



A new insight in the structure, composition and functioning of central African moist forests



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ABSTRACT

The greater part of the semi-deciduous moist forests of the Congo basin has been given to logging companies for exploitation. In the next decades, very few of these forests will remain intact. In this paper, we aimed to identify large-scale variations in the structure, composition and functioning of African moist forests that could serve as a baseline for both management and conservation purposes. Commercial forest inventory data were assembled for 49,711 0.5-ha plots, covering an area of more than six million hectares, crossing the borders of Cameroon, Central African Republic and Republic of Congo. Floristic composition was analyzed for a subset of 176 genera reliably identified in the field. Three key functional traits of tropical trees: regeneration guild, leaf phenology, and wood specific gravity, were collected at the species level from various sources, and assigned at the genus level. We first investigated the main variations in forest structure and composition, and identified seven forest types based on these variations. Differences in the percentage of pioneer and deciduous stems, and mean wood specific gravity were tested between forest types. Most of the study area was composed of a mosaic of the structural variations of the forests characterized by the occurrence of *Celtis* (Ulmaceae) species, which are mostly composed of frequent and abundant genera that formed the common floristic pool of the region. Secondary *Musanga* (Moraceae) forest is located in repeatedly disturbed areas, along roads and around main cities; mixed *Manilkara* (Sapotaceae) forest covers a huge area in the southern Central African Republic and in the northern Republic of Congo; and monodominant *Gilbertiodendron* (Fabaceae) forest is sparsely distributed along rivers. The contrasted structure, composition, and functioning of the forest types imply pronounced differences in population and ecosystem processes, and call for adapted management and conservation strategies.

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1. Introduction

The need to manage and conserve tropical forests has never been greater, with a unique challenge to develop strategies that are suitable for sustainable timber production, biodiversity conservation and carbon storage. The tropical forests of central Africa comprise the second largest continuous block of tropical forests in the world, possibly harbouring up to 20,000 different plant

species including c. 8000 species of trees (White, 1983) and storing more than 200 t of carbon per hectare in live trees (Lewis et al., 2009, 2013).

Patterns of diversity and endemism are now well established for sub-Saharan Africa (Küper et al., 2004; Linder, 2001). In central Africa, high rates of diversity and endemism in the Cameroon–Gabon (Lower Guinea) and Kivu areas have been generally recognized (Linder, 2001; White, 1983), and these hotspots of biodiversity have been considered as priorities for conservation (Küper et al., 2004). In between these centres of diversity and endemism, immense areas are covered by lowland semi-deciduous moist forests that are not particularly species-rich and mostly composed of widely distributed species (White, 1983). Since the

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1950s most of these forests, with the exception of the Democratic Republic of Congo, have been granted to private logging companies and impacted by selective logging (Nasi et al., 2012; Ruiz Pérez et al., 2005). In the next decades, very few of the forests outside protected areas will remain intact, yet they have never received particular attention as a whole.

Information on the composition, and to the lesser extent the structure, of these forests are available from phytogeographical maps at the national (Boulvert, 1986 in the Central African Republic; Caballé, 1978 in Gabon; Lebrun and Gilbert, 1954 in the Democratic Republic of Congo; Letouzey, 1985 in Cameroon) and continental (Aubréville et al., 1958; De Namur, 1990; White, 1983) scales. Thematic (e.g. carbon maps) or land use maps have also been obtained by remote sensing techniques (e.g. Baccini et al., 2008; Mayaux et al., 2004; Verhegghen et al., 2012). On the one hand, phytogeographical maps have mainly been based on expert knowledge and basic statistical analyses of forest inventory data. On the other hand, remote sensing maps generally distinguish between only a few broad forest types, without additional details. Maps derived from MODIS imagery, which take advantage of canopy phenology, are likely to bridge the gap between phytogeographical maps and remote sensing (Gond et al., 2013; Viennois et al., 2013). To date, however, no work has been attempted that integrates detailed forest inventory data with ecological knowledge on forest structure, tree species composition and functioning to produce a comprehensive forest map for decision makers.

The lack of such a comprehensive map of the Congo basin forests has limited their management on a sound ecological basis as discussed in Gourlet-Fleury et al. (2013b). At the same time, extensive areas of forests have been sampled by logging companies to quantify the timber resource and its spatial variations, providing a unique opportunity to study these forests in detail and at a large scale. Data from commercial forest inventories have generally been regarded as imprecise or incomplete by academic standards, despite the quantitative information they contain. However, since diameters of all trees are measured in plots of known areas, following similar protocols, they provide accurate quantitative information for the analysis of structural variations (Couteron et al., 2003). Moreover, it has been demonstrated that commercial forest inventory data are suitable to detect compositional gradients (Réjou-Mechain et al., 2011). We here hypothesize that large-scale commercial forest inventories combined with species functional traits and modern statistical techniques are an efficient and more detailed alternative to remote sensing to define informative forest types over large areas using ground-based information.

In this paper we used the spatially extensive data collected by logging companies to identify large-scale variations in structure and both floristic and functional composition of the semi-deciduous moist forests of the Congo basin. To do so, we used three key functional traits for tropical trees that influence the forest's response to disturbance, soil fertility and climate: shade tolerance, leaf phenology and wood specific gravity (Fayolle et al., 2012; Maharjan et al., 2011; Slik et al., 2008). We specifically aimed to (i) detect large scale variations in forest structure and composition; (ii) identify and label forest types with regards to their structural, compositional and functional characteristics; and (iii) produce a distribution map of these forest types that could serve as a baseline for forest management (including conservation) and sampling (e.g. to estimate carbon stocks) purposes. We also discussed how the combined information on forest structure, composition and function gained from this work might help orientate future management options in the study area.

2. Material and methods

2.1. Study area

The study area covers more than 6 million ha of lowland moist forests located in southeastern Cameroon, in southern Central African Republic and in northern Republic of Congo. A humid tropical climate prevails in the area with a dry season of up to 3-months. Mean annual rainfall varies between 1400 and 1700 mm. Altitude ranges from 300 to 800 m a.s.l. The vegetation belongs to the mixed, moist, semi-deciduous forests of the Guineo-Congolian region where the Malvaceae, Ulmaceae (now Cannabaceae), Sapotaceae and Meliaceae families are abundant (Boulvert, 1986; Harris, 2002; Letouzey, 1985; White, 1983).

2.2. Inventory data

In this study, we used data from large-scale forest inventories from 22 logging concessions (six in Cameroon, six in the Central African Republic, and ten in the Republic of Congo) completed by logging companies prior to the implementation of forest management. The sampling design was systematic, irrespective of forest types. It consisted of parallel transects 2 or 3 km apart, and divided into consecutive rectangular plots (25 × 200 m or 20 × 250 m, i.e. 0.5 ha). Due to restricted access to data in five Congolian concessions, we only used half of the inventoried plots (i.e. every other plot). Within each plot, all trees with a diameter at breast height (dbh) ≥ 30 cm were measured and identified. Trees with diameters up to 140 cm were assigned to 10 cm wide dbh classes and larger trees were grouped in the dbh ≥ 150 cm class. Vernacular names were converted to species-level scientific names when possible. Taxonomy was revised and homogenized according to the African plant database (available online <http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php>).

The analyses were conducted at the genus level because vernacular names are more reliable at the genus level than at the species level (Réjou-Mechain et al., 2011), and because the genus resolution captures most of the floristic variation in tropical forests (Higgins and Ruokolainen, 2004; Slik et al., 2003; ter Steege et al., 2006). A total of 343 genera were identified in the 49,711 inventoried plots. The unidentified trees represented between 0 and 5 stems, and between 0 and 0.92 m² basal area per plot, with a mean of 0.6 stem (1.7% of total stem number) and 0.1 m² (1.3% of total basal area) per plot. Within the 49,711 inventoried plots, a total of 35,930 plots (72% of plots) did not contain any unidentified tree at genus level. We further restricted the analyses to a set of 176 tree genera for which we had confidence in the identification across the study area following a set of rules. The selected genera should (1) be present in at least two logging concessions and represented by at least 30 trees across the study area; (2) show a mean diameter distribution across the study area in agreement with the genus biology (genera known to contain only understory species should not reach large diameter); and (3) show a coherent spatial pattern across the study area (no major gap in the distribution, absence in one concession while present in all the neighboring concessions, and that could correspond to the local misidentification by tree spotters). Despite an extensive check of data and taxonomy, minor misidentifications may have persisted. The set of genera analyzed represented, on average, 85% of plot stem number and 88% of plot basal area. Among the 49,711 plots, we only considered the 38,363 plots for which the 176 genera contributed to more than 80% of plot total stem number.

2.3. Functional traits

We collected information on shade tolerance, leaf phenology, and wood specific gravity at the species level from local floras, published databases and field observations. Information on shade tolerance was collected for 298 tree species. Shade tolerance was based on the species' regeneration guilds identified in Ghana (Hawthorne, 1995). Pioneers require gaps for establishment, non-pioneer light-demanding species can establish in shade but need a gap to grow to their full height, and shade tolerant species can be found in shade both as young and older plants. We obtained a reliable shade tolerance at the genus level for 147 genera, among which 47 were considered pioneers, 37 non-pioneer light demanders and 63 shade tolerant. Information on leaf phenology was collected for 309 tree species. We obtained a reliable leaf phenology at the genus level for 146 genera, among which 99 were considered evergreen and 47 deciduous. Wood specific gravity values were extracted from the International Cooperation Centre in Agronomic Research for Development (CIRAD) database on wood properties (http://www.cirad.fr/ur/bois_tropicaux). We obtained wood specific gravity values at the genus level for 48 genera. When no information was available for the genus, we assigned family, order or global mean value by following a set of rules intended to reduce sampling bias within the various taxonomic levels (see Gourlet-Fleury et al., 2011). In the genus set considered, wood specific gravity ranged between 0.216 and 0.876 g cm⁻³ for *Ricinodendron* (Euphorbiaceae) and *Bobgunnia* (Fabaceae), respectively, with a mean of 0.580 g cm⁻³. In contrast to wood specific gravity, for the two qualitative traits (shade tolerance and leaf phenology) when there was no information available or no tendency of trait conservatism at the genus level the genus was ignored in the trait calculation.

2.4. Data analyses

2.4.1. Structure

We calculated the abundance (number of stems) of the 13 diameter classes in each 0.5 ha plot. We performed a correspondence analysis (CA) of the plot × diameter matrix to detect the main axes of structural variation (Couteron et al., 2003).

2.4.2. Composition

We calculated the abundance of the 176 genera in each 0.5 ha plot. We performed a non-symmetrical correspondence analysis (NSCA) of the plot × genus matrix to detect the main axes of compositional variation (Couteron et al., 2003). Intuitively, the NSCA can be seen as a weighted CA where genera are weighted by their abundance. The results of the NSCA are thus less sensitive than that of CA to particular correspondences between poor plots and taxa that are globally rare but locally abundant. In addition, we used a Monte Carlo permutation test (RV test) with 999 repetitions to test for a link between the CA structure and NSCA composition to test for a significant link between forest structure and composition.

2.4.3. Clustering

We used the *k*-means method to identify forest types based on both structural and compositional variations (plot scores on the axes 1 and 2 of the CA structure and on the axes 1–4 of the NSCA composition were used in the same cluster analysis). The *k*-means method partitions the points into *k* groups such that the within-group variance is minimized. It is equivalent to a model-based clustering with equal-shape equal-volume within-cluster variances. We built all clusterings for *k* = 1–20. We then examined the weighted mean of variance per group to select the number of groups.

2.4.4. Dominant and indicator genera

We identified the dominant and indicator genera for each forest type. Genera with more than one stem per plot (two stems per hectare) within each forest type were considered dominant. Indicator genera were identified with the method of Dufrêne and Legendre (1997). The method calculates an indicator value (IV) for each genus *i* in each forest type *j* which is an integrated measure for the relative mean abundance (A_{ij}) and the relative frequency (B_{ij}).

$$IV_{ij} = A_{ij} \times B_{ij}$$

IVs can vary between 0 (no association of the genus with the forest type) and 1 (all individuals of a particular genus were found in all plots belonging to a particular forest type, and was absent in all other plots). A Monte Carlo random permutation test based on 999 iterations was used to test whether the observed IV of a genus in a forest type was significantly greater than zero.

2.4.5. Traits

We calculated, at plot level, the percentage of pioneer stems, the percentage of deciduous stems and the mean wood specific gravity weighted by genus abundance. We tested for functional differences across forest types with non-parametric analyses of variance and identified pair-wise differences with Wilcoxon tests.

All statistical analyses were performed within the open source R statistical software. We used the following packages: *ade4* for multivariate analyses (CA and NSCA), *cluster* for the *k*-means clustering, and *labdsv* for the calculation of indicator values and the associated significance.

3. Results

3.1. Structural variation

Trees in our combined dataset of 38,363 0.5-ha plots numbered more than one million (i.e. 1,388,566 trees with a dbh ≥ 30 cm). Stand structure strongly varied across the study area encompassing recently disturbed areas, more or less old-growth secondary forests and mature forests. Stem density and basal area (dbh ≥ 30 cm) ranged between 17–54 stems and 3.8–14 m² per 0.5-ha plot, respectively (5% and 95% quantiles). Mean diameter distribution across the whole study area showed the classical reverse-J shape of old-growth tropical forests.

The CA of the plot × diameter abundance matrix highlighted two major structural axes (Fig. 1). The first axis (13.1% of variance explained) opposed plots rich in small trees (30–40 cm dbh) with positive scores to plots rich in large trees (≥ 80 cm) with negative scores (i.e. successional forests recovering after disturbance versus 'old growth' forests). The second axis (10.2% of variance explained) opposed plots rich in medium-sized trees (40–80 cm dbh) to plots rich in large trees.

3.2. Compositional variation

The trees belonging to the 176 study genera numbered more than one million (i.e. 1,250,382 trees with a dbh ≥ 30 cm). The ten most frequent genera in the study area (Appendix S1) were *Celtis* (Ulmaceae), *Strombosia* (Olacaceae), *Polyalthia* (Annonaceae), *Petersianthus* (Lecythidaceae), *Entandrophragma* (Meliaceae), *Anonidium* (Annonaceae), *Chrysophyllum* (Sapotaceae), *Angylocalyx* (Fabaceae), *Staudtia* (Myricaceae) and *Xylopia* (Annonaceae). The locally abundant *Manilkara* (Sapotaceae), *Terminalia* (Combretaceae) and *Macaranga* (Euphorbiaceae) genera belonged to the ten most abundant genera but were less evenly distributed and thus less frequent than *Angylocalyx*, *Chrysophyllum* and *Xylopia*.

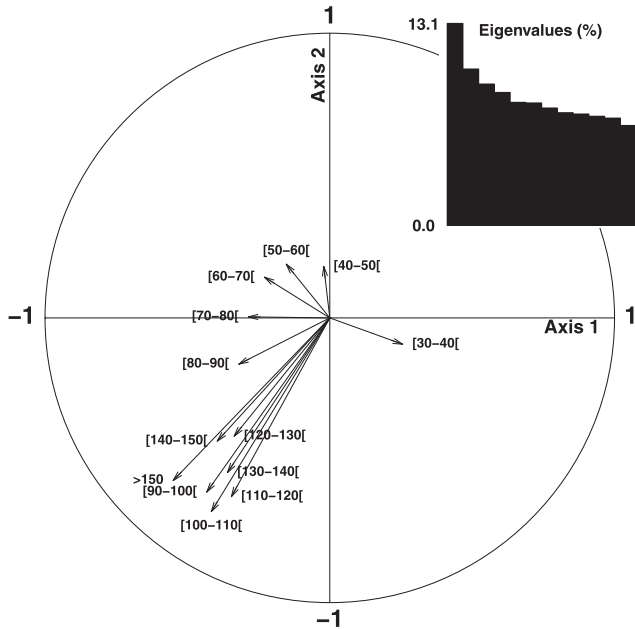


Fig. 1. Analysis of stand structure. The factorial plane defined by the first two axes of a correspondence analysis of the abundance matrix of the 38,363 plots × 13 diameter classes is given. Variance explained by each axis is given in the inserted barplot.

The NSCA of the genus abundance matrix highlighted four major compositional axes which together explained 29.3% of variance (Fig. 2). The first axis (10.4% of variance) highlighted plots rich in *Celtis*. The second axis (7.4% of variance) opposed two contrasted assemblages: plots rich in *Manilkara* with positive scores and plots dominated by *Gilbertiodendron* (monodominant stands) with negative scores. The third axis (6.4% of variance explained) reinforced the uniqueness of plots dominated by *Gilbertiodendron* with negative scores. The fourth axis (5.1% of variance explained) opposed two contrasted assemblages: plots rich in *Celtis*, *Polyalthia* and

Strombosia (shade tolerant species) with positive scores to plots rich in *Musanga* and *Petersianthus* (both pioneers). These results were obtained with the number of stems as a measure of abundance. The same trends emerged with basal area since stem number and basal area were highly correlated (Pearson's correlation coefficient, $r = 0.98$, $P < 0.001$).

We identified a slight but significant link between the results of the CA structure and that of the NSCA composition. The RV coefficient was low (0.012) but significant according to the simulated p -value ($P < 0.001$) based on 999 repetitions indicating a slight but significant link between forest structure and composition.

3.3. Forest types

We identified seven forest types reflecting the large-scale variations in the diameter structure, floristic composition and functional traits across the study area (Table 1, Figs. 3 and 4). Among the 176 study genera, a total of 139 genera were significant indicators of a particular forest type (Appendix S1). Although significant indicators, *Celtis*, *Petersianthus*, *Polyalthia*, *Terminalia*, and *Strombosia* were widespread across the whole study area and also dominant species of most forest types (Table 1). We thus considered this set of abundant and generalist genera to form the common floristic pool of the semi-deciduous forests of the Congo basin. *Celtis* is definitely the most ubiquitous genus in the moist semi-deciduous forests of central (and western) Africa, and these forests have been formerly described as moist semi-deciduous forests rich in Ulmaceae because of the abundance and diversity of the *Celtis* genus (White, 1983 and references therein).

The old-growth *Celtis* forest showed the classical reverse-J shape distribution of diameters, with no particular deviation from the mean diameter structure (Fig. 3). This forest type was characterised by *Celtis*, and to a lesser extent, by the other genera of the common floristic pool, *Petersianthus*, *Strombosia* and *Terminalia*. The old-growth *Celtis* forest was distributed across the whole study area (6166 plots, 16.1%), with the exception of the northern Republic of Congo, and showed the highest level of deciduousness (Fig. 4).

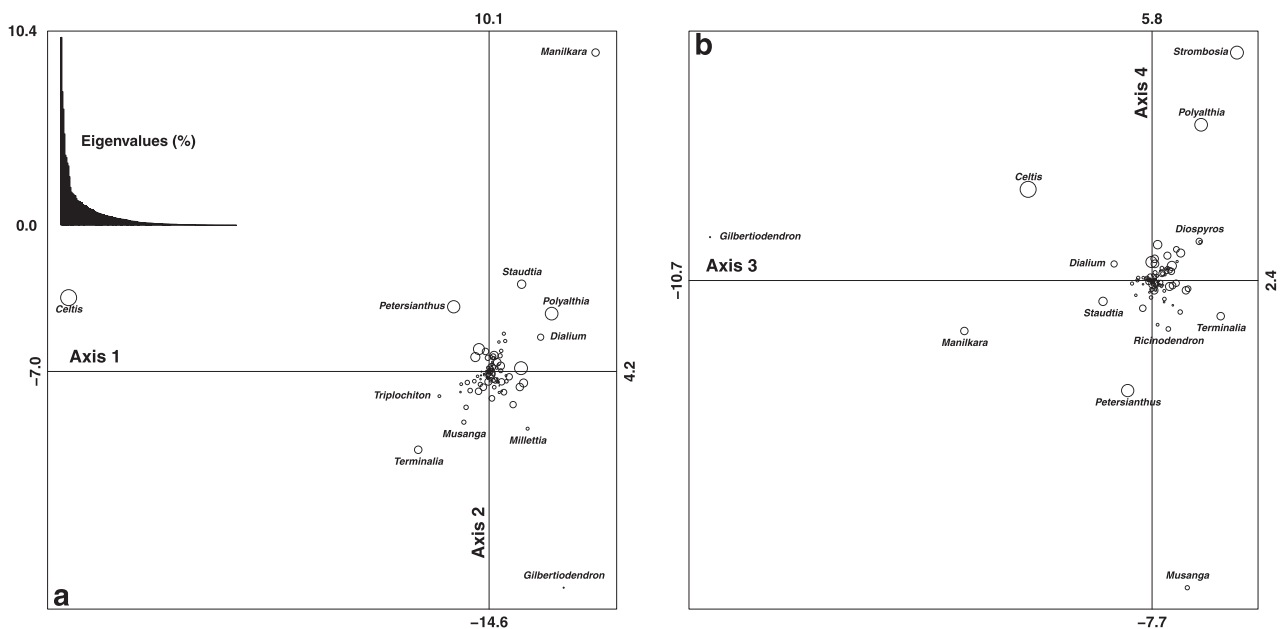


Fig. 2. Analysis of genus composition. The factorial plane defined by the first two axes (a), and defined by the third and fourth (b) axes of the non-symmetrical correspondence analysis of the abundance matrix of the 38,363 plots × 176 genera are given. The size of the symbols is proportional to the genus frequency other the study area. Variance explained by each axis is given in the inserted barplot.

Table 1

Dominant and indicator genera of the seven forest types. The number of plots and representativeness is given for each forest type. The mean stem number per plot and the indicator value are given in bracket for dominant and indicator genera, respectively.

Forest type	Dominant genera	Indicator genera
Old-growth <i>Celtis</i> forest 6166 plots 16.1%	<i>Celtis</i> (7.6) <i>Petersianthus</i> (1.7) <i>Strombosia</i> (1.2)	<i>Celtis</i> (0.47 ^{***}) <i>Terminalia</i> (0.12 ^{***}) <i>Chrysophyllum</i> (0.10 ^{***}) <i>Eribroma</i> (0.09 ^{***}) <i>Triplochiton</i> (0.09 ^{***})
Poorly regenerating <i>Celtis</i> forest 5616 plots 14.6%	<i>Celtis</i> (1.9) <i>Terminalia</i> (1.2) <i>Polyalthia</i> (1.2) <i>Strombosia</i> (1.2) <i>Petersianthus</i> (1.1)	<i>Alstonia</i> (0.09 ^{***})
Degraded <i>Celtis</i> forest 8788 plots 22.9%	<i>Strombosia</i> (1.7) <i>Polyalthia</i> (1.2) <i>Celtis</i> (1.2)	<i>Strombosia</i> (0.14 ^{***}) <i>Millettia</i> (0.11 ^{***}) <i>Diospyros</i> (0.09 ^{***}) <i>Panda</i> (0.09 ^{***})
Young <i>Celtis</i> forest 9047 plots 23.6%	<i>Polyalthia</i> (2.0) <i>Celtis</i> (1.5) <i>Strombosia</i> (1.5) <i>Petersianthus</i> (1.1)	<i>Xylopia</i> (0.10 ^{***}) <i>Macaranga</i> (0.09 ^{***})
Secondary <i>Musanga</i> forest 1901 plots 5.0%	<i>Musanga</i> (6.0) <i>Petersianthus</i> (1.8) <i>Celtis</i> (1.6) <i>Terminalia</i> (1.2) <i>Trilepisium</i> (1.0)	<i>Musanga</i> (0.74 ^{***}) <i>Trilepisium</i> (0.18 ^{***}) <i>Ricinodendron</i> (0.17 ^{***})
Mixed <i>Manilkara</i> forest 6223 plots 16.2%	<i>Manilkara</i> (5.6) <i>Staudtia</i> (1.9) <i>Celtis</i> (1.9) <i>Polyalthia</i> (1.9) <i>Petersianthus</i> (1.8) <i>Strombosia</i> (1.3) <i>Dialium</i> (1.2)	<i>Manilkara</i> (0.73 ^{***}) <i>Staudtia</i> (0.3 ^{***}) <i>Prioria</i> (0.24 ^{***}) <i>Synsepalum</i> (0.20 ^{***}) <i>Polyalthia</i> (0.18 ^{***}) <i>Dialium</i> (0.16 ^{***}) <i>Ganophyllum</i> (0.15 ^{***}) <i>Petersianthus</i> (0.15 ^{***}) <i>Tessmannia</i> (0.14 ^{***}) <i>Entandrophragma</i> (0.11 ^{***}) <i>Ongokea</i> (0.11 ^{***}) <i>Angylocalyx</i> (0.10 ^{***}) <i>Blighia</i> (0.10 ^{***}) <i>Maranthes</i> (0.10 ^{***}) <i>Hexalobus</i> (0.09 ^{***}) <i>Pycnanthus</i> (0.09 ^{***})
Monodominant <i>Gilbertiodendron</i> forest 622 plots 1.6%	<i>Gilbertiodendron</i> (15.9)	<i>Gilbertiodendron</i> (0.97 ^{***})

*** Significant indicator genera at $P < 0.001$ are indicated.

Among the seven forest types, a total of three groups differed only slightly in composition (similar scores on the compositional axes) but showed strong differences in diameter distribution. We choose to consider these three forest types as derivatives of the old-growth *Celtis* forest for these reasons. (1) No distinctive composition. These forest types are dominated by the genera of the common floristic pool and there are few indicator genera. (2) High floristic similarity. These three forest types share many species with the old-growth *Celtis* forest according to the analysis of floristic dissimilarity (Table 2). (3) No coherent distribution. These three forest types were distributed across the whole of the study area and did not show any structured spatial pattern. The derivative forest types were labelled according to their structural variation of the old-growth *Celtis* forest: poorly regenerating, degraded and young.

The poorly regenerating *Celtis* forest tended to be poor in small trees but rich in large trees. The composition of this forest type, dominated by the genera of the common floristic pool, was similar to that of the old-growth *Celtis* forest (Table 2). The scattered distribution across the whole study area (5616 plots, 14.6%), the specific diameter structure, the common floristic pool and the absence of any specific indicator except *Alstonia* suggest that it is a variant of the old-growth *Celtis* forest locally rich in large trees.

The degraded *Celtis* forest tended to be poor in both small and large trees. The composition of this forest type, dominated by the genera of the common floristic pool, was similar to that of the old-growth *Celtis* forest. The scattered distribution across the whole study area (8788 plots, 22.9%), the specific diameter structure and the common floristic pool but the presence of *Millettia*, *Diospyros* and *Panda* as indicators suggests that it is a variant of the old-growth *Celtis* forest that developed locally due to soil factors and/or due to degradation by past human disturbance.

The young *Celtis* forest was rich in small trees but poor in medium-sized and large trees. The composition of this forest type, dominated by the genera of the common floristic pool, was similar to that of the old-growth *Celtis* forest. The scattered distribution across the whole study area (9047 plots, 23.6%), the specific diameter structure, the common floristic pool and the presence of *Xylopia* and *Macaranga* as indicators suggest that the type represents *Celtis* forest recovering from small-scale disturbance due to natural gap formation or logging.

The secondary *Musanga* forest was poor in medium-sized and large trees. The composition of this forest type, dominated by the genera of the common floristic pool in addition to the strong dominance of *Musanga* (with a mean of 6 stems per 0.5 ha plot), was otherwise similar to that of the old-growth *Celtis* forest. The localized distribution along roads and around main cities (1901 plots, 5.0%), the specific diameter structure and the presence of *Trilepisium* and *Ricinodendron* (pioneers) as indicators, suggest a forest regrowing after farming that may lead to old-growth *Celtis* forest as succession proceeds. This forest type was rich in pioneer stems and had a low mean wood specific gravity (Fig. 4).

The mixed *Manilkara* forest showed no major deviation from the mean diameter structure, except a slight deficit in big trees. The composition of this forest type, characterised by *Manilkara* and *Staudtia*, and to a lesser extent, by the genera of the common floristic pool, and with several other indicator genera, *Prioria*, *Synsepalum*, and *Dialium*, differed strongly from that of the *Celtis* forest. The *Manilkara* forest covered a huge area in southern Central African Republic and in northern Republic of Congo (6223 plots, 16.2%), tended to be poor in pioneer and deciduous stems, and to have a high mean wood specific gravity.

The *Gilbertiodendron* forest tended to be poor in both small and very large trees. This forest type was strongly dominated by a single genus, *Gilbertiodendron* (with a mean of 16 stems per 0.5 ha plot) with no other characteristic or indicator genus. The monodominant *Gilbertiodendron* forest, sparsely distributed along rivers in the northern Republic of Congo, and to a lesser extent in southeastern Cameroon and southern Central African Republic (622 plots, 1.6%), tended to be poor in pioneer and deciduous stems, and to have a high mean wood specific gravity.

4. Discussion

In this paper we used the spatially extensive data collected by logging companies to identify large-scale variations in the structure and both the floristic and functional composition of the semi-deciduous moist forests of the northern Congo basin. These variations across forest types imply pronounced differences in population and ecosystem processes, and call for different

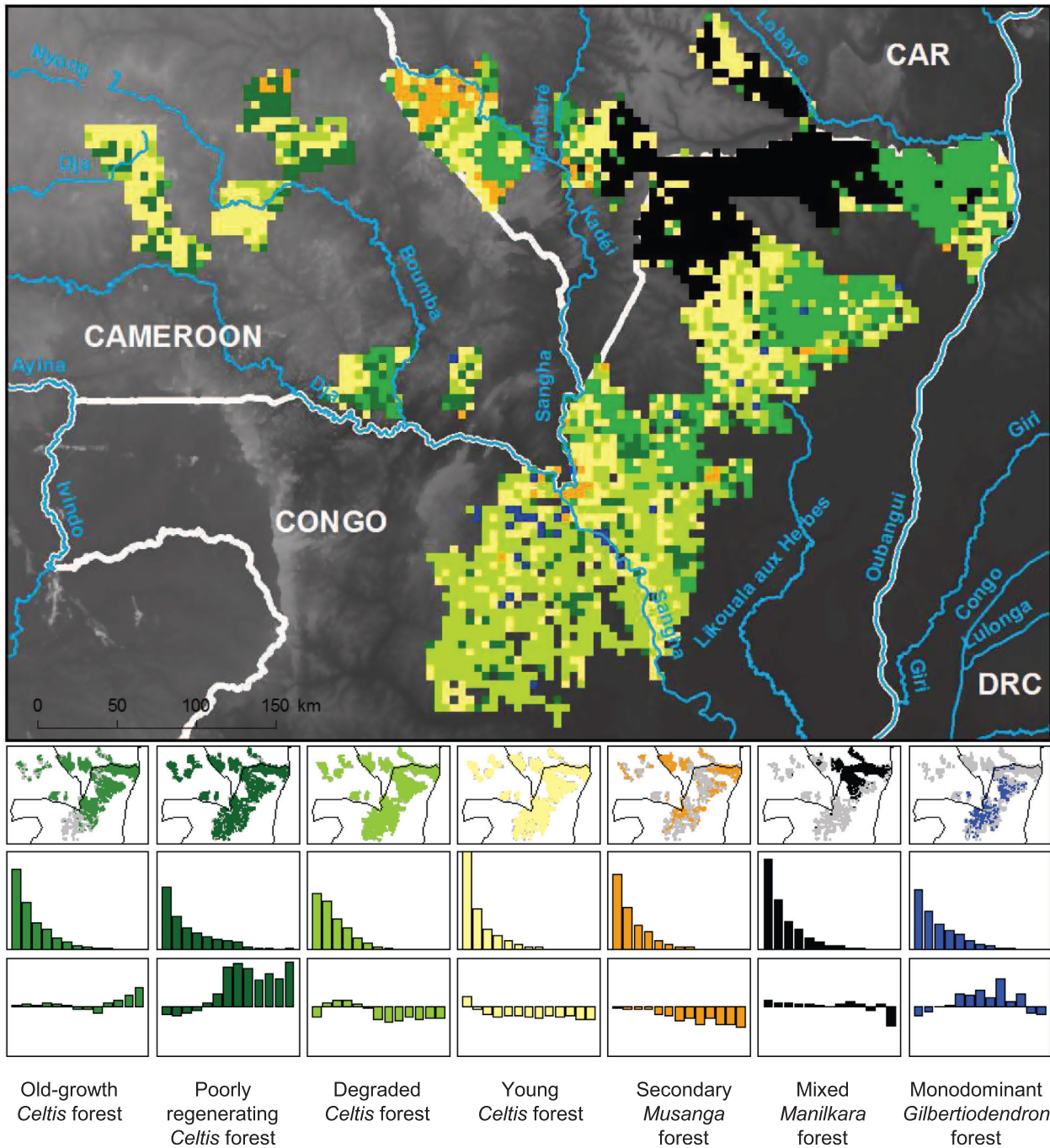


Fig. 3. Map of the forest types. The presented map has been smoothed based on a 5×5 km grid. Country borders and main rivers are indicated. The topography is shown in background. Individual forest type maps, types of diameter structure and their deviation from the mean diameter structure for all 38,363 0.5-ha plots are shown in the lower panels.

management and conservation strategies. The distribution map of these forest types could serve as a baseline for both management and conservation purposes.

4.1. Contrasted structure, composition and functioning within African moist forests

The forest types identified in this study agreed reasonably well with previous descriptions of the vegetation in the study area from phytogeographical maps (Bégué, 1967; Boulvert, 1986; Letouzey, 1985), commented checklists (Gillet and Doucet, 2012; Harris, 2002), floristic analyses (Fayolle et al., 2012; Gourlet-Fleury et al., 2011; Réjou-Méchain et al., 2008) and remote sensing studies

(Betbeder et al., 2014; Gond et al., 2013). For the first time, we offer a homogenized view of the forest types occurring in the study area, highlighting the links between them, and identifying the probable environmental and historical drivers.

The old-growth *Celtis* forest associated with the genera of the common floristic pool, *Petersianthus*, *Terminalia* and *Triplochiton* for large emergent trees, and *Polyalthia* and *Strombosia* for small understory trees, can be considered as the old-growth forest typical of the study area, the dense semi-deciduous forests rich in Ulmaceae and Sterculiaceae described by Aubréville (1950), White (1983), and Letouzey (1985). The Ulmaceae family is mostly represented by the abundant and diverse *Celtis* genus (represented by *C. adolfi-friderici*, *C. mildbraedii*, *C. philippensis*, *C. tessmannii*, and

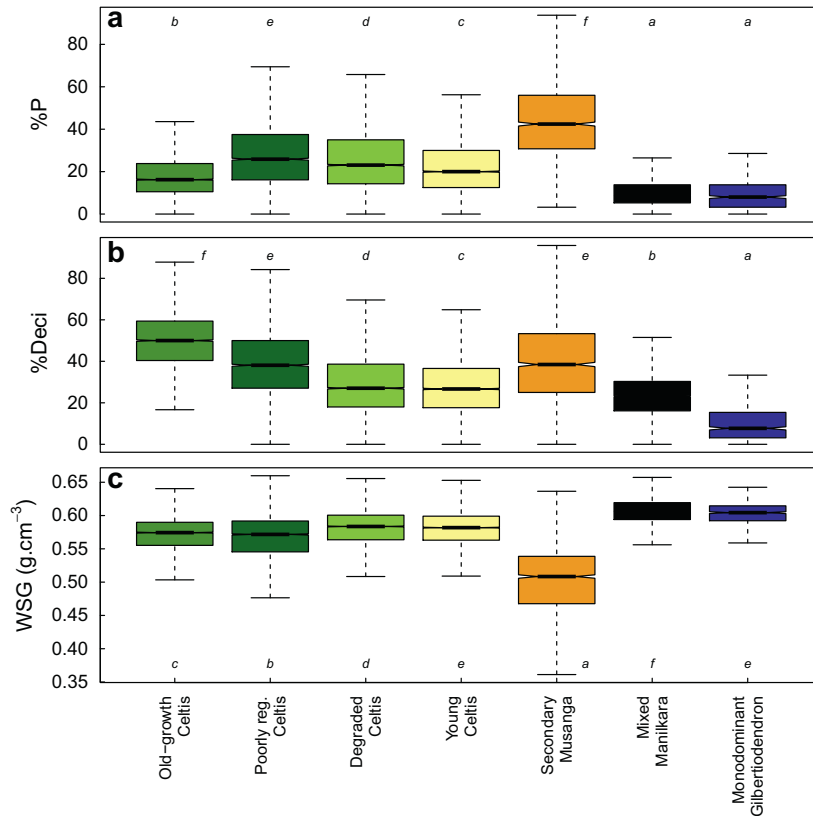


Fig. 4. Analysis of functional traits across forest types. Differences in the % of pioneer stems (a), the % of deciduous stems (b), and the mean wood specific gravity (i) were tested between forest types. Different lowercase letter indicate significant differences at $P < 0.001$.

Table 2

Floristic dissimilarity among forest types. Values of Jaccard and Morisita–Horn index are given in the upper and lower half matrix, respectively. Pairs of forest types with low dissimilarity, i.e. similar genus composition, are shown in bold.

	Celtis forest				Secondary Musanga forest	Mixed Manilkara forest	Monodominant Gilbertiodendron forest
	Old-growth	Poorly regenerating	Degraded	Young			
Celtis forest							
Old-growth	–	0.023	0.023	0.023	0.075	0.168	0.186
Poorly regenerating	0.324	–	0.071	0.070	0.544	0.442	0.931
Degraded	0.454	0.000	–	0.039	0.074	0.461	0.925
Young	0.412	0.000	0.000	–	0.074	0.395	0.205
Secondary Musanga forest	0.559	0.074	0.618	0.597	–	0.711	0.955
Mixed Manilkara forest	0.516	0.176	0.176	0.176	0.122	–	0.161
Monodominant Gilbertiodendron forest	0.932	0.205	0.205	0.926	0.175	0.933	–

C. zenkeri in the study area), and to a lesser extent, by the mono-specific *Holoptelea*, *Trema* and *Chaetacme* genera. The former Sterculiaceae family (now included in the Malvaceae) was represented by the monospecific *Chlamydocola*, *Eribroma*, *Mansonia*, *Triplochiton* and diverse *Cola*, *Pterygota*, *Sterculia* genera. The local abundance of extremely large trees of light-demanding species such as *Triplochiton scleroxylon* and *Terminalia superba*, in the old-growth and poorly regenerating *Celtis* forests indicates old-growth secondary forest rather than pristine forest (Van Gernerden et al., 2003). These forests most probably developed after land abandonment between three to four centuries ago (e.g. White and Oates, 1999; Van Gernerden et al., 2003). Evidence of human occupation and activities between 675 and 90 years BP has been recently highlighted (Morin-Rivat et al., 2014). Although hotly debated in the past, there is growing evidence for the idea that the old-growth ‘virgin’ tropical forest is a myth (Willis et al., 2004).

We identified structural variations of the old-growth *Celtis* forest that were widely distributed and not spatially homogeneous, reflecting the mosaic nature of tropical forests due to small scale natural gap dynamics and also possibly recent (<50 years) or long-term (>200 years) human disturbances. Contrary to common belief, the impacts of human occupation and activities on African moist forests is not restricted to the last few decades (Brcic et al., 2007; Van Gernerden et al., 2003; White and Oates, 1999). Mechanized logging could explain the deficit in large trees in particular places and the abundance of small and pioneer trees in other places due to the recent colonization of logging roads and gaps. In northern Congo, the huge area dominated by a degraded type of the *Celtis* forests, lacking both small and large trees, partially corresponds to the previously described open canopy Marantaceae forest (De Namur, 1990; Gillet and Doucet, 2012). In these forests tree regeneration is prevented by the dominance

of giant herbs and lianas of the Marantaceae and Zingiberaceae families. Field observations show that there is a gradient from forests with relatively closed canopies to forests with extremely open canopies all lacking trees in small diameter classes due to giant herbs and lianas. The mechanism shaping the dominance of these herbs and lianas has not yet been identified and specifically the role of past human disturbance (Brncic, 2002; Gillet, 2013) has not been determined. The spatial extent of the open Marantaceae forest remains to be determined since remote sensing studies still fail to distinguish this forest type from the rural complex because of similar spectral reflectance (Verhegghen et al., 2012).

The secondary forests dominated by *Musanga* and other pioneer genera were found in repeatedly human-disturbed areas along roads and around main cities (Fayolle et al., 2012). *Musanga cecropioides* has been recognized to dominate the first stages of forest succession in the whole Guineo-Congolian region (White, 1983), in Cameroon (Letouzey, 1985), and in the Democratic Republic of Congo (Lebrun and Gilbert, 1954). The low dissimilarity with the structural derivatives of the *Celtis* forest suggests that, in the study area, the secondary *Musanga* forest corresponds to the early stages of succession after field abandonment leading to the old-growth *Celtis* forest.

We identified a major floristic discontinuity in the southern Central African Republic and in the northern Republic of Congo with the abrupt shift from *Celtis* to *Manilkara* forest. The mixed *Manilkara* forest has been shown to be associated with the sandstone substrate (Fayolle et al., 2012) and the extremely sandy soils that developed on sandstone in this area (Gourlet-Fleury et al., 2011; Réjou-Méchain et al., 2008). In this study, we showed that the *Manilkara* forest tended to have a lower level of deciduousness and denser wood than the adjacent *Celtis* forest. The filtering of tree species with a particular set of functional traits such as slow growth rates, shade tolerance, evergreen leaves, and high wood specific gravity, have indeed been previously highlighted on the huge sandstone plateau that crosses the border of the Central African Republic and the Republic of Congo, and associated with nutrient rather than water limitation (Fayolle et al., 2012; Gourlet-Fleury et al., 2011).

We identified a sparsely distributed old-growth forest type along rivers in northern Congo, with a particular composition and function, the monodominant *Gilbertiodendron* forest, which is the only evergreen forest type in the area. *Gilbertiodendron* is a diverse and endemic genus of the Guineo-Congolian region (White, 1983). In the study area, the *Gilbertiodendron* forest is defined by the dominance of the gregarious, evergreen and shade tolerant *Gilbertiodendron dewevrei*, which is locally abundant (more than 15 stems per 0.5-ha plots) and occurs at different development stages, with an abundant regeneration of the same species (Gillet and Doucet, 2012; Harris, 2002; Lebrun and Gilbert, 1954; Letouzey, 1985). Monodominant *Gilbertiodendron* forests have developed on a variety of soil types, but tend to occur along forest streams very similar to the position of gallery forests in savanna areas (Harris, 2002). Some other species of the former Caesalpiniaceae family also tend to form monodominant forests (*Brachystegia*, *Cynometra*, *Julbernardia*) and potential mechanisms of monodominance have been thoroughly discussed (see Peh et al., 2011 and references therein).

4.2. Correspondence with previous work at the country scale

The identification and mapping of broad forest types among central African moist forests will be useful for developing appropriate forest management and conservation strategies, as well as for developing a sampling protocol suitable for estimating forest carbon stocks. Since the major decisions will be made at the country

level, we describe (and discuss) below the forest types found in each individual country.

In the Central African Republic, the dense semi-deciduous forests rich in Ulmaceae and Sterculiaceae have been additionally described as rich in Sapotaceae and Meliaceae but poor in Caesalpiniaceae (Boulvert, 1986). Three main forest types have long been recognized within the southwestern forest area (Boulvert, 1986; Lanly, 1966a, 1966b). The forests of the Mbaere district on the sandstone substrate were first described as primary forests characterized by *Oxystigma* (=Prioria), *Petersianthus*, *Lovoa*, and *Autranella*. In this study, we clearly identified this forest type as the mixed *Manilkara* forests, with *Prioria*, *Petersianthus*, *Lovoa* and *Autranella* as significant indicators for large emergent trees. *Staudtia*, *Synsepalum* and *Polyalthia* were also significant indicator genera for small understory trees. The two other forest types previously identified as old-growth secondary forests characterized by huge trees of long-lived pioneers such as *Triplochiton* and *Terminalia* (Boulvert, 1986; Lanly, 1966a, 1966b) are located outside the sandstone plateau: the Lobaye district in the eastern part, and the Upper Sangha district in the western part, with additional Cameroonian genera such as *Mansonia* and *Holoptelea* in the western part. In this study, we were only able to characterize the forests of the Upper Sangha district in the eastern part, which appeared to be characterized by both the old-growth *Celtis* forest, with *Terminalia* and *Triplochiton* as significant indicators, and by the secondary *Musanga* forest, with both *Mansonia* and *Holoptelea* as significant indicators. Our results thus confirmed the secondary character of the forests of the Upper Sangha district where only a little old-growth forest remains. At smaller scale in the Dzanga-Sangha National Park, Harris (2002) additionally distinguished the monodominant *Gilbertiodendron* forest from the mixed species terra firme forest. The monodominant *Gilbertiodendron* forest is little represented in the Central African Republic due to the sparse river system, but may have also been under-sampled by the logging companies.

The northern Republic of Congo has long been an under-sampled area (White, 1983). Apart from the recent publication of a commented checklist (Gillet and Doucet, 2012), only a little published information was available on vegetation composition and distribution in the area. Bégué (1967) distinguished the pure stands of *Macrobium* (=Gilbertiodendron), which correspond to the monodominant *Gilbertiodendron* forest, from mixed lowland terra firme forests, which correspond to a mix between our *Celtis* and *Manilkara* forests, and the secondary *Musanga* forest. He also identified and located several patches of open forests, rich in medium size trees and dominated by giant herbs of the Marantaceae family in the understory, which correspond to the open Marantaceae forest. Guillot (1981) additionally identified, around Ouesso, a difference in forest composition between geological substrates and soil types that were later re-examined (Fayolle et al., 2012). Specifically, he first identified the requirements of *Triplochiton scleroxylon* for fertile soils based on a combined analysis of forest composition, soil chemical properties (exchangeable bases) and cocoa yields (Guillot, 1981). These early results for the high nutrient requirement of *Triplochiton* were later experimentally confirmed in Ghana (Veenendaal et al., 1996).

In Cameroon, Letouzey (1985) distinguished the monodominant *Gilbertiodendron* forests along river streams from mixed species terra firme forest, and additionally analyzed the variations within the mixed species terra firme forest in terms of degree of degradation and deciduousness. This work has recently been re-examined with refined remote sensing techniques (Gond et al., 2013). The semi-deciduous forest with Sterculiaceae and Ulmaceae in the eastern part of Cameroon corresponds to the young and old-growth *Celtis* forests, while the western evergreen forests of the Dja reserve and of the Atlantic coast that are rich in Caesalpiniaceae were not represented in the study area.

The forest types identified in this study match reasonably well the phytosociological classification of the forests of the Democratic Republic of Congo that distinguished between moist evergreen forest, moist semi-deciduous forest and secondary forest, and sub-divisions among these types (Lebrun and Gilbert, 1954). The evergreen monodominant *Gilbertiodendron* forest, corresponding to the moist evergreen equatorial forest of Congo, as opposed to montane forest, was recognized by the same authors to form a single phytosociological order, the *Gibertiendretalia Dewevrei*. The old-growth *Celtis* forest and its structural variants were recognized to form a single phytosociological order within the moist semi-deciduous forests: the *Piptadenio-Celtidetalia* due to the abundance of *Piptadeniastrum africanum* and several *Celtis* species. In this study, we showed the ubiquity and indicator value of the *Celtis* genus across the study area. We found, however, that *Piptadeniastrum* was slightly associated to another forest type, the mixed *Manilkara* forest that does not occur in the Democratic Republic of Congo (Lebrun and Gilbert, 1954). The secondary *Musanga* forest was also recognized by Lebrun and Gilbert (1954) to form a single phytosociological order, the *Musangetalia*.

4.3. Implications for conservation and management

Whether timber can be produced sustainably in tropical forests, and thus preserving ecosystem services and the forest's inherent value (including biodiversity and carbon), has been a highly controversial topic (see Putz et al., 2012 for a review of arguments in favour; and see Zimmerman and Kormos, 2012 for arguments against). It is difficult to make sound recommendations without a thorough consideration of the ecological context but management practices should be adapted to forest types when they have been identified as we have done here.

In this study, we used trait information in addition to forest structure and composition to get insight into forest functioning. Indeed, community trait average has been shown to be a useful tool to detect ecological patterns, and infer the underlying processes (e.g. ter Steege and Hammond, 2001; ter Steege et al., 2006). The hypothesis behind the approach is that species converge in functional traits because of establishment, survival and/or growth barriers imposed by the abiotic environment and that mean trait differences across forest types are driven by environmental or historical factors. By combining the three types of information, we can propose relevant management options for each forest type based on a diagnostic on forest potential for timber production and future response to disturbance.

The percentage of pioneers has been shown to be significantly positively correlated with disturbance level, to decrease with time elapse since disturbance, and to increase with repeated disturbance (Slik, 2005). In this study, we identified a strong correlation between the structural gradient and the density of pioneers, both highlighting the secondary *Musanga* forest, even though the forest structure analysis was independent of taxa identity. Forests with a high percentage of pioneers have most probably experienced frequent and/or recurrent disturbance events in the past. These secondary forests offer a well suited environment for the survival and growth of valuable light-demanding species of the canopy. They should be managed for future timber production, with adapted diameter cutting limits and felling cycles allowing the recovery of these valuable species, possibly complemented by artificial regeneration.

Dry season deciduousness has many consequences for ecosystem functioning, affecting the availability of resources for herbivores and decomposers (van Schaik et al., 1993). In this study we interpreted the spatial distribution of evergreen monodominant *Gilbertiodendron* forest as driven by water availability, while we have already demonstrated that the lower deciduousness of

Manilkara forest compared with that of *Celtis* forest might be due to soil infertility (Fayolle et al., 2012). Forests exhibiting low deciduousness might be less resilient to disturbance. In particular, forests on nutrient poor soils might be slow to recover after logging and this, in addition to the link between wood specific gravity and slow growth (see below) would call for particular caution in *Manilkara* forests, in favour of low logging intensities, longer felling cycles and larger conservation areas.

Wood specific gravity has been proposed as a conservation tool to quantify past disturbance and conservation priority areas (Slik et al., 2008). This is especially true in the context of biomass and carbon storage (Gourlet-Fleury et al., 2011). In this study, we identified two forest types with high wood specific gravity, the *Gilbertiodendron* and the *Manilkara* forests, that could both be regarded as old-growth forests and could be targeted for conservation priority (Slik et al., 2008). Old-growth forests in the tropics are important for conservation because they frequently harbour a higher proportion of vulnerable species (disturbance-sensitive) and species of restricted distribution (plants and animals) that are not found elsewhere. Wood specific gravity is negatively correlated to growth rate (Chave et al., 2009) and accordingly, the main species found in those forest types are characterized by slow growth rates (Fayolle et al., 2012; Gourlet-Fleury et al., 2011). This, combined with low deciduousness and a low percentage of pioneers re-inforce the need for low intensity management practices. In contrast, the productive *Celtis* forests that developed on more fertile soils than *Manilkara* forests, and that apparently experienced a long history of disturbance, might be more suitable for silviculture.

Two study cases led in the Central African Republic well illustrate our argument. In forests that can be assigned to the *Manilkara* forest type, Hall et al. (2003) compared unlogged, 6-month and 18-year post-harvest stands. They found little difference in species composition and diversity between treatments, but strong differences in stand structure. Stem densities were significantly lower 18 years after logging than in the unlogged treatment, suggesting low recovery after disturbance as expected from the mean trait values exhibited by the set of species characterizing this type. In contrast, in *Celtis* forests located near M'Baiki, only little difference in species composition, diversity, stem density, basal area and biomass were identified between silvicultural treatments more than 20 years after logging and thinning (Gourlet-Fleury et al., 2013a, 2013b; Ouédraogo et al., 2011). This fast recovery rate after disturbance again is fully consistent with the trait analysis.

We identified three structural derivatives of the old-growth *Celtis* forests: forests exhibiting a deficit of small trees (poorly regenerating and degraded *Celtis* forest), or of medium and large trees (young *Celtis* forest) most probably due to a variety of factors including past and recent human disturbance. While the last would require lengthening felling cycles, the first two deserve special attention to giant herbs and lianas which are most probably impeding tree recruitment. More research is needed to better understand the dynamics of this regeneration stratum and how it might be fostered by logging operations.

5. Conclusion

We identified the large scale variations in forest structure, composition and functioning within the semi-deciduous moist forests of the northern part of the Congo basin. These variations across forest types imply pronounced differences in population and ecosystem processes, and call for different management and conservation strategies. The distribution map of these forest types and a better accounting of the underlying determining factors help devise better targeted management options that produce a more sustainable use of central African moist forests. The approach could be

extended beyond the study area, in all places where commercial forest inventories are available.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.06.014>.

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