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Stand structure and species co-occurrence in mixed and monodominant Central African tropical forests

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Abstract: We compare forests dominated by *Gilbertiodendron dewevrei* at the Dja Biosphere Reserve (Cameroon) with adjacent high-diversity mixed forests in terms of tree-species composition and stand structure, in order to understand the co-occurrence of mixed forest tree species in the monodominant forest. A total of 18 1-ha permanent plots were established in the two forest types. In each plot, all trees with dbh ≥10 cm were identified as were those <10 cm dbh within a subsample of 300 m^2. Species richness was significantly different between the two forest types. Mixed forest had an average of 109 species ha^{-1} for trees ≥10 cm dbh and 137 species for trees <10 cm dbh. By contrast, *G. dewevrei*-dominated forest had an average of 47 species ha^{-1} (≥10 cm dbh) and 92 species (<10 cm dbh). There was no significant difference in terms of stem density of the trees with dbh <10 cm between the two forests (mixed: 3.7 stems m^{-2}; monodominant: 3.1 stems m^{-2}). As *G. dewevrei* is a shade-tolerant species that can regenerate under its own shade, its higher stem density and basal area can reduce species richness of an area.

Key Words: Diversity, Dja Biosphere Reserve, mixed forest, monodominant forest, natural regeneration, structure

INTRODUCTION

Tropical forests are among the most diverse plant communities worldwide (Hart *et al.* 1989, Whitmore 1998). They contain about 50–80% of the Earth's species diversity (Fays 2008, Puig 2002). However, there is still a knowledge gap in our understanding of the structure and diversity of tropical forests. Factors controlling tree density and diversity in rain forest include natural and anthropogenic disturbances, climate, soil drainage, other soil characteristics (Ghazoul & Sheil 2010, Richards 1996) and biotic interactions between species which play a fundamental role in the stability of ecological communities (Thébault & Fontaine 2010).

Contrary to the association of tropical forests with high biodiversity, some patches within these systems are found to have low diversity (Connell & Lowman 1989, Djuikouo 2012, Hart *et al.* 1989, Sonké 2005). Such monodominant forests may cover large areas (up to hundreds of square kilometres) and occur adjacent to significantly more-diverse forest types (Hart *et al.* 1989). In African and Neotropical monodominant forests, the dominant species mostly belong to Caesalpiniaceae whereas in Asia they usually belong to Dipterocarpaceae and Lauraceae (Anbarashan & Parthasarathy 2013, Degagne *et al.* 2009, Peh *et al.* 2011a).

It has been hypothesized that, in tropical regions, mixed forests are found on the most productive soils whereas single-species dominance (monodominance) depends on unfavourable soils characteristics (Richards 1996). However, when comparing monodominant and mixed forest stands, there was no significant difference in soil texture and chemical composition in many cases (Hart 1995, Peh *et al.* 2011b). This implies that monodominance of these systems is not readily explained by edaphic limitations.

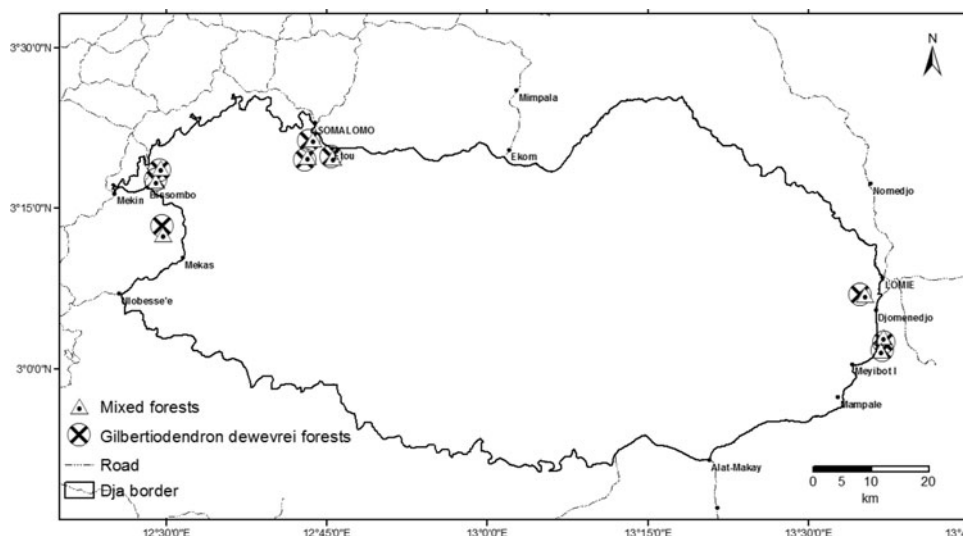[1] Corresponding author. Email: kamdem_marienoel@yahoo.fr

Figure 1. Location of sampling sites within the Dja Biosphere Reserve, Cameroon.

By contrast, a positive feedback mechanism of species-specific life-history traits may explain the existence of such 'classical monodominant' forests (Peh *et al.* 2011a). For example, a monodominant species of a closed canopy could cast a deep shade and form a deep leaf litter layer that provide favourable conditions for its large seeds to develop into shade-tolerant saplings and deter seedling regeneration of other non-dominant species.

Gilbertiodendron dewevrei (De Wild.) J. Leonard (Fabaceae-Caesalpinioideae) is an important example of a classical monodominant species which forms large stands from south-eastern Nigeria and eastern Cameroon across the entire Guineo-Congolian rain-forest zone to Eastern Democratic Republic of Congo (Gerard 1960, Hart 1990, Richards 1996). It can form extensive, sometimes almost pure stands, reaching more than 10 000 ha. Typically, *G. dewevrei* accounts for more than 75% of the total basal area and above-ground biomass (Djuikouo *et al.* 2010, Makana *et al.* 2011) and more than 90% of the canopy-level trees (Hart 1995, Torti *et al.* 2001). As a consequence, in various ecological studies, forests dominated by *G. dewevrei* have been recognized as a distinct formation (White 1983). This paper compares tree-species composition, structure and regeneration patterns between the *G. dewevrei* forests and their adjacent high-diversity mixed forests at the Dja Biosphere Reserve in Cameroon, critically focusing on smaller stems as these are ignored in most studies utilizing tropical forest inventory plots (e.g. Lewis *et al.* 2009). Specifically, we aimed to test the following hypotheses: (1) mixed-forest species were established well in the understorey of monodominant forest; (2) dominance by a single species can modify the overall forest structure and tree species richness i.e. including the structure and

diversity of the regenerating canopy trees as compared with mixed-species stands.

MATERIALS AND METHODS

Study sites

We conducted this study in the 526 000-ha Dja Biosphere Reserve located in south-east Cameroon (2°50′–3°30′N, 12°20′–13°40′E, ∼600 m asl). The habitat of the reserve is classified as moist evergreen forests (Letouzey 1985), comprising a heterogeneous terra firme system with large patches dominated by *G. dewevrei*. The soil beneath the monodominant and mixed-forest stands does not differ (Peh *et al.* 2011b).

The mean annual temperature is 24.3 °C, with minimum average monthly temperatures of 23.4 °C in October and maximum average monthly temperatures of 26.5 °C in February (Djuikouo 2012). The annual rainfall averages 1512 mm (average from 1979 to 2008), with monthly precipitation less than 100 mm occurring between December and February.

Data collection

We studied the floristic structure and regeneration patterns in 18 1-ha (100 × 100 m) permanent sample plots, nine plots established in *G. dewevrei*-dominated forest and nine in mixed forest (Figure 1). By using remote-sensing images, plot locations were chosen based on the presence of *G. dewevrei* stands which are patchily distributed throughout the reserve. Three locations, Bissombo (BIS), Somalomo (DJK) and Lomié (DJL) were

selected based on their phytogeographic influence on the reserve (Senterre 2005, Sonké 2005).

First a patch of *G. dewevrei* was located, and within that a plot set at a random location (using a random compass bearing and random distance from an arbitrary start location). For each *G. dewevrei*-dominated-forest plot, a corresponding mixed-forest plot was established nearby to minimize potential differences between these plots in terms of edaphic and topographical characteristics. Again randomization was used to avoid local-scale biases in plot locations. These sites were also selected such that the plot was within a homogeneous forest type; if a plot was not homogeneous a new random location was chosen. Each plot was further divided into small quadrats of 20×20 m to assist in the enumeration. All the trees with a diameter at breast height (dbh) ≥ 10 cm within a plot were tagged, mapped and measured using standard methods (Lewis *et al.* 2009, White & Edwards 2000).

Within each plot, we also surveyed the trees of small size classes (height ≥ 10 cm and dbh <10 cm) that included juvenile individuals of large-statured (canopy) species plus juvenile and adult individuals of small-statured (understorey) species. Specifically, three parallel strips, 19 m apart, of 100×1 m each were enumerated for stems <10 cm dbh within each 1-ha plot (i.e. 300 m^2; 3% of plot area). We recorded the height of all plants within these strips, and also recorded their dbh if they were taller than 3 m. Because sample sizes are generally low for individual species given the limited sampling, we classified all the individuals (dbh <10 cm and dbh ≥ 10 cm) recorded in the plots into four categories: G1, height <5 m; G2, height ≥ 5 m and dbh <20 cm; G3, dbh between 20–40 cm; and G4, dbh > 40 cm. Voucher specimens were collected for each plant to confirm the field identification by using existing floras and herbarium specimens at the National Herbarium of Cameroon and National Botanical Garden of Belgium.

Data analysis

We used diversity indices to describe diversity patterns across the study plots. Shannon (ISH) and Simpson (D') diversity indices are the most widely used, and thus facilitate comparisons. These indices take into account not only the number of species but also whether species are more or less equally abundant, or whether in contrast one or a few species dominate. Hurlbert's species richness curves that were rescaled to the number of individuals were employed to compare species richness among different size classes (G1, G2, G3, G4). These rarefaction curves give the expected number of species $E(Sx)$ in a sample of x individuals selected at random (without replacement) from a plot containing n individuals and S species (Hurlbert 1971).

$$E(Sx) = \sum 1 - C_{n-nj}^{N} / C_{n}^{N}$$

In addition, we used Entropart in the R package which employs the state-of-the-art method of entropy partitioning (http://CRAN.R-project.org/package-entropart) to estimate the effective species number of each size class of each forest type. This approach, which assumes that community species follow multinomial distributions (Marcon *et al.* 2012, 2014), enables us to correct sampling biases and compare 95% confidence intervals between corresponding size classes of the two forest types, and among size classes within each forest type.

Since the plots of monodominant and mixed forests were paired, we used Student's t-test to determine if the two forest types are different in terms of species richness and structure. In addition, we used chi-square test to determine if the distribution of stems is associated with size classes. Cluster analysis was conducted using WARD algorithm and NNESS Index to verify the similarities between plots. The NNESS Index takes into consideration the number of species and the number of stems per species. Statistical analyses were performed using MVSP 3.2 (Kovach Computing Service) and STATISTICA 6 (StatSoft France, Maisons – Alfort, France).

RESULTS

Forest structure

We recorded a total of 18 272 small stems (i.e. trees with dbh <10 cm) within the 5400 m^2, representing 387 species, 226 genera and 62 families. Some 72.6% were identified to species level, 16.5% identified to genus level, 5.1% identified to family level, and 5.8% remain unidentified. Small-stem density was not significantly different between mixed forest (3.7 ± 0.6 stems m^{-2}) and monodominant forest (3.1 ± 0.6 stem m^{-2}) (Table 1).

A total of 7755 stems with dbh ≥ 10 cm were recorded within the 18 1-ha permanent plots, representing 263 species, 167 genera and 44 families. About 91.4% were identified to species level, 4.7% identified to genus level, 2% identified to family level and 1.9% remain unidentified. The mixed forest had significantly more stems than *G. dewevrei* forest (500 ± 37.1 and 362 ± 25.7 stems ha^{-1}, respectively). Although both monodominant and mixed forests had decreasing stem numbers along the gradient of size classes (Figure 2a), the mixed forest had significantly higher density of trees at the threshold of 10 cm and fewer large trees (> 40 cm) than monodominant stand (Chi-square test, $\chi^2 = 10.8$, df $= 1$, P <0.001). Furthermore, total basal area was significantly different between the two forest types. Average basal area of *G. dewevrei* forest was 32.7 ± 2.6 m^2 ha^{-1}, whereas that of mixed forest

Table 1. Structural parameters and diversity of *Gilbertiodendron dewevrei* and mixed forests of 18 1-ha plots of trees with dbh ≥10 cm and 18 300-m^2-subplots of trees with dbh <10 cm at the Dja Biosphere Reserve, Cameroon. Differences between forest types analysed by Student's t-test, df = 16;* denotes P <0.05 (significant); ** denotes P <0.001 (highly significant).

|	Parameters	Mixed forest	*G. dewevrei* forest	P
dbh ≥10 cm	Number of individuals	500 ± 37.1	362 ± 25.7	**
	Number of species	109 ± 5.72	46.7 ± 9.4	**
	Mean dbh (cm)	21.6 ± 0.67	26.1 ± 0.71	*
	Basal area (m^2 ha^{-1})	27 ± 1.57	32.7 ± 2.57	*
	Shannon index (ISH)	4.07 ± 0.10	1.73 ± 0.39	**
	Simpson index (D')	0.97 ± 0.01	0.53 ± 0.10	**
dbh <10 cm	Number of individuals	1107 ± 188	924 ± 164	0.17
	Number of species	137 ± 9.7	92.4 ± 3.81	**
	Shannon index (ISH)	3.93 ± 0.10	2.93 ± 0.18	**
	Simpson index (D')	0.96 ± 0.01	0.87 ± 0.03	**
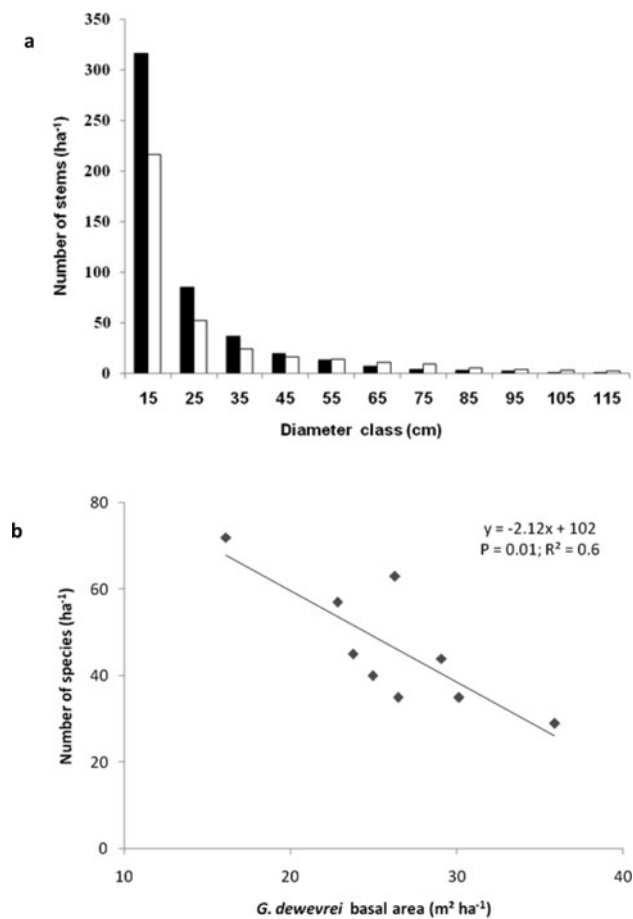
Figure 2. Distribution of stems density in mixed (dark bars) and *Gilbertiodendron dewevrei* (white bars) stands (a). Labels on the x-axis are midpoints of diameter intervals. Relationship between *G. dewevrei* basal area and number of species at the Dja Biosphere Reserve, Cameroon (b).

was 27 ± 1.6 m^2 ha^{-1} (Student's test, t = 3.76, df = 16, P <0.05).

In *G. dewevrei* forest, 80% of the total basal area of trees with dbh ≥10 cm was accounted for solely by the dominant species. The mixed-forest species made a relatively small contribution to the total basal area of the monodominant forest; these species were *Desbordesia glaucescens* (1.5%), *Erythrophloeum suaveolens* (1.6%), *Pentaclethra macrophylla* (1.1%), *Irvingia gabonensis* (0.7%), *Alstonia boonei* (0.7%), *Petersianthus macrocarpus* (0.6%) and *Carapa procera* DC. (0.6%). These species had a relatively greater contribution to the total basal area of the mixed forest (e.g. *P. macrocarpus*, 6.9%; *P. macrophylla*, 4.7%; *C. procera*, 2.5%; *D. glaucecens*, 2.2% and *E. suaveolens*, 1.24%).

Floristic relationship

Cluster analysis based on overall floristic composition (i.e. including trees with dbh <10 cm), clearly shows a floristic link between mixed forest and *G. dewevrei* forest (Figure 3). Despite the relatively low similarity between both forest types in terms of structure, the floristic composition of monodominant forest was relatively similar to that of their adjacent mixed forest of the same locality. Distinction of each locality without clear differentiation of forest types was observed.

Forest composition

Mixed forest was significantly more diverse than *G. dewevrei* forest in terms of species richness in both trees with dbh ≥10 cm and dbh <10 cm, as measured by Simpson's and Shannon's diversity indices (Table 1). Mixed forest had an average of 109 ± 5.7 species ha^{-1} of trees with dbh ≥10 cm, and 137 ± 9.7 species of trees with dbh <10 cm, whereas *G. dewevrei* forest had an average of 46.7 ± 9.4 species ha^{-1} and 92.4 ± 3.8 species for stems with dbh ≥10 cm and dbh <10 cm, respectively. Many species were represented by only one individual with dbh
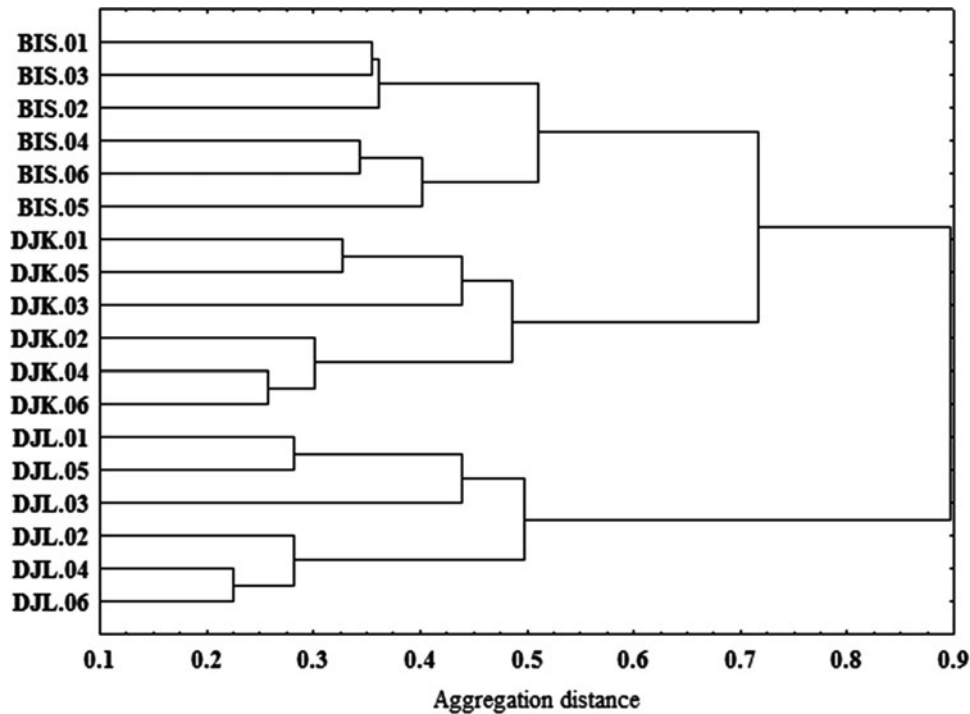
Figure 3. Cluster analysis based on overall floristic composition (i.e. including trees with dbh <10 cm) across all 18 plots at the Dja Biosphere Reserve, Cameroon: Bissombo BIS; Lomié DJL; Somalomo DJK. Odd-numbered plots (e.g. BIS. 01) denote *Gilbertiodendron dewevrei*-dominated forest; even-numbered plots (e.g. BIS. 02) denote mixed forest.

≥10 cm in the monodominant forest (48 spp. across the nine 1-ha plots).

Thirty-eight families were identified in the *G. dewevrei* forest. Fabaceae-Caesalpinioideae was the dominated (sub)family which constituted more than 82% of the relative basal area of the monodominant forest (with 80% solely by *G. dewevrei*). *Irvingia gabonensis* with 0.7% of the relative basal area was the only species occurring in all plots of *G. dewevrei* forest. Apart from *G. dewevrei* which constituted 32.2% of trees with dbh <10 cm, other relatively important tree species in the monodominant forest included *Tabernaemontana crassa* Benth. (1.2%), *T. pendulifolia* K. Schum (1.3%), *Angylocalyx pynaertii* De Wild. (0.9%), *Strombosia pustulata* Oliv. (0.7%) and *Polyalthia suaveolens* Engl. & Diels (0.5%).

In mixed forest, we identified 44 families dominated by Euphorbiaceae (20% of the relative basal area) with 32 different species. Families such as Euphorbiaceae, Rubiaceae and Annonaceae were well-represented by individuals with small diameters in both forest types.

There was no significant relationship between the diversity of stems with dbh ≥10 cm and dbh <10 cm for both forest types (mixed forest: $R^2 = 0.01$, $P = 0.78$; monodominant forest: $R^2 = 0.10$, $P = 0.4$). However, a significant negative correlation was observed between the basal area and species richness in the *G. dewevrei* forest (Figure 2b).

Table 2. Effective species numbers (± 95 %) of each size class (G1, height <5 m; G2, height ≥5 m and dbh <20 cm; G3, dbh between 20–40 cm; and G4, dbh > 40 cm) of the *Gilbertiodendron dewevrei* and mixed forests at the Dja Biosphere Reserve, Cameroon.

Size class	*G. dewevrei* forest	Mixed forest
G1	292 ± 12.3	338 ± 12.4
G2	188 ± 9.82	307 ± 11.4
G3	88.4 ± 6.69	191 ± 9.62
G4	69.2 ± 7.08	139 ± 10

Vertical structure of species

The species richness of different size-class distributions was evaluated using Hurlbert's curve for both forest types. The asymptotic smoothed species accumulation curves for the mixed forest are higher than that of monodominant forest across all size classes, suggesting that, for similar number of stems, a monodominant forest has fewer species than mixed forest in both trees with dbh ≥10 cm and dbh <10 cm (Figure 4). In accordance with the Hulbert's species curves, effective species numbers of all size classes of the mixed forest were significantly higher than the corresponding size classes of the monodominant forest (Table 2). The significant decline in effective species numbers along the increasing size classes (i.e. confidence intervals of all size classes did not overlap) was observed in both forest types.
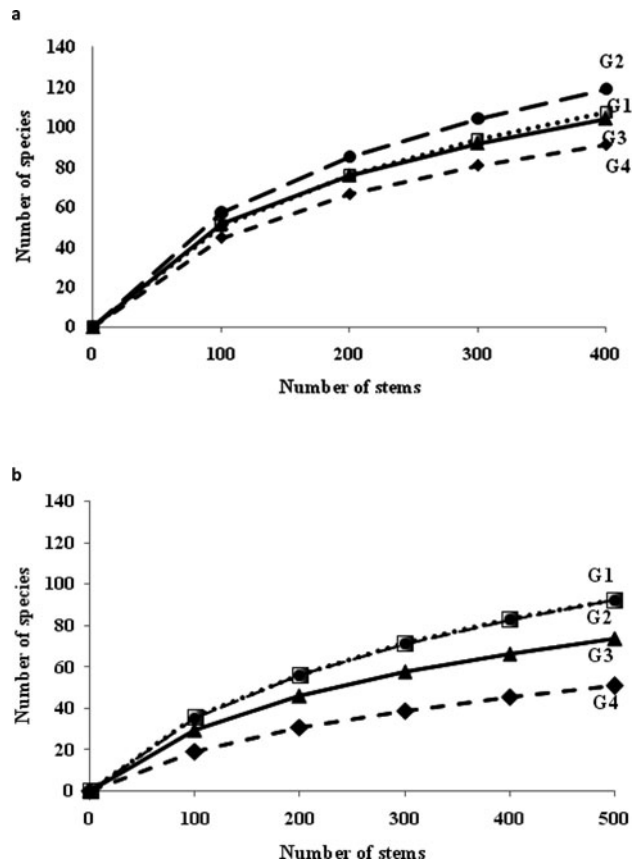
Figure 4. Species richness (Hurlbert Curve) in mixed forest (a) and *Gilbertiodendron dewevrei* forest (b) at the Dja Biosphere Reserve (Cameroon), for four different size classes: G1, height <5 m; G2, height ≥5 m and dbh <20 cm; G3, dbh between 20–40 cm; and G4, dbh > 40 cm.

Regardless of forest type, most species with large trees (dbh > 40 cm) were also well represented in other size classes (Table 3). However, species number of trees > 40 cm dbh is significantly different between the two forest types (Student's test, t = 7.34, df = 16, P <0.001). The species number of the subcanopy size class (dbh between 20 cm and 40 cm), was highly significantly different between the two forest types (Student's test, t = −12.6, df = 16, P <0.001). In both forest types, this size class was dominated by Olacaceae, Annonaceae, Myristicaceae, Rubiaceae and Sterculiaceae. Natural regeneration was observed in most subcanopy species. These species included *T. crassa*, *A. pynaertii*, *S. pustulata*, *Santiria trimera* (Oliv.) H. J. Lam ex Aubrév. and *Polyathia suaveolens*. For both forest types, the stem numbers occurring in size class between 20 cm and 40 cm correlated positively and significantly with those in the smaller size class (mixed forest: r = 0.32, P <0.05; monodominant forest: r = 0.54, P <0.001).

Because these datasets are strongly clumped by plots, we could not analyse the size class distributions of each canopy species in monodominant and mixed stands. Nevertheless when combining the plots together for exploratory purposes (Table 3), we observed that (1) some species, such as *Distemonanthus benthamianus*, were abundant in the mixed forest but absent in the monodominant forest; and (2) while non-dominant species in monodominant stand are generally associated with mixed forest, three mixed-forest species (*E. suaveolens*, *I. gabonensis*, *Mammea africana*) had higher numbers of large trees in monodominant forest.

DISCUSSION

Based on our survey of nine 1-ha plots of *Gilbertiodendron dewevrei* forest, this study confirms the floristic homogeneity of monodominant forest at the canopy level (Connell & Lowman 1989, Makana *et al.* 1998). A similar pattern was observed by Hart *et al.* (1989) at Ituri forest in the Democratic Republic of the Congo: the monodominant stands of this forest, *G. dewevrei* accounted for 80% of the total basal area, and diversity index scores were lower than those of the mixed forest. In terms of total based area, our study shows that the *G. dewevrei* forest at Dja Biosphere Reserve (32.7 ± 2.6 m^2 ha^{-1}) was not significantly different from the same forest type at Uele in the Democratic Republic of the Congo (29.9 m^2 ha^{-1}) (Gerard 1960). These *G. dewevrei* forests were also not different in terms of stem density of trees with dbh ≥10 cm (Dja Biosphere Reserve: 362 ± 25.7 trees ha^{-1}; Uele: 419 trees ha^{-1}).

Higher species richness in both stems with dbh ≥10 cm and dbh <10 cm was observed in mixed forest after controlling for the stem density. Using another approach, Makana *et al.* (2004, 2011) compared the monodominant and mixed forests directly using two 10-ha plots of each forest type and showed that, despite the dominance of *G. dewevrei*, species diversity of the monodominant forest was high and comparable to their adjacent mixed forest. The discrepancy between our results is probably because our sites were selected in such a way that the entire area was within a homogeneous 1-ha of forest.

Surprisingly, species diversity in the smaller size classes of the monodominant forest, though lower than that of the mixed forest, was still relatively high. In the monodominant forest, the higher diversity of stems with dbh <10 cm compared with that of the established stems implies the following: first, most propagules were originated from the adjacent mixed forest and are capable of penetrating into *G. dewevrei* forest. Second, a significant number of non-dominant species were able to overcome deep shade and deep litter to germinate successfully.

Table 3. Twenty canopy species in the *Gilbertiodendron dewevrei* and mixed forests at the Dja Biosphere Reserve, Cameroon. Juveniles: dbh <10 cm; Subcanopy: 10 cm ≤ dbh <40 cm; Canopy: dbh ≥40 cm (the values in the table indicate number of individuals).

	Mixed forest			G. dewevrei forest		
	Juveniles	Subcanopy	Canopy	Juveniles	Subcanopy	Canopy
Gilbertiodendron dewevrei (De Wild.)J. Léonard				2510	1896	470
Uapaca paludosa Aubrév. & Léandri	81	46	82	42	11	5
Petersianthus macrocarpus (P.Beauv.) Liben	47	148	42	4	7	4
Pentaclethra macrophylla Benth.	50	90	22	10	13	11
Panda oleosa Pierre		27	14		9	
Alstonia boonei De Wild.		1	13		1	5
Hexalobus crispiflorus A.Rich.		2	13		3	1
Uapaca acuminata (Hutch.) Pax & Hoffm.	49	26	13	15	4	1
Desbordesia glaucescens (Engl.) Tiegh.	34	62	12	36	16	11
Heisteria trillesiana Pierre	15	56	11	21	21	1
Celtis tessmannii Rendle	38	36	10	2	3	1
Guarea cedrata (A.Chev.) Pellegr.	49	82	10	3	3	
Gambeya lacourtiana (De Wild.) Aubr.	15	15	7	7	1	3
Distemonanthus benthamianus Baill.	2	40	6			
Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill.	13	18	3	29	26	6
Erythrophleum suaveolens (Guil. & Perr.) Brenan	2	1	5	1	2	12
Pterocarpus soyauxii Taub.	5	33	5	6	12	5
Mammea africana Sabine	14	6		35	26	4
Ongokea gore Pierre		7	5		2	3
Coula edulis Baill.	1	5			5	3

Third, most of these mixed-forest species however still failed to establish at the canopy level.

Our estimated average stem density of trees with dbh <10 cm in *G. dewevrei* forest was 3.1 stems m^{-2}, which is not significantly different from that of the mixed forest (3.7 stems m^{-2}). But our estimated average stem density of trees with dbh ≥10 cm was significantly lower in the monodominant forest (362 stem ha^{-1}) as compared with the mixed forest (500 stems ha^{-1}). This indicates that *G. dewevrei* was able to outcompete most stems of the mixed-forest species, despite having a significant number of the latter successfully dispersed into the monodominant system. Generally, hypotheses about the origin and maintenance of classical monodominance usually refer to one or a suite of species-specific life-history traits, such as the ability to stage massive and synchronous fruiting, avoidance of predation and herbivory, and low soil nutrient availability. Also, low light availability and deep litter in the monodominant forest could inhibit the establishment of seedlings of mixed-forest species (Gross *et al.* 2000, Hart 1995, Peh *et al.* 2011a, Torti *et al.* 2001). Nevertheless, some shade-tolerant mixed-forest species (such as *Desbordesia glaucescens*, *Irvingia gabonensis*, *Polyalthia suaveolens*, *Strombosia pustulata*, *Santiria trimera*) were able to attain a relative high sapling density in the monodominant despite the biophysical barriers imposed by the dominant species (Makana *et al.* 2011). In addition, the presence of gap colonizers or high-light-demanding species such as *Alstonia boonei*, *Distemonanthus benthamianus* and *Petersianthus macrocarpus* in the mixed forest suggests the occurrence of periodic succession in response to gap formation. However, these species were unlikely to co-exist with *G. dewevrei* in significant numbers for two reasons: first, there are significantly fewer and smaller gaps in this forest type, compared with their adjacent mixed forest, indicating very lower exogenous disturbances (Hart *et al.* 1989, Peh *et al.* 2011a). Second, under the shade of these colonizers that occasionally established in the monodominant forest, their new recruits were unlikely to compete successfully with the more abundant, shade-tolerant saplings of *G. dewerei*.

Both structure and composition of the two forests may provide us with new insights on the processes leading to monodominance in *G. dewevrei* forest, and also on the mechanisms for maintaining species diversity in the mixed forest (Hart *et al.* 1989). The size-class distributions of canopy species in monodominant and mixed forests at Dja Biosphere Reserve suggest that, without severe large-scale disturbance, both forest types are likely to continue to be dominated by their current dominant species. The dominant canopy species of the monodominant (*G. dewevrei*) and mixed forests (e.g. *U. paludosa*, *P. macrocarpus*, *P. macrophylla*, *D. glaucescens*) are all well represented in the subcanopy layers and had abundant juveniles.

Most small individuals of mixed-forest species in the monodominant forest would likely be out-competed by individuals of *G. dewevrei*. This is an example of diffuse competition (Hubbell & Foster 1983) whereby a

positive feedback of the biotic conditions created by the monodominant stands (Peh *et al.* 2011a) is having a broad negative impact on all other tree species. Our observation also suggests that *G. dewevrei* only suppresses rather than eliminates the presence of mixed-forest species (Makana *et al.* 2011).

Interestingly, each locality of our sampling sites was distinct in terms of their floristic composition, which included species of trees with dbh ≥10 cm and dbh <10 cm. This implies that the floristic composition of both forest types may not be homogeneous throughout the reserve and there may be a spatial differentiation of floristic characteristics in the region. Earlier studies on classical monodominant forests had also observed a change in the floristic composition with geographical distances (Condit *et al.* 2005, Gerard 1960).

The results of this study support the assumption that there is a floristic inflow from the mixed forest into the monodominant *G. dewevrei* forest (Djuikouo *et al.* 2010, Hart *et al.* 1989, Makana *et al.* 2004, Peh *et al.* 2014). Many species had abundant juveniles in the undergrowth of these monospecific forests. But species richness in monodominant forest decreased along a gradient of increasing tree size classes, and very few species could establish well into the monodominant canopy. Therefore, this observation does not support the hypothesis that the structure of the canopy tree diversity of the monodominant forests might shift towards diversification. No doubt some mixed-forest species were well-represented in the subcanopy and canopy layers in *G. dewevrei*-dominated forest. Their presence in the smaller size classes was proportionate to their population size in the canopy, indicating that these non-dominant species have *in situ* regeneration potential in the monodominant systems. Nevertheless, in the absence of severe disturbance, *G. dewevrei* would likely to remain dominant in the canopy, and possibly expand at the expense of adjacent mixed forest.

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