.9±1.8	40.0±4.9	11.1±1.0	-	-
Intermediate level	46.0±9.3	16.8±1.3	35.7±6.5	8.1±0.6	20.0±0.0	4.5±2.5
Lower level	64.3±7.2	0.6±0.1	57.1±7.8	1.6±0.2	35.7±7.2	0.7±0.2
F4: *Hymenocardia ulmoides - Milletia comosa* Secondary Forest						
Emergent/very high level	25.0±6.5	21.3±2.4	-	-	-	-
Upper level	60.6±3.1	17.9±1.2	45.0±7.8	9.3±0.4	-	-
Intermediate level	48.9±3.1	13.1±1.9	46.1±4.4	5.8±0.4	25.9±4.9	3.8±0.6
Lower level	28.8±4.8	0.9±0.1	41.1±6.0	1.4±0.2	38.5±6.1	1.1±0.2
F5: *Manilkara obovata - Manotes expensa - Symphonia globulifera* Cirque Forest						
Emergent/very high level	60.0±0.0	25.0±0.0	-	-	-	-
Upper level	56.0±5.1	15.6±3.1	45.0±15.0	9.0±1.0	-	-
Intermediate level	57.5±11.1	10.3±3.4	46.7±5.7	4.5±0.8	50.0±40.0	2.0±0.0
Lower level	30.0±6.8	0.6±0.1	50.0±8.9	1.3±0.2	59.2±8.2	1.1±0.2
F6: *Mangifera indica - Chrysobalanus icaco* Anthropogenic Forest						
Emergent/very high level	55.0±5.0	35.0±5.0	-	-	-	-
Upper level	59.3±4.1	19.5±1.3	30.0±5.8	10.7±2.3	-	-
Intermediate level	52.3±4.4	13.3±1.4	34.0±3.2	6.7±0.5	53.8±7.3	2.7±0.4
Lower level	30.0±4.1	0.8±0.1	37.1±3.7	1.8±0.2	61.4±4.4	1.0±0.1
F7: *Manilkara obovata - Borassus aethiopica - Chrysobalanus icaco* Coastal Thicket						
Emergent/very high level	-	-	-	-	-	-
Upper level	53.3±8.8	15.7±4.7	-	-	-	-
Intermediate level	66.7±8.8	10.7±4.8	38.3±13.6	5.3±1.5	-	-
Lower level	17.7±7.9	0.8±0.2	40.0±11.5	1.3±0.3	50.0±10.0	1.0±0.0
F8: *Manikara obovata - Syzygium guineense* Ecotonal Forest						
Emergent/very high level	-	-	-	-	-	-
Upper level	67.5±4.8	15.5±2.5	-	-	-	-
Intermediate level	60.0±5.8	10.5±1.7	45.0±8.7	5.5±0.9	-	-
Lower level	40.0±4.1	0.5±0.0	47.5±4.8	1.9±0.1	50.0±22.2	1.0±0.8

Contd...

	Tree stratum		Shrub stratum		Herbaceous stratum	
	Cover (%)	Height (m)	Cover (%)	Height (m)	Cover (%)	Height (m)
F9: *Lasimorpha senegalensis* Coastal Swamp Forest						
Emergent/very high level	30.0±10.8	26.3±1.3	-	-	-	-
Upper level	57.0±13.4	19.0±2.4	27.5±2.5	9.0±1.0	-	-
Intermediate level	47.5±4.8	12.0±1.8	35.8±1.8	5.0±0.3	30.0±20.0	3.5±1.5
Lower level	42.5±13.8	1.4±0.4	25.0±8.1	1.0±0.2	49.3±12.8	1.4±0.1
F10: *Anthostema aubryanum - Xylopia rubescens* Lowland Swamp Forest						
Emergent/very high level	43.3±4.8	31.3±1.5	43.3±12.0	13.3±1.7	-	-
Upper level	55.3±3.5	25.3±1.1	28.6±6.3	10.9±1.1	-	-
Intermediate level	41.4±3.7	16.8±1.3	31.4±5.0	6.6±0.6	33.9±8.7	3.1±0.3
Lower level	41.3±4.8	1.3±0.2	38.7±7.0	1.7±0.1	59.7±6.8	1.3±0.1
F11: *Rhizophora racemosa* Mangrove Forest						
Emergent/very high level	20.0±0.0	25.0±0.0	-	-	-	-
Upper level	62.5±11.8	20.0±2.0	-	-	-	-
Intermediate level	47.5±11.1	15.0±2.0	48.0±10.7	4.0±0.6	50.0±0.0	1.0±0.0
Lower level	33.3±12.0	1.0±0.1	45.0±15.8	1.7±0.4	32.5±14.4	0.6±0.1

villensis. Nine sub communities were distinguished. Overall, species composition was highly variable and dependent on the time since disturbance or abandonment of the fallows.

The most common tree species included *Musanga cecropioides, Pentaclethra eetveldeana, Millettia comosa* and *Xylopia aethiopica*. Species such as *Trema orientalis, Cogniauxia podolaena*, *Vernonia brazzavillensis* and *Ricinodendron heudeloti* were locally prominent. The shrub layer was represented predominantly by *Alchornea cordifolia*, *Croton haumanianus*, *Mussaenda chippii, Chromolaena odorata, Manihot esculenta* and the scandent shrub *Argocoffeopsis eketensis. Megastachya mucronata* and *Panicum brevifolium* were the most prominent grass species and *Scleria boivinii* the most abundant sedge. Although the species composition of the herbaceous layer varied among subcommunities, the dominant contributing species were *Haumania liebrechtsiana*, *Cissus oreophila, Cyathula prostrata* and *Aframomum longipetiolatum.*

Fig. 3 represents an ordination on only F1 - F4. Several plots were on fallow land and the age since abandonment of the cropland has been indicated in the figure. Recently abandoned cropland within F1 occurred predominantly towards the top of the ordination plane, whereas the oldest fallow sites occurred towards the bottom of the ordination plane in communities F1 but also F2. All the fallow sites within community F4 were closely grouped and lay adjacent to F1.

Structurally, the tree stratum was well developed in the emergent and upper canopy levels (Table 2). The shrub stratum had the highest cover values for the intermediate and lower levels(Table 2). Only two levels were distinguished for the herbaceous stratum, with the intermediate level being best developed (Table 2).

F2. *Haumania liebrechtsiana - Cynometra lujae* Marantaceae Forest

These Marantaceae forests covered ~17% of the study area and occurred in valleys of the Mayombe Mountain foothills furthest inland of the current study area. Mean distance to the coast was 29.8 km and mean altitude 51 m above sea level. The community occupied sandy soil and erosion was low to non-existent. Human influence such as logging and plant and firewood collecting was observed. The mean distance of the sample plots to human infrastructure was 180 m.

This community (except subcommunity 2d) was differentiated by species group S (full differential table - source from corresponding author) with diagnostic species such as *Staudtia kamerunensis, Synsepalum longecuneatum, Diospyros hoyleana* and *Pausinystalia johimbe* the most noteworthy. Four subcommunities were identified.

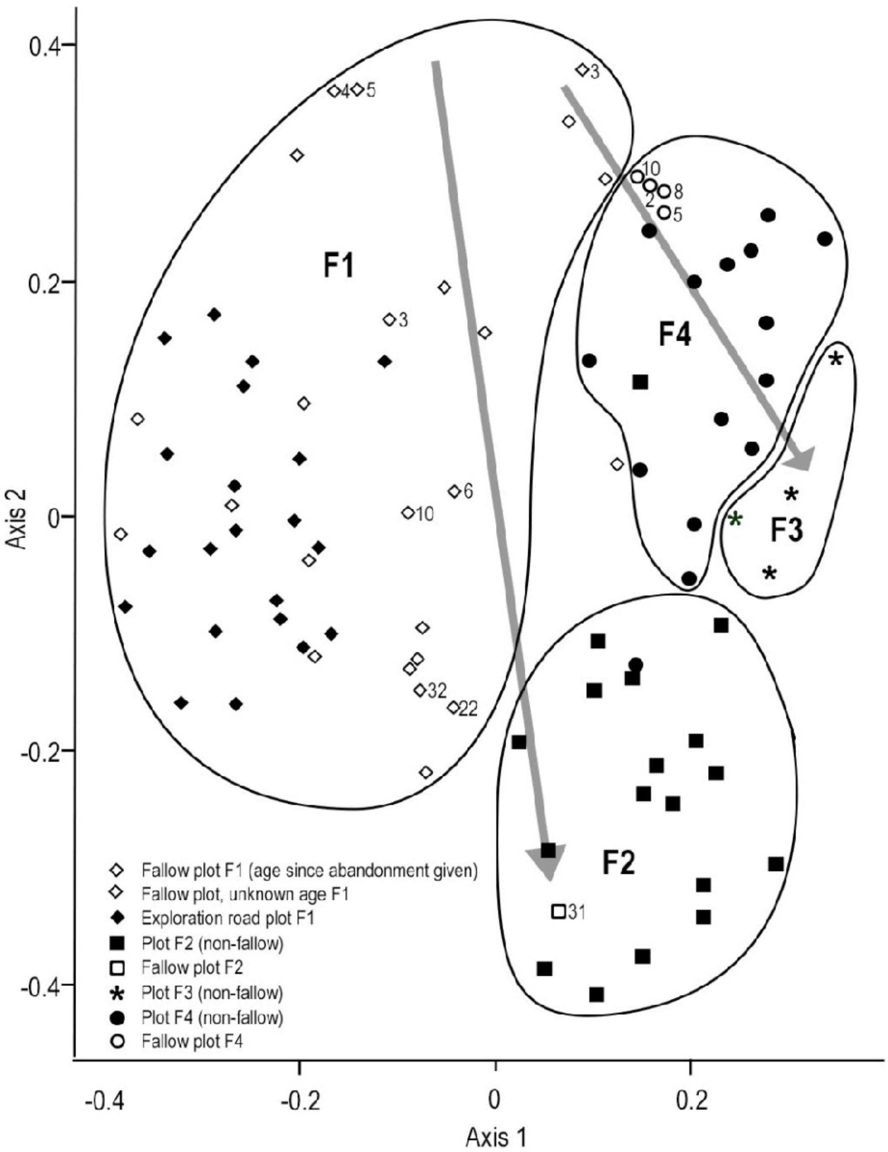

Fig. 3. Principal coordinate analysis scatter diagram of Group 1-forest communities indicating possible successional pathways. Fallow sites (open symbols) of known age are qualified by the number of years since abandonment and the arrows indicate possible successional sequences. F1, Degraded forest; F2, Marantaceae forest; F3, Okoumé forest; and F4, Secondary Forest.

The most prominent tree species included the diagnostic species mentioned above as well as *Garcinia kola, Dicranolepis laciniata, Caloncoba welwitschii, Dialium polyanthum, Dichostemma glaucescens, Pentaclethra eetveldeana* and *Trichilia heudelotii*. Other conspicuous tree species were *Tabernaemontana crassa, Croton mayumbensis, Dracaena reflexa, Panda oleosa* and *Coula edulis*. Shrub species included *Diospyros hoyleana*, *Dialium polyanthum*, *Thomandersia butayei* and the liana *Manniophyton fulvum*. The herbaceous layer was represented by *Haumania liebrechtsiana, Agelantha villosiflorum, Mostuea brunonis* and *Nephthytis afzelii*. *Haumania liebrechtsiana* was the dominant herbaceous species often forming an almost impenetrable lower canopy. *Guaduella oblonga* was the only grass species recorded.

The multilayered tree canopy was best developed in the upper and lower levels (Table 2). Woody liana in the shrub layer extended to a mean height of 15 m, but mean crown cover was highest at the intermediate and lower levels. The herbaceous stratum was best developed at the lower level (cover 31%) primarily due to the abundance of Marantaceae species.

F3. *Aucoumea klaineana - Klainedoxa gabonensis - Chrysobalanus icaco* Okoumé Forest

The okoumé forests covered ~12% of the study area and formed a discontinuous band seawards of the Marantaceae forests (F2). Mean distance to the coast was 25.6 km and mean altitude was 37 m a.s.l. The community occupied sandy soil and erosion was low to non-existent. Although soils were not permanently waterlogged, seasonal inundation could occur, especially in subcommunity 3a. This is demonstrated by the position of these plots within the wetland sites in the ordination (Fig. 1). Signs of human activity were represented by logging and plant collecting, especially of *Gnetum africanum,* and firewood collecting. The mean distance to human infrastructure was 479 m.

Community F3 was differentiated by species group Y (full differential table - source from corresponding author) containing diagnostic species such as *Aucoumea klaineana, Klainedoxa gabonensis* and *Quassia gabonensis*. The two subcommunities could be distinguished by the presence of *Sacoglottis gabonensis* (tree) and the creeping herb *Geophila afzelii* respectively.

The most prominent tree species included the diagnostic tree species as well as *Sacoglottis gabonensis, Chrysobalanus icaco, Symphonia globulifera, Cassipourea* sp.*, Sorindeia juglandifolia* and *Raphia hookeri*. The shrubs *Chrysobalanus icaco*, *Cnestis iomalla*, *Gaertnera paniculata*, *Thomandersia butayei*, *Raphia hookeri* and lianas all featured prominently. Due to the dense cover of the woody layer, sunlight penetration to the lower canopy was limited and no grass species were recorded. Vines and lianas such as *Dioscorea smilacifolia, Agelaea poggeana, Smilax anceps, Geophila afzelii* and *Cnestis iomalla* were abundant.

Crown cover of the emergent (32%) and lower tree levels (45%) was among the highest of all communities in the study area (Table 2). The shrub stratum was best developed in the lower level, although high cover values were also found at the upper and intermediate levels because of the abundance of liana. The herbaceous stratum was best developed in the lower level.

F4. *Manotes expansa - Millettia comosa* Secondary Forest

These secondary forests covered ~17% of the study area and were found predominantly on southfacing footslopes on sandy soil. Mean distance from the coast was 16.6 km although the community occurred along almost the entire coast to inland gradient. Mean altitude was 46 m above sea level. Human influence, such as logging and plant collecting, was low. The mean distance of the sample plots to human infrastructure was 488 m.

Four subcommunities were distinguished, but there was no diagnostic species group that differentiated the community (full differential table - source from corresponding author).

A large number of tree species were common, e.g. *Hymenocardia ulmoides, Chaetocarpus africanus, Carapa procera, Anthocleista schweinfurthii, Manotes expansa, Greenwayodendron suaveolens*, *Cola heterophylla* and locally *Pentaclethra macrophylla* and *Pentaclethra eetveldeana.* Although species such as *Sorindeia juglandifolia*, *Greenwayodendron suaveolens* and *Chaetocarpus africanus* can exceed the current mean crown height, the woody composition was dominated by species such as *Hymenocardia ulmoides* and *Manotes expansa,* which generally do not become such tall trees. Prominent shrub species included *Psychotria peduncularis, Heinsia crinita, Morinda morindoides, Caloncoba welwitschii*, *Brenandendron donianum* and scandent shrubs such as *Tetracera alnifolia, Cnestis iomalla* and *Millettia comosa* were conspicuous.*Thomandersia butayei* and *Morinda morindoides* were typically found along the fringes of the community. No grass species were recorded and the herbaceous layer consisted of species such as *Gnetum africanum* (liana), *Aframomum citratum* and *Palisota* spp.

The multi-layered tree stratum was best developed in the upper canopy and the crown cover of the shrub stratum was almost equally developed in the intermediate and lower levels (Table 2). The herbaceous stratum had the highest cover (31%) at the lower level.

F5. *Manilkara obovata - Manotes expansa - Psydrax moandensis* Cirque Forest

These forests covered ~4% of the study area and were associated with the coastal zone. The community occurred mainly on steep slopes, in cirques, at a mean distance of 2.1 km from the coast and a mean altitude of 56 m above sea level. Soils had low clay content and erosion was moderate to high. Human influence was low, but firewood and plant collecting were noted. The mean distance to human infrastructure was 376 m.

There was no species group that differentiated this community, and it showed strong floristic relationships with both F6 and F8 (full differential table - source from corresponding author). The most conspicuous woody species were *Manilkara obovata, Symphonia globulifera, Chrysobalanus icaco, Elaeis guineensis, Syzygium guineense, Psydrax moandensis, Anthocleista schweinfurthii, Xylopia aethiopica, Heinsia crinita* and *Chaetocarpus africanus.*

Although the mean height of the emergent tree level was low, several species had the potential to reach almost double this height. High cover values were recorded for the upper and intermediate tree canopy, while in the shrub stratum the intermediate and lower levels were best developed (Table 2). Mean crown cover of the herbaceous stratum was 51% at the lower level.

F6. *Mangifera indica - Chrysobalanus icaco* Anthropogenic Forest

These anthropogenic forest patches were found on the coastal plain and covered <1% of the study area. Mean distance from the coast was 4.9 km and mean altitude was 51 m above sea level. Soils had a low clay content and no erosion was visible. Current human influence was low although signs of plant collecting were observed. The mean distance to human infrastructure was 917 m.

The community was differentiated by species group AK (full differential table - source from corresponding author) with *Mangifera indica, Millettia versicolor, Bambusa vulgaris* and *Rauvolfia vomitoria* representing the diagnostic species.

The tree layer was represented by the above-mentioned diagnostic tree species as well as by *Chrysobalanus icaco, Xylopia aethiopica, Anthocleista schweinfurthii, Elaeis guineensis* and *Macaranga spinosa*. The dominant tree was *Mangifera indica*. *Rauvolfia vomitoria*, *Tetracera alnifolia* (liana) and the alien *Lantana camara* were the dominant shrub species. *Manilkara obovata* occurred predominantly in a shrub form in this plant community, although it can attain heights exceeding 30 m. Almost no grass species were recorded and herbaceous species included *Gnetum africanum, Vismia affinis, Abrus canescens* and the fern *Nephrolepis biserrata*. Where *Bambusa vulgaris* had established, it formed virtually impenetrable monocultures that excluded all other plant species.

Mean height of the emergent tree level was the highest of all communities, although crown cover at this level was low (Table 2). Shrubs contributed fairly evenly to crown cover in the intermediate (40%) and lower levels (43%). The herbaceous cover was highest at the lower level.

F7. *Manilkara obovata - Borassus aethiopicum - Dalbergia ecastaphyllum* Coastal Thicket

These thickets covered ~3% of the study area and occurred in a narrow strip along the coast at a mean distance of 0.32 km from the coast. The mean altitude within the community was 15 m above sea level. Soils had a low clay content and no erosion was visible. Human influence was low and plant collecting was the only activity noted. The mean distance to human infrastructure was 1102 m.

This community was differentiated by species group AN (full differential table - source from corresponding author) including diagnostic species such as *Borassus aethiopicum, Heterotis rotundifolia, Dalbergia ecastaphyllum* and *Phoenix reclinata.*

Palms, *Borassus aethiopicum* and *Phoenix reclinata,* were a prominent feature of this community. The most conspicuous trees were *Manilkara obovata, Chrysobalanus icaco, Anthocleista vogelii* and *Syzygium guineense.* In the shrub layer *Psychotria peduncularis* and *Tricalysia coriacea* were noticeable together with the liana *Dalbergia ecastaphyllum,* which could extend into the upper canopy to a height of 10 m. No grass species were recorded and the most conspicuous herbaceous species were *Asystasia gangetica*, *Heterotis rotundifolia, Aframomum sericeum, Sansevieria longiflora* and *Abrus canescens*.

The tree stratum was best developed at the intermediate level (Table 2). Shrubs covered around 30 % of the area in the intermediate and lower levels, while the herbaceous stratum was prominent only at the lower level. A substantial amount of litter was present on the forest floor.

F8. *Manilkara obovata - Syzygium guineense* Ecotonal Forest

These coastal forests were not mapped separately since they represented a narrow ecotone on the fringe of community F5. The community occurred at a mean distance of 1.8 km from the coast and a mean altitude of 52 m above sea level. Soils had low clay content and no erosion was recorded. Some plant collection by the local inhabitants was noted. The mean distance to human infrastructure was 1090 m.

This species-poor community had no diagnostic species group and was characterised by the dominance of *Manilkara obovata* and *Syzygium guineense*.

The emergent layer was absent and the upper and intermediate tree canopy levels had high cover values although the height was not particularly high (Table 2). The herbaceous and shrub strata were co-dominant at the lower level.

F9. *Lasimorpha senegalensis* Coastal Swamp Forest

Community F9 covered ~1% of the study area at a mean distance of 3.3 km from the coast and mean altitude of 20 m above sea level. It occurred mostly in the southern littoral zone on flat, seasonally-flooded terrain with small raised promontories. Soils had a low to medium clay content and no erosion was discernible. Signs of plant collecting by local inhabitants were visible. The mean distance to human infrastructure was 969 m.

This community was differentiated by species group AS (full differential table - source from corres-ponding author) with *Lasimorpha senegalensis, Voacanga thouarsii, Stipularia africana* and *Panicum parvifolium* representing the diagnostic species.

The most prominent tree species were *Anthocleista vogelii, Syzygium guineense, Elaeis guineense* and *Chrysobalanus icaco*. Mayor contributors to the shrub layer were *Voacanga thouarsii, Stipularia africana, Landolphia incerta* and *Tetracera alnifolia*. The most prominent grass species was *Panicum parvifolium*, which was particularly abundant along the periphery of the swamps. Other conspicuous herbaceous species included *Gloriosa superba, Lasimorpha senegalensis* and *Aframomum sericeum*. The latter species generally exhibits a preference for slightly drier environments such as the raised promontories.

The tree stratum was best developed at the upper canopy level, although a distinct emergent layer was also present (Table 2). The shrub stratum was best developed at the intermediate and lower levels. In the herbaceous stratum cover was highest at the lower level (49 %).

F10. *Anthostema aubryanum - Xylopia rubescens* Lowland Swamp Forest

These lowland swamp forests were predominantly associated with the Kouilou River and covered ~7 % of the study area. They occurred on flat terrain at a mean distance of 11.9 km from the coast and a mean altitude of 23 m above sea level. Soils were seasonally or permanently inundated and areas of open water were often present. Very low levels of human activity were observed. The mean distance to human infrastructure was 956 m.

The community was differentiated by species group AZ (full differential table - source from corresponding author) with *Anthostema aubryanum, Xylopia rubescens, Podococcus barteri, Baphia* sp., *Laccosperma secundiflorum* and *Coelocaryon preussii* some of the diagnostic species. Four subcommunities were distinguished.

The woody layer was represented by the diagnostic tree species as well as *Chrysobalanus icaco, Symphonia globulifera, Vitex grandifolia, Gilbertiodendron dewevrei, Fleroya stipulosa* and *Anthocleista vogelii.* Palm species were prominent e.g. *Elaeis guineensis, Raphia hookeri*, *Podococcus barteri* and *Laccosperma secundiflorum.* The dominant shrub and small tree species included *Tetracera alnifolia, Warneckea membranifolia, Piper guineensis* and *Entada abyssinica. Nymphaea lotus* was found only in open water habitats.

This swamp forest had the highest crown cover (35 %) for the emergent tree level of all forest communities observed in the current study. Overall, the tree layer was fairly well developed at all levels and the high crown cover value for the very high shrub level was noteworthy (Table 2). The herbaceous stratum was well developed at the lower level with a cover of 60 %.

F11. *Rhizophora racemosa* Mangrove Forest

These mangroves covered ~1 % of the study area and occurred in saline swampy conditions. The sampled sites were located at a mean distance of 3.3 km from the coast. Mean altitude within the community was 30 m above sea level. Soils had a low to medium clay content. No signs of animal or human activity were observed. The mean distance to human infrastructure was 840 m.

This mangrove community was characterised by *Rhizophora racemosa, Hibiscus tilliaceus, Raphia subnuda, Eugenia* sp. and *Dracaena mannii* (species group BB, full differential table - source from corresponding author).

The mangrove *Rhizophora racemosa* formed an almost impenetrable monoculture. Other tree species that were visually dominant in the emergent level were *Terminalia superba* and *Ceiba pentandra* although neither were encountered within the sampling sites. Typical shrub species included *Hibiscus tilliaceus* and *Dracaena mannii.* Although not recorded within the sampling sites, *Vossia cuspidata* and *Cyperus papyrus* does occur along the river embankments.

The tree stratum was best developed in the upper canopy, while the shrub layer had high

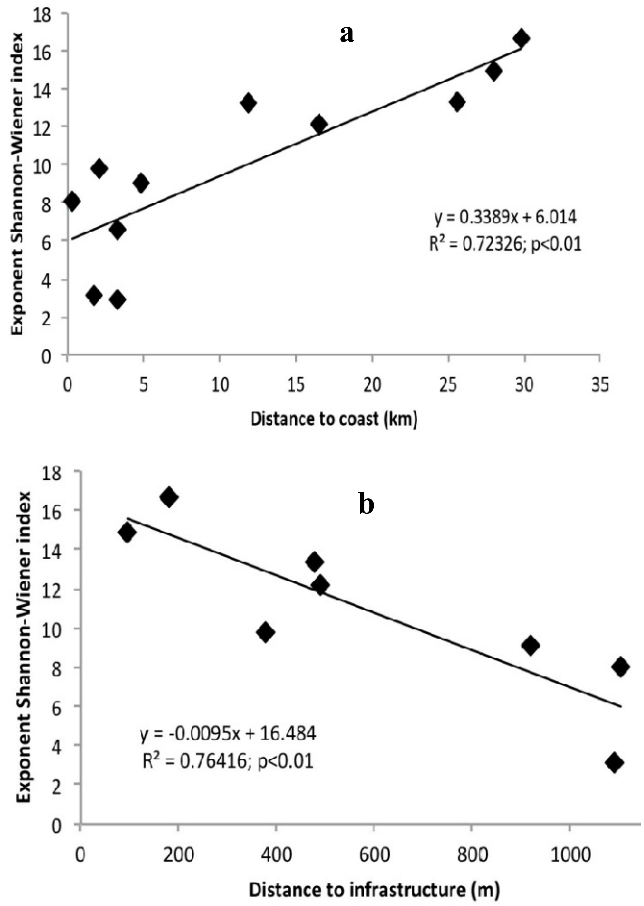

Fig. 4. Linear relationship between plant diversity (indicated by the exponent of the Shannon-Wiener index) and a. the distance to the coast and b. the distance to infrastructure.

cover values at the intermediate and lower levels (Table 2). The herbaceous stratum was present only at a lower level.

Forest diversity and Red Data species

In total 465 taxa were recorded in the 156 forest plots sampled across eleven communities. The mean number of species was highest in F2 and F3 (28 species per plot), whereas the exponent H´ and inverse Simpson, which both compare effective number of species, pointed to F2 and F1 as being the most diverse (Table 3). Evenness, Shannon-Wiener (H´) and Simpson's index were all also highest for F1 and F2. All measures of diversity indicated that F8 and F11 were the most species-poor communities.

There was no relationship between mean altitude of a community and the mean exponent H´ (R^2 = 0.0637, $P > 0.05$; not illustrated). However, there was a significant *positive*, linear relationship between the mean distance to the coast and mean exponent H´ of a community (Fig. 4a). In contrast, there was a significant *negative* relationship between the distance to the nearest human infrastructure and mean exponent H´ of a community. This relationship was even stronger if the swamp forest communities were excluded because of possible problems of accessibility (Fig. 4b). Exponent H´ did not show a trend along the northwest-southeast coastal gradient (not illustrated) in communities F3 and F4, which both occurred along this gradient.

Five Red Data species were recorded in the sample plots: *Aucoumea klaineana* (F1, F2 & F3) and *Fleroya stipulosa* (F10) are both classified as Vulnerable, whereas *Gnetum africanum* (all communities except F5 & F11) is classified as Near Threatened and both *Irvingia gabonensis* (F10) and *Milicia excelsa* (F1) are classified as Near Threatened/Lower Risk (www.iucnredlist.org).

Discussion

Phytogeography and endemism

Phytogeographically, the forest communities fall within the Guineo-Congolian Region of Endemism as defined by White (1979, 1983). Three subcentres (White 1979) are recognized within this region: Upper Guinea, Lower Guinea and Congolia. The study area falls within the Lower Guinea subcentre.

White (1983) described the Mayombe region as part of the dry semi-deciduous forest (seasonal forest), an interpretation that is not shared by Dowsett & Dowsett-Lemaire(1991), Hecketsweiler & Mokoko-Ikonga (1991) and Doumenge (1992), who all regard the vegetation as wet, semi-evergreen tropical forest. In their reconstruction of the biomes, based on a pollen analysis, Lebamba *et al.* (2009) concurred with the latter authors that floristically the Mayombe region had more affinities to the wet, semi-evergreen rainforest than the dry, seasonal forests. Although the rainfall in the Mayombe region is less than 1500 mm/annum and the dry season more than three months long, Lebamba *et al.* (2009) contend that the high cloud cover and high relative atmospheric humidity during the dry season are more important than the annual rainfall amount and dry season length in determining the floristic composition of the rain forest. In their recent analysis of patterns of tree species composition across African tropical forests

Fayolle *et al.* (2014b) distinguished six clusters. On the basis of the floristic evidence the vegetation in the study area was classified by Fayolle *et al.* (2014b) as part of the Wet Central African cluster.

Plant communities

Eleven plant communities were described and mapped at a much finer scale than has been done previously. Two gradients could be established: a disturbed - relatively undisturbed gradient (running from bottom to top in Fig. 1); and a wet - dry gradient running from lower right to upper left in Fig. 1). The least degraded communities, and consequently those with the highest conservation value were the swamp forests (F9, F10 and F11) and the okoumé forest (F3).

Three purely descriptive botanical studies were conducted in the Kouilou Département in the late 1980s and 1990s (Cusset 1989, Dowsett & Dowsett-Lemaire 1991, Hecketsweiler & Mokoko-Ikonga 1991). Although these studies were based on physiognomy and plant lists of earlier vegetation descriptions, the units described could be related fairly confidently to the communities distinguished by the classification approach performed in the current study.

Communities F1, F2, F4 and F6 all showed clear signs of human influence. In the previously mentioned studies these communities were described as anthropogenically degraded rainforest. These communities were predominantly found within the drier (Group 1) communities to the right in ordination space or in the lower part of the ordination space of Group 2 communities (Fig. 1). Community F1 was a degraded forest community containing most fallow sites as well as sites where recent (2010 - 2012) mine exploration activities had occurred. Although a fair number of mature forest species still occurred, the community was composed primarily of pioneer species such as *Chromolaena odorata, Harungana madagascariensis, Croton haumanianus, Trema guineense, Macaranga barteri, Xylopia aethiopica, Pteridium aquilinum, Ricinodendron heudelotii* and *Musanga cecropioides*. Several of these pioneer species are known to be common in repeatedly human-disturbed areas along roads and around settlements (Fayolle *et al.* 2014a) and consequently F1 is believed to be in a young successional stage.

The successional sequence on the fallows in the study area seems to follow a similar route to that described by Moutsamboté *et al.* (2000) who recognized four stages. The first stage is dominated by *Chromolaena odorata*, followed by *Hymenocardia ulmoides, Harungana madagas-cariensis, Trema guineensis* and *Xylopia aethiopica* after 3 - 4 years in the second and third stages. More phanerophytes occur in the fourth stage, when the vegetation corresponds to a pre-forest stage. Several authors have commented on an apparent change in the successional sequence in recent years. Originally the successional pathway on abandoned cultivated land in Mayombe was through a *Musanga cecropioides* dominated stage (De Foresta & Schwartz 1991). However, since the permanent settling of villages and associated increased population density, fallows of shorter duration than previously are applied. This increased cultivation intensity has led to fallow fields being invaded by *Chromolaena odorata* or sometimes *Pteridium aquilinum* (De Foresta & Schwartz 1991, Ngobo *et al.* 2004) as was reported in the current study. When considering the age of the fallows, the successional pathway seemed to run from F1 to F2 (Fig. 3). Alternatively, the progression could proceed from F1 through F4 to an okoumé forest stage (F3).

Community F4 was also a degraded or secondary forest. It had a lower mean tree height for the emergent, upper and intermediate levels than F2 and was consequently considered to represent a younger successional stage than F2 (Marantaceae forest).

Marantaceae forests, such as represented by F2 in the current study, are common in the lowland rainforest in the Congo Basin and have been described by various authors (Cusset 1989, Vande Weghe 2004). These forests are characterized by an almost impenetrable layer of Marantaceae, in particular *Haumania liebre-chtsiana*, and Zingiberaceae (e.g. *Aframomum* species and *Costus* species). These species quickly fill gaps in disturbed forest and form extensive shrubberies in logged areas. The aggressively growing Marantaceae can prevent further forest development, although several young secondary species were encountered in these forests in the study area. Brncic *et al.* (2007) speculated that Marantaceae forests indicate sites of previous human occupancy. This view is supported by Tovar *et al.* (2014) who investigated the hypothesis that the four major forest types in central African rainforest (mixed forest, Marantaceae forest, *Gilbertiodendron* monodominant forest and swamp forest) are the consequence of different intensities of past human activity, in particular fire. Tovar et al. (2014) found that the areas currently covered by

Marantaceae forest underwent more frequent burning events than the other forest types over the past 2500 years.

Mango forests (F6) clearly have an anthropogenic origin. Most villages in the region are associated with orchards constituted of many edible fruit-bearing species, usually including mango trees. Old and abandoned settlements (50 - 100 years) can often be identified by the remaining mango trees, although most of the other planted and edible alien species have disappeared and been replaced by some native species (Dowsett & Dowsett-Lemaire 1991). After abandonment these patches may act as nuclei for forest succession. Although the structure of F6 resembled a mature forest, there was a lack of many mature indigenous forest tree species, which could hinder progression towards a more advanced successional stage.

The coastal evergreen rainforest, or 'Atlantic littoral forest' (Letouzey 1968, 1985), characterised by *Aucoumea klaineana* and *Sacoglottis gabonensis* (F3) is one of the main wet Guineo-Congolian forest types (White 1983). In the Congolese littoral *Sacoglottis gabonensis* occurs at its southern distribution limit and is no longer co-dominant with *Aucoumea klaineana* as is the case in the Cameroono-Gabonese littoral (Kimpouni *et al.* 2013). Low numbers of *Sacoglottis gabonensis* were noted in the study area, with the species only being present in one of the subcommunities of F3. Although F3 cannot be regarded as a primary forest it represented the most mature successional stage in the study area. *Aucoumea klaineana* is a long-lived pioneer species and therefore often a remnant within mature or even primary forest. In the study area the okoumé forests showed healthy regeneration. According to Pangou *et al.* (2006) successful seedling establishment of *Aucoumea klaineana* occurs only every 20-30 years when an abundance of seeds are present and favourable climatic conditions for seedling established are present. Furthermore, in soils with high clay content, high grass cover and an abundance of hardwood species and Cecropiaceae, the successful regeneration of *Aucoumea klaineana* is hindered.

The cirque forests (F5) occurred within close proximity to the coastline and were comparable to the *Symphonia* gorge forest described by Dowsett & Dowsett-Lemaire (1991) and part of the 'melange sublittoral' described by Cusset (1989). Natural disturbances are common within the cirques and could explain the young successional stage of this community. All the dominant species in F5 (*Anthocleista schweinfurthii, Symphonia globulifera, Elaeis guineense* and *Chrysobalanus icaco*) are typical of disturbed or pioneer forest sites. The species-poor community F8 formed a narrow band around the cirque forests and is probably best seen as an ecotone between the cirque forest and the adjoining savanna vegetation.

The low-canopy, coastal thicket (F7) grew up to a few meters immediately inland of the beach zone. The community was comparable to the *Manilkara/Chrysobalanus* coastal thickets previously described by various authors (Dowsett & Dowsett-Lemaire 1991, Mbatchou 2004).

Communities F9, F10 and F11 were wetland communities and were grouped towards the top left in the ordination (Group 2, Fig. 1). Community F9 occurred in small patches along the coast and was a seasonally-flooded forest, whereas F10 was a permanently-flooded forest associated with *Cyperus papyrus* stands. The mangroves (F11) were found near the mouth of the Kouilou River at the interface between land and sea. The mangrove species possess physiological traits enabling them to overcome high salinity and frequent tidal inundation. Both the permanently-flooded swamp forest (F10) and mangroves (F11) showed little signs of human impact and could be regarded as mature forest communities.

It must be noted that the highly preferred timber species, *Terminalia superba,* was not recorded in any sampling sites. It was however noted while travelling through the study area in inaccessible places on the banks of the Kouilou River or on islands of higher ground within the swamp forest (F10) and the mangroves (F11). In 1991, Dowset & Dowsett-Lemaire reported it as a conspicuous species. The species decline is most likely a result of legal and illegal logging during the past 20 years. The species is classified as a pioneer species and usually regenerates well after forest exploitation. Since no saplings were encountered in the current study the lack of regeneration could possibly be due to a shortage of seeds (Daïnou *et al.* 2011).

Although several studies have shown that African forests are fairly resilient to climate and past anthropogenic disturbances (Brncic *et al.* 2007, Gourlet-Fleury *et al.* 2013; Kassi *et al.* 2008; Oslisley *et al.* 2013; Rudel 2013; Willis *et al.* 2004) there is no historical analogue to mechanized logging or vegetation destruction by mining activities. Destruction of the topsoil is expected to have severe long-lasting effects and intervention would be necessary for forest recovery. Active rehabilitation of sites where topsoil had been removed should explore patterns of forest survival that have allowed these forests to recover quickly in the past and attempt to recreate suitable conditions.

Plant diversity

The current study could quantitatively confirm the west to east gradient between the coast and the Mayombe mountain range with respect to plant diversity, which is linked to topography and climate as suggested by Hecketsweiler & Mokoko-Ikonga (1991), Dowsett & Dowsett-Lemaire (1991) and Vande Weghe (2004). Forest plant diversity was lowest at the coast and increased further inland.

The relationship between plant diversity and distance from human infrastructure produced an unexpected result, with the highest diversity closest to human infrastructure where the human pressure and disturbance is at its highest. This relationship could be interpreted in two ways: a. humans are selecting the most diverse plant communities for their activities or b. human impacts are increasing plant diversity. Previous reports of human impacts and disturbance on plant diversity in African rain forests have been contradictory. Von Gemerden *et al.* (2003) reported a decrease in diversity after disturbance, whereas Kassi *et al.* (2008) reported that shifting cultivation could increase diversity on condition that the fields were small and embedded in a forest matrix, cultivation lasted only a few years, remnant trees were preserved and fire was excluded. The present results support this hypothesis.

Diversity parameters are difficult to compare if plot sizes are not equal among studies, the values provided in Table 2 can therefore only serve to indicate broad trends. The Shannon-Wiener index was 4.90 if data of all 156 plots were combined (9.8 ha) and ranged from a low of 1.23 to 4.10 for individual communities. By comparison, Shannon-Wiener values of 3.34 to 4.14 have been reported for forests with gregarious species (Lope forest, Gabon; in Senterre & Lejoly 2001) and from 5.24 to 5.46 in mixed forests (Dja forest, Cameroon; in Senterre & Lejoly 2001) to 5.79 in rainforest (Nsork, Equatorial Guinea, in Senterre & Lejoly 2001). In Campo-Ma'an, Cameroon, Shannon-Wiener index values ranged from 0.12 for mangroves (0.2 ha) to 5.33 (1.4 ha) for entire communities with the total for the entire Campo-Ma'an (14.7 ha) being 5.54. Mean values for 1 ha plots in Central Africa range from 3.72 to 4.00 (Gonmadje *et al.* 2011). Overall, the values reported within the current study area are within the range reported for other tropical forests in Central Africa.

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