

Determinants of spatial patterns of canopy tree species in a tropical evergreen forest in Gabon

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Abstract

Questions: We examined the spatial patterns of dominant canopy species in a tropical forest to investigate: (a) what is the niche occupancy of canopy species with respect to topographic gradients; (b) what are the dominant ecological processes that explain their distribution; (c) what are the interactions among the most prevalent canopy species; and (d) what are the interactions between canopy species adults and juveniles trees?

Location: Rabi permanent CTFS-ForestGEO plot, Gabon.

Methods: We selected the four most abundant canopy species and one timber species. We used Berman's test to determine the effect of three topographic variables on the distribution of each species and univariate analysis to model the spatial pattern of each species using either an inhomogeneous Poisson process or an inhomogeneous Cox process. We also used a bivariate form of the pair correlation function (PCF) to determine the spatial interaction between species and the correlation among conspecific adult and juvenile trees.

Results: Four of the five species had aggregated spatial patterns while *Lophira alata* showed spatial randomness. Most of the variance in the local tree density was explained by within-population dispersal processes rather than environmental factors. Bivariate PCF tests showed significant segregation between species associations. Two species exhibited aggregation at small distances between young and adult trees, while others showed either complete spatial randomness at small inter-tree distances or segregation at large distances.

Conclusions: This study showed that the spatial pattern in the majority of canopy species was aggregation. Seed dispersal limitation mainly explained the observed aggregation pattern. Habitat filtering, as evidenced by the influence of topographic variables on niche occupancy, marginally, yet significantly, explained this pattern. The different spatial patterns of the principal species permit their coexistence. Spatial segregation among adult and juvenile trees reveals a strong pattern of either species-specific seed predation or pathogens.

KEYWORDS

canopy tree species, Gabon, large-diameter trees, permanent plot, Rabi, Smithsonian ForestGEO, spatial patterns, topographic variables, tropical evergreen forest

1 | INTRODUCTION

Large-diameter trees of canopy species dominate the structure, dynamics, and function of many temperate and tropical forests (Lutz, Larson, Freund, Swanson, & Bible, 2013). It has been shown that about 50% of the aboveground biomass of forests is associated with large-diameter trees representing between 1% (Lutz et al., 2018) and 1.5% (Bastin et al., 2014) of the total stems. These large-diameter trees are also responsible for the variation in aboveground biomass across the tropics (Slik et al., 2013). Tree species that can reach large diameters also have a disproportionate economic value. *Aucoumea klaineana* and *Lophira alata* are both canopy trees species that are the most important timber species in Gabon. In 2007, 931,473 m³ of *Aucoumea klaineana* and 37,700 m³ of *Lophira alata* entered mills, constituting 82% and 3% of the total timber production of Gabon, respectively (de Wasseige et al., 2009). Timber harvest may, therefore, lead to a high level of future change in the large-diameter abundance of these species.

In a forest stand, trees are subject to competitive pressures for water and soil nutrients and access to light (Ward, Parker, & Ferrandino, 1996). To the extent that symmetric competition drives demography (survival, recruitment, and growth), tree spatial patterns will become more regular over time. Regular spatial structure is commonly interpreted as a signal of high competition in forest stands, while aggregation signals abundant regeneration without subsequent self-thinning (Kenkel, 1988; Pelissier, 1998). Asymmetric competition between canopy trees and smaller conspecifics or heterospecifics can also lead to more regular patterns at small inter-tree distances (Lutz et al., 2014).

Conversely, if dispersal limitations or niche preferences are dominant factors, patterns should be more clustered. In tropical forests, aggregation is the main pattern of tree spatial distribution (Hubbell, 1979; Réjou-Méchain et al., 2011). According to Borcard, Legendre, and Drapeau (1992), the environmental control model (Bray & Curtis, 1957; Whittaker, 1956) and biotic factors such as horizontal or vertical interactions (Connell & Janzen, 1970) are responsible for observed variations in the presence or abundance of the organisms. Aggregation can also be explained by habitat filtering (Weiher & Keddy, 1995) and coexistence among tree species in a community (Pielou, 1961). The relationships between trees and environmental factors such as soil types are also well documented (Condit, Engelbrecht, Pino, Pérez, & Turner, 2013; John et al., 2007; Paoli, Curran, & Slik, 2008). Studies in Asian forests show the effects of topography (elevation, slope, convexity) on species distribution (Legendre et al., 2009; Lin et al., 2013). In addition, changes in spatial patterns have also been observed between adult and juvenile trees (Detto & Muller-Landau, 2016; Janzen, 1970; Lutz, Larson, Swanson,

& Freund, 2012; Lutz et al., 2013). These arguments support the niche theory (Grinnell, 1917; Hutchinson, 1957), which predicts that the presence and abundance of species in a given area depend on differences in abiotic and biotic factors. In fact, tree species variability in different types of forest follows from the fact that the abiotic component of forest ecosystems varies and that forests are functionally related to their abiotic environment. Spatial patterns of all trees in a forest are driven by the more numerous small-diameter trees, and this may obscure important patterns among the less numerous large-diameter trees. Furthermore, even if all trees of a given species show clustering at a particular point in time, we cannot infer that some (or any) of these small trees will persist in the presence of their large conspecifics until they too reach a large diameter.

The dominance of the forest canopy in Gabon by Fabaceae is generally interpreted as an indication of mature forest (Caballé, 1978). Fabaceae dominate the canopy of the forest in Rabi in terms of abundance, aboveground biomass and number of species (Memiaghe, Lutz, Korte, Alonso, & Kenfack, 2016). Although spatial pattern analyses of trees have been done in tropical and temperate forests, the structure of forests in Africa has been rarely examined, perhaps under the assumption that African forests are similar to tropical forests elsewhere (Newbery & Van Der Burgt, 2004). However, Richards (1996) has suggested important differences among tropical forest types necessitating re-examination of forest patterns. In addition, Hardy and Sonké (2004) aimed at assessing the species diversity of the forest. Engone Obiang et al. (2010) aimed at characterizing the overall spatial pattern of all trees irrespective of their species. None of these previous studies focused on specific species to better understand their ecology from their spatial pattern. Here, we examined the spatial distribution of dominant upper canopy tree species. The seeds of these species are dispersed either ballistically or by gravity, and therefore, the distribution of juveniles around adults is expected to be spatially aggregated. In light of the ecological and commercial importance of upper-canopy species, our objectives were to examine (a) niche occupancy of canopy species with respect to topographic gradients; (b) spatial patterns of canopy species to infer the dominant ecological processes shaping the community; (c) interactions among the most prevalent canopy species; and (d) interactions between canopy dominants and their smaller conspecifics.

2 | METHODS

2.1 | Study site

The study site was the 25-ha Rabi plot located in southwestern Gabon (1°55'28" S, 9°52'48" E). The vegetation of the area is a mixture of swamp and mixed moist semi-evergreen forests (Bonnefille,

2011). The soils are ferralitic and hydromorphic, with a mixture of sandy clay and clay sand (Thibault, Fisher, & Goodman, 2004). Mean annual temperature is 26.1°C and annual precipitation averages 2,299 mm (Lee, Alonso, Dallmeier, Campbell, & Pauwels, 2006). The plot is 500 m × 500 m, with elevations between 28 m and 54 m above sea level. The 25-ha plot was subdivided into 625 quadrats of 20 m × 20 m, with elevation recorded at the 676 grid corners. Plot establishment followed the Smithsonian–ForestGEO standard methods (Anderson-Teixeira et al., 2015; Condit, 1998) with all trees ≥1 cm dbh (diameter at breast height; 1.30 m) tagged, mapped, measured and identified. For establishment details, see Memiaghe et al. (2016).

2.2 | Species selection

We selected upper canopy species (those that reach heights ≥30 m and dbh ≥60 cm) according to the classification methods of Kenfack, Thomas, Chuyong, and Condit (2007). From the resulting 61 species in 51 genera and 26 families (out of a total of 345 species in 192 genera and 54 families; Memiaghe et al., 2016), we selected the four most abundant upper canopy species (Appendix S1); *Tetraberlinia moreliana* (Fabaceae), *Gilbertiodendron ogoouense* (Fabaceae), *Tetraberlinia bifoliolata* (Fabaceae), *Amanoa strobilacea* (Phyllanthaceae), and one important timber species, *Lophira alata* (Ochnaceae).

Most species of *Tetraberlinia* are strictly confined to upland forests on nutrient-poor soils except *Tetraberlinia bifoliolata* which sometimes is found in riverine forests where the temporary inundations do not last very long (Wieringa, 1999). In Gabon, flowering of *Tetraberlinia moreliana* coincides with the first rains after the long dry season, mid-September to October, while it occurs between March and June for *Tetraberlinia bifoliolata*. Like *Tetraberlinia bifoliolata*, *Gilbertiodendron ogoouense* is a large tree of evergreen rain forests on well-drained or periodically inundated soil (Van der Burgt, Mackinder, Wieringa, & de la Estrella, 2015). Seeds of these Fabaceae are dispersed by dehiscence, and the maximum ballistic seed dispersal distance of the highest tree species is likely around 60 m, measured horizontally from the edge of the tree crown (Van Der Burgt, 1997). Explosive dehiscence is also the dispersal seed mechanism in the *Amanoa* genus (Adam, 1971). *Amanoa strobilacea* species, restricted largely to swampy areas within lowland evergreen rainforest, is classified as vulnerable species according to IUCN criteria (Hawthorne, 1998). *Lophira alata* is a non-pioneer light-demanding species whose seedlings can settle under the forest cover and need light only at a given development stage (Palla, Louppe, & Doumenge, 2002). It is a monoecious deciduous wind-dispersed species, with a leafless period during one or two weeks in December (Engone Obiang et al., 2012).

2.3 | Spatial analysis

We analyzed the spatial distribution using point process theory (Cressie, 1993). The first-order moment of a spatial point process is its intensity $\lambda(x)$ that represents the density of trees at location x .

Homogeneous point process has a constant intensity across a given area. A second-order moment of a spatial point process is its pair correlation function (PCF) $g(r) = \lim_{|dx|, |dy| \rightarrow 0} p(r) / [\lambda(x) \lambda(y) |dx||dy|]$, where $p(r)$ is the probability of finding two trees at locations x and y separated by a distance r , where dx denotes an infinitesimal region in the vicinity of x , and $|dx|$ denotes the area of dx (Cressie, 1993; Law et al., 2009; Wiegand & Moloney, 2004). If there is no second-order structuring of points, the probability of finding one tree in dx and one tree in dy is $\lambda(x) \lambda(y) |dx| |dy|$, i.e., $g(r) = 1$. Second-order structuring corresponds either to clustering [$g(r) > 1$], or to regular spacing [$g(r) < 1$]. The null hypothesis in point process theory is complete spatial randomness (CSR) where points are spatially distributed at random in the study area. Departure from CSR in plant communities may occur because the first-order density of points is responding to an environmental covariate (spatial inhomogeneity), and/or because points have a second-order structuring, often due to biotic interactions. Inhomogeneous point patterns with no second-order structuring are modeled with an inhomogeneous Poisson process, for which the number of trees in any bounded region A follows a Poisson distribution with mean $\int_A \lambda(x) dx$. The PCF of a Poisson process is $g(r) = 1$. All spatial analyses were conducted using the Spatstat package in the R software, version 1.47 (Baddeley, Rubak, & Turner, 2015).

2.4 | Test of topographical variables

We performed a χ^2 test of complete spatial randomness at a 1-ha scale, which showed the non-uniformity of populations ($\chi^2 = 916.23$, $df = 24$, $p < 0.001$). Accordingly, we conducted population analyses as inhomogeneous point processes with an intensity driven by topographical variables. We superimposed a regular grid of 5 m × 5 m quadrats on the study area and calculated three topographic variables (elevation, slope, and convexity) for each quadrat (Gunatilleke et al., 2006; Harms, Condit, Hubbell, & Foster, 2001; Valencia et al., 2004). The elevation of each quadrat was calculated as the mean of the elevation at its four corners. Slope was calculated as the mean angular deviation from horizontal of each of the four triangular planes formed by connecting three of its corners. Convexity of a quadrat was estimated by subtracting the mean elevation of the eight surrounding quadrats from the elevation of the focal quadrat. Exploratory analyses based on smoothing estimates of the intensity as functions of covariates were used to assess whether the relationship between the logarithm of the intensity and covariates was linear or quadratic.

We used Berman's test (Berman, 1986) to determine the effect of each topographical variable separately on tree density. This test is based on the mean S of the covariate values at the locations of trees as compared to its expected mean μ across all locations in the study area under the null hypothesis of CSR. Departure from the null hypothesis of no dependence of tree density on the covariate is assessed using the test statistic $Z_1 = (S - \mu) / \sigma$, where σ is the standard deviation of the covariate across all locations in the study area under CSR.

2.5 | Univariate analyses

The spatial pattern of each species was modeled using either an inhomogeneous Poisson process (no second-order structuring) or an inhomogeneous Cox process (Jalilian, Guan, & Waagepetersen, 2013). Cox processes generate second-order clustering that can be interpreted as the outcome of within-population dispersal processes. Model goodness-of-fit was assessed using the inhomogeneous PCF and confidence envelopes generated using 100 Monte Carlo simulations of the model. For goodness-of-fit assessment, the inhomogeneous PCF was estimated (both for the observed and for simulated patterns) using a non-parametric estimator based on a smoothing kernel, i.e., without taking into consideration the predicted intensity. The intensity was modeled using a log-linear relationship: $\lambda(x) = \exp(\mathbf{z}(x) \beta^T)$, where $\mathbf{z}(x)$ denotes the vector of the three topographical covariates at location x , β is a vector of parameters to estimate (including the intercept), and T denotes the transpose of β .

Different inhomogeneous Cox processes were tested, including inhomogeneous log Gaussian Cox processes and inhomogeneous Neyman–Scott processes. In the former case, the underlying Gaussian field was modeled using either an exponential or a Matérn covariance function. The dispersal kernel of the Neyman–Scott processes was either Gaussian (Thomas process), uniform on a disk (Matérn cluster process), a variance Gamma kernel, or a Cauchy kernel (see Jalilian et al., 2013 for details on the definition of these processes). The inhomogeneous Cox processes were fitted using the two-step procedure described by Waagepetersen and Guan (2009) using the minimum contrast method based on the PCF to fit the Cox process. Goodness-of-fit of the observed point patterns to the models was tested using the Diggle–Cressie–Loosmore–Ford (DCLF) test based on Monte Carlo simulations of the model because differently structured tests of spatial patterns may identify significant patterns (Furniss, Larson, & Lutz, 2017; Harms et al., 2001).

The first-order dependence of the intensity on topographical covariates and the second-order clustering due to within-population dispersal processes both influence the variance of the number of trees found in a bounded region of the study area. To partition the variance between these two sources, we used the R^2 statistic defined by Jalilian et al. (2013) as:

$$R^2 = \frac{\sigma_z^2}{\sigma_z^2 + \sigma_0^2(\sigma_z^2 + \rho_z^2)}$$

where ρ_z is the mean of the predicted intensity across all locations in the study area, σ_z^2 its variance, and $\sigma_0^2 = g_0(0) - 1$ where g_0 is the theoretical PCF of the fitted Cox process. When the density of trees is not related to topographical covariates, $R^2 = 0$, and when the observed structure in the spatial pattern of trees follows entirely from their response to topographical covariates, $R^2 = 1$. Stronger clustering of trees due to within-population dispersal processes decreases R^2 .

2.6 | Bivariate spatial patterns

We used the bivariate PCF to determine interactions between species pairs, and also between adult and juvenile conspecifics after dividing the species into four diameter classes: $1 \text{ cm} \leq \text{dbh} < 5 \text{ cm}$ (juvenile trees), $5 \text{ cm} \leq \text{dbh} < 12 \text{ cm}$, $12 \text{ cm} \leq \text{dbh} < 25 \text{ cm}$, and $\text{dbh} \geq 25 \text{ cm}$ (adult trees). The inhomogeneous bivariate PCF $g_{ij}(r)$ is intuitively defined as: $\lim_{|dx|, |dy| \rightarrow 0} p(r) / [\lambda_i(x) \lambda_j(y) |dx| |dy|]$, where $p(r)$ is the probability of finding two trees, of types i and j respectively, at locations x and y separated by a distance r , dx denotes an infinitesimal region in the vicinity of x , and $|dx|$ denotes the area of dx (Wiegand & Moloney, 2004). When there is no interaction between type i and type j , $g_{ij}(r) = 1$. If the two populations attract, $g_{ij}(r) > 1$ and is significant when the bivariate PCF is greater than the upper bound of the confidence interval. If the two populations repulse themselves, $g_{ij}(r) < 1$ and is significant when the function is less than the lower bound of the confidence interval.

3 | RESULTS

The five most common canopy species represented 45.5% (11,971 stems) of all canopy stems. The diameter distribution of *Lophira alata* was predominantly concentrated in the large-diameter class, whereas the other species exhibited a reverse-J diameter distribution (Table 1).

3.1 | Topographic variables

Within the study area, elevation varied between 33.4 and 60.8 m above sea level, slope varied between 0° and 26° , and convexity varied between -2.87 and 1.72 . The Berman test showed a negative effect of all variables on the spatial distribution of all species except *Lophira alata* (Table 2). Slope influenced the tree density of four of five species, elevation three or five, and convexity two of five (Table 2).

Species	All stems	Diameter class (cm)			
		1–5	5–12	12–25	>25
<i>Tetraberlinia moreliana</i>	149.6	137.6	5.7	2.2	4.2
<i>Gilbertiodendron ogoouense</i>	135.8	111.2	16.2	5.2	3.2
<i>Tetraberlinia bifoliolata</i>	123.3	95.2	14	7.9	6.2
<i>Amanoa strobilacea</i>	65.4	36.9	14.9	8.8	4.8
<i>Lophira alata</i>	4.7	2.1	0.5	0.2	1.9

TABLE 1 Density (stems per ha) of the five most abundant canopy species in the 25-ha plot at Rabi

TABLE 2 Result of Berman's test between species and the topography variables based on the null hypothesis of complete spatial randomness

Species	All		Elevation		Slope		Convexity	
	Z ₁	p						
<i>Tetraberlinia moreliana</i>	-6.06	<0.001	-5.22	<0.001	8.12	<0.001	14.9	<0.001
<i>Gilbertiodendron ogoouense</i>	-7.56	<0.001	-4.16	<0.001	7.26	<0.001	1.39	0.16
<i>Tetraberlinia bifoliolata</i>	-5.10	<0.001	-3.76	<0.001	9.77	<0.001	2.99	<0.001
<i>Amanoa strobilacea</i>	-2.02	0.04	-1.62	0.10	3.53	<0.001	1.92	0.054
<i>Lophira alata</i>	-1.46	0.14	-0.09	0.90	0.05	0.95	0.40	0.061

3.2 | Univariate spatial patterns

The inhomogeneous PCF showed clustering in the spatial pattern of all trees for distances <30 m (Figure 1a; DCLF test: $u = 4.6, p = 0.01$). *Lophira alata* was the only species exhibiting CSR for all inter-tree distances (Figure 1d; DCLF test: $u = 18.7, p = 0.054$). The spatial pattern

of all other species could be modeled by an inhomogeneous point process with second-order clustering (Figure 1). A different model was used for each species (Table 3), but all models produced heavy-tailed covariance functions, reflecting the fact that isolated trees could be found far from the main clusters of trees (see Appendix S2). Although topographic variables played a very significant role in

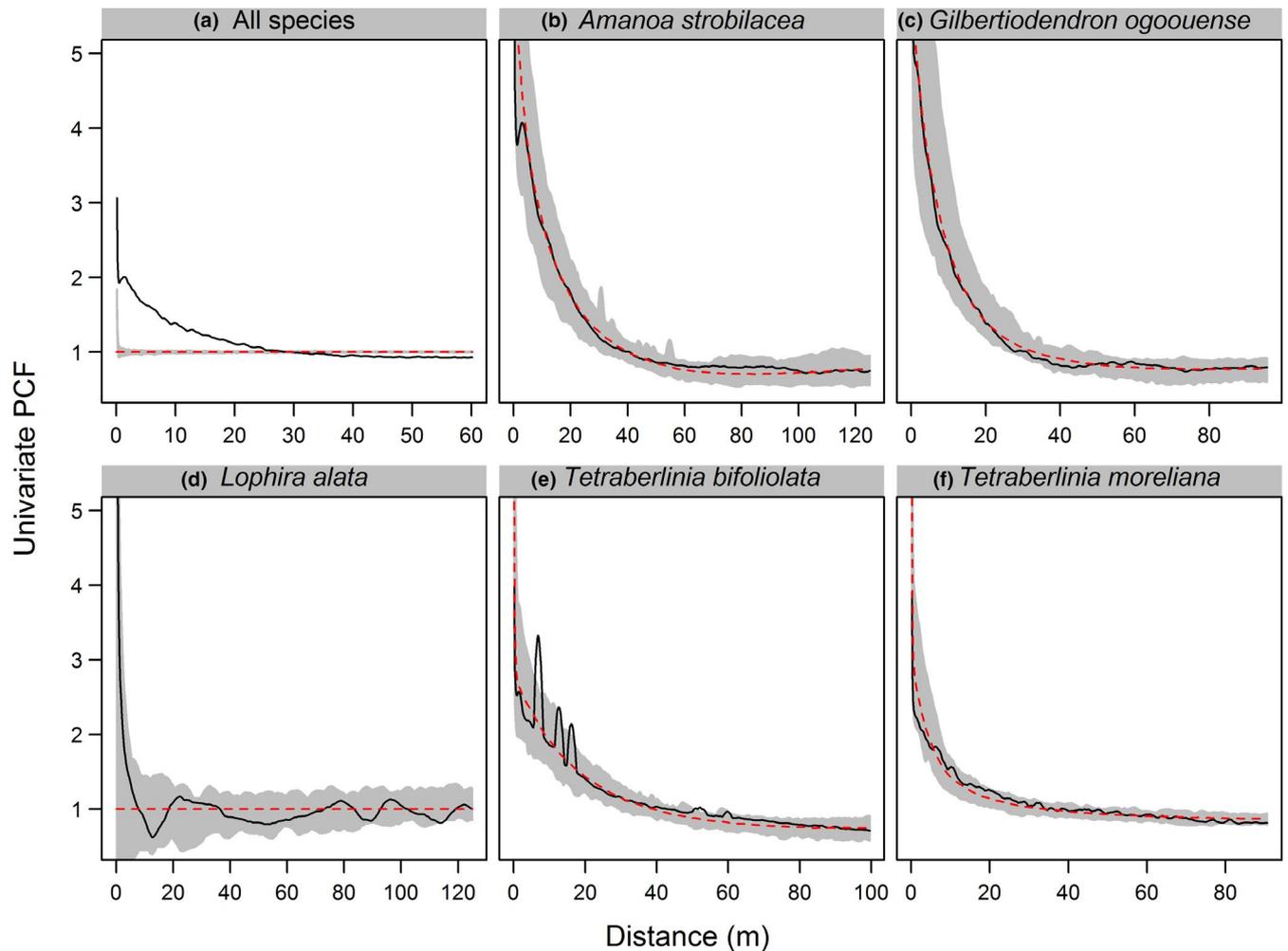


FIGURE 1 Univariate spatial patterns of the five dominant canopy species in the 25-ha plot at Rabi. Solid black lines represent the observed pattern of inter-tree distances; dashed red lines represent the predicted inhomogeneous PCFs under the fitted point process (all species [a] and *Lophira alata* [d]): homogeneous Poisson process; *Amanoa strobilacea* (b): inhomogeneous Neyman–Scott process with variance Gamma dispersal kernel; *Gilbertiodendron ogoouense* (c): inhomogeneous log Gaussian Cox process with exponential covariance function; *Tetraberlinia bifoliolata* (e): inhomogeneous log Gaussian Cox process with Matérn covariance function; *Tetraberlinia moreliana* (f): inhomogeneous log Gaussian Cox process with Cauchy covariance function. Gray areas show the 95% confidence limits around the predicted PCF estimated from 100 random simulations of the point process

predicting the local density of trees (Table 3), R^2 values were low (less than 6%), meaning that most of the variance in the local number of trees was explained by within-population dispersal processes rather than by environment-driven variation in tree density.

3.3 | Canopy tree species interactions

The bivariate PCF (Figure 2) showed segregation between species association according the Monte Carlo goodness-of-fit test: *Gilbertiodendron ogoouense*–*Amanoa strobilacea* ($u = 3.68, p = 0.01$); *Tetraberlinia bifoliolata*–*Amanoa strobilacea* ($u = 7.1, p = 0.01$), *Tetraberlinia moreliana*–*Gilbertiodendron ogoouense* ($u = 1.71, p = 0.01$); *Tetraberlinia moreliana*–*Tetraberlinia bifoliolata* ($u = 3.47, p = 0.01$), *Tetraberlinia moreliana*–*Amanoa strobilacea* ($u = 6.75, p = 0.01$); *Lophira alata*–*A strobilacea* ($u = 4.77, p = 0.03$). The only association where there was no interaction (CSR) was that of *Lophira alata*–*Gilbertiodendron ogoouense* ($u = 1.93, p = 0.1$). *Tetraberlinia moreliana*–*Lophira alata* and *Tetraberlinia bifoliolata*–*Lophira alata* associations also exhibited CSR at short distances, respectively $r < 20$ m ($u = 46, p = 0.46$) and $r < 40$ m ($u = 1.68, p = 0.01$).

3.4 | Spatial patterns of adult and juvenile conspecifics

Exploratory analysis of interactions between adult and juvenile trees (Figure 3) revealed two species with aggregation at small inter-tree

distances (<30 m): *Tetraberlinia bifoliolata* ($u = 2.38, p = 0.01$) and *Amanoa strobilacea* ($u = 33.63, p = 0.01$). These same species were segregated at inter-tree distances >30 m ($p = 0.01$ for the two species). Other species exhibited either CSR at small scales ($r < 40$ m): *Tetraberlinia moreliana* ($u = 1.82, p = 0.09$); all species ($u = 0.12, p = 0.09$) or segregation at larger scales ($p = 0.01$ for all species and *Tetraberlinia moreliana*).

4 | DISCUSSION

The five chosen canopy species (11,854 stems) represent more than 45% of all canopy trees species (26,288 stems): *Tetraberlinia moreliana* (14%), *Gilbertiodendron ogoouense* (13%), *Tetraberlinia bifoliolata* (11.7%), *Amanoa strobilacea* (6%) and *Lophira alata* (0.65%). *Tetraberlinia moreliana* can attain a height of 51 m, and this representative of canopy species is confined to west Gabon and a small area in south-west Cameroon (Rietkerk, Ketner, & De Wilde, 1995). Although present at low density (4.6 stems per ha), *Lophira alata* has the highest aboveground biomass (25 Mg/ha) followed by *Tetraberlinia moreliana* (16.5 Mg/ha), *Librevillea klainei* (11.51 Mg/ha), and *Odyndyea gabonensis* (10.57 Mg/ha; Appendix S1). The diameter distribution of *Tetraberlinia moreliana*, *Gilbertiodendron ogoouense*, *Tetraberlinia bifoliolata* and *Amanoa strobilacea* follows a reversed J-shape, indicating that these species have good regeneration under the existing canopy. In comparison, the *Lophira alata*

TABLE 3 Type and parameter values of the univariate point process fitted to the spatial patterns of the five dominant canopy species in the 25-ha plot at Rabi

Species	Density (Stem ha ⁻¹)	1st order non-stationary intensity				2nd order structuring				
		Variable	$\hat{\beta}$	SE $\hat{\beta}$	p	Model	Kernel or covariance	Parameter	Estimate	R^2
<i>Amanoa strobilacea</i>	65.4	Elevation	-0.37	0.05	<0.001	Neyman-Scott	variance Gamma	κ	8.56×10^{-5}	0.004
		Elevation ²	3.65×10^{-3}	6×10^{-4}	<0.001			Scale	27.1	
<i>Gilbertiodendron ogoouense</i>	135.8	Elevation	-0.13	0.005	<0.001	LGCP	Exponential	Variance	2.48	0.029
		Convexity	0.30	0.06	<0.001			ν	-0.47	
		Slope	-0.028	0.005	<0.001			Scale	19.6	
		Convexity	0.32	0.045	<0.001					
<i>Lophira alata</i>	4.7								NA	
<i>Tetraberlinia bifoliolata</i>	123.2	Elevation	0.21	0.065	<0.001	LGCP	Matérn	Variance	2.22	0.030
		Elevation ²	-3.60×10^{-3}	7×10^{-4}	<0.010			Scale	51.1	
		Slope	0.16	0.023	<0.001			ν	0.5	
		Slope ²	-1.31×10^{-2}	0.001	<0.001					
		Convexity	0.42	0.050	<0.001					
<i>Tetraberlinia moreliana</i>	149.6	Elevation	0.63	0.061	<0.001	LGCP	Cauchy	Variance	1.60	0.057
		Elevation ²	-8.27×10^{-3}	7×10^{-4}	<0.001			Scale	2.74	
		Slope	-0.038	0.006	<0.001			γ	0.25	
		Convexity ²	-0.35	0.048	<0.001					

Note: The definition of the parameters of the point processes follows the 'spatstat' package of R (version 1.47). Abbreviations: LGCP, log Gaussian Cox process; SE, standard error.

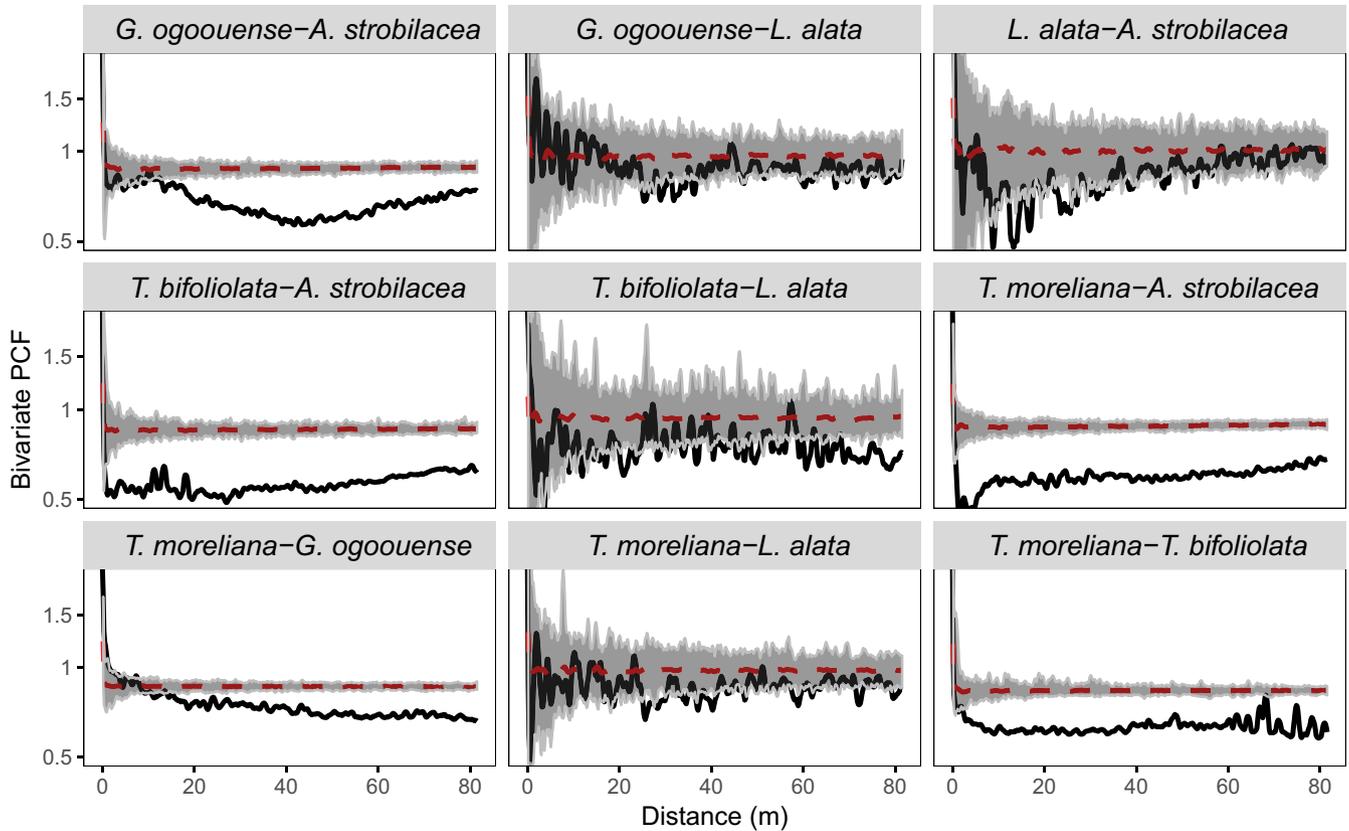


FIGURE 2 Bivariate spatial interactions between canopy species in the 25-ha plot at Rabi. Solid lines represent the observed patterns; gray areas shows 95% confidence limits estimated from 99 random simulations of Monte Carlo under the heterogeneous Poisson null model (dashed lines)

population contains more adult trees than juveniles, as expected for this shade-intolerant species. However, *Lophira alata* can sometimes regenerate easily within shady mature forests, like in the northwest Gabon (Engone Obiang et al., 2012) where it presents a unimodal or bimodal dbh distribution pattern (Biwolé, 2015; Doucet, 2003; Letouzey, 1957; Palla et al., 2002).

Slope is known to influence both forest dynamics and the spatial pattern of trees (Baldeck et al., 2013; Ferry, Morneau, Bontemps, Blanc, & Freycon, 2010; Robert & Moravie, 2003). Steeper slopes enhance the growth of large trees while having little influence on the growth of small trees, but see Lin et al. (2013), who found that steep slopes limit colonization rates. The density of smaller trees (diameter < 5 cm) at Rabi was greater than the density of trees in larger diameter classes (Table 1). Thus, topography does not necessarily favor the maintenance of high species numbers at a given area. Here, heterogeneity seems to be the main factor that controls the distribution of many species (Hutchinson, 1957), and niche differentiation appears to be affecting spatial pattern (Ward et al., 1996). The observed aggregation pattern could be partially explained by the preference and the filtering of species in the habitat (Harms et al., 2001; Lin et al., 2013).

Spatial aggregation is perhaps the most common pattern for tropical trees species (Fangliang, Legendre, & LaFrankie, 1997; Hubbell, 1979). The high-density canopy species (*Tetraberlinia moreliana*,

Gilbertiodendron ogoouense, *Tetraberlinia bifoliolata* and *Amanoa strobilacea*) also exhibited aggregation at small distances. These species differed by the decreasing shape of their PCF, which was reflected by the different covariance functions of the fitted models. In agreement with past studies that have shown that light-tailed covariance functions are inappropriate for tropical forests (Jalilian et al., 2013), all these functions had heavy tails. In contrast, *Lophira alata* had low density but a random pattern at all distances, perhaps indicative that conspecific density-dependent mechanisms have become subordinate to density-independent controls for this species (LaManna et al., 2017).

Whereas other studies have shown that aggregation intensity decreases with abundance (Condit et al., 2000; Wang et al., 2010), our results do not follow that pattern. Species with low abundance (i.e., *Lophira alata*) exhibited CSR, and abundant species had high levels of aggregation. Here, dispersal mechanism likely explains the aggregation (Hubbell, 1979; Plotkin et al., 2000). However, habitat filtering as evidenced by the influence of topographic variables on niche occupancy also marginally, yet significantly, explains this pattern. Other studies suggest the influence of soil on the spatial distribution of trees (John et al., 2007; Russo, Davies, King, & Tan, 2005; Ward et al., 1996). Because at the scale of 25 ha, differences in soil are often correlated with microtopography (Tange, Yagi, Sasaki, Niiyama, & Kassim, 1998), including topographical variables like elevation, convexity and slope also account, to some extent, for soil

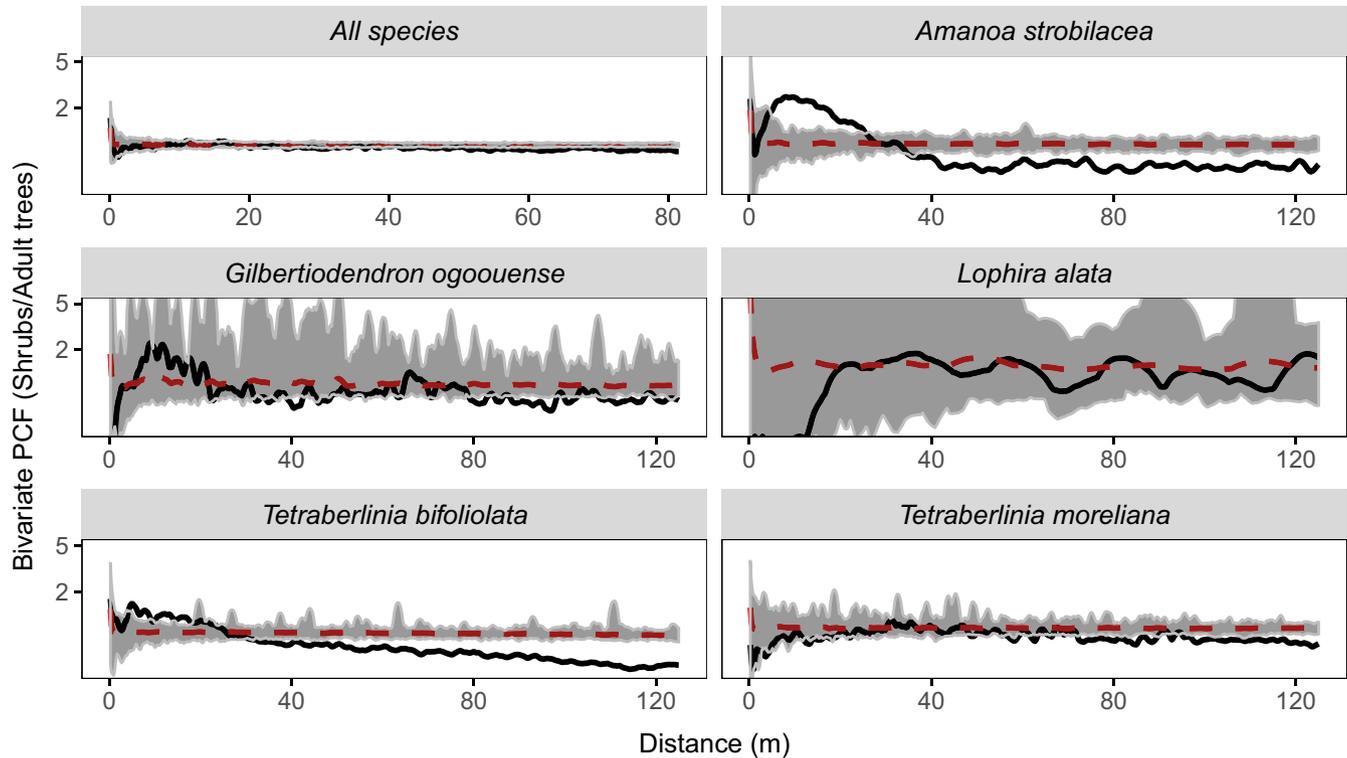


FIGURE 3 Spatial interaction between adult and juvenile tree conspecifics in the 25-ha plot at Rabi. Solid lines represent the observed patterns; gray areas show 95% confidence limits estimated from 99 random simulations of Monte Carlo under the heterogeneous Poisson null model (dashed lines). Positive values indicate spatial attraction and negative values spatial repulsion

differences. Furthermore, other relationships between topographical variables and soil components have also been well established (Pachepsky, Timlin, & Rawls, 2001). According to Condit et al. (2000), species whose seeds are dispersed by animals are assumed to be better dispersed than those of species dispersed by wind or explosively. One detailed study carried out in the Rabi area on *Tetraberlinia moreliana* (Van Der Burgt, 1997) concluded that explosive dehiscence is the main dispersal mode of this species and the dispersal distance varied between 40 m and 60 m from the parent trees. Explosive dehiscence is also the dispersal seed mechanism in the *Amanoa* genus (Adam, 1971). The aggregation pattern observed in these species supports, in fact, the dispersal limitation hypothesis. *Lophira alata*, a wind-dispersed species (Satabie, 1982), can disperse its seeds up to 200 m from the parent tree (Biwolé, 2015; Palla et al., 2002). This longer dispersal distance could explain the CSR pattern even if other wind-dispersed species of Dipterocarpaceae exhibited more aggregation (Condit et al., 2000). Furthermore, this light-demanding species can develop everywhere where the canopy is accidentally opened (Letouzey, 1968).

Spatial repulsion between species was found except for the *Lophira alata*–*Gilbertiodendron ogoouense* association. Negative associations are documented in closely related species (Pei et al., 2011). In Gabon, most of the observed negative associations were of species from the same family. Because these species can prefer the same habitat, this could indicate the dominance of competitive processes (Tilman & Pacala, 1993). Our results support the segregation

hypothesis of coexistence between species (Chesson, 2000; Pacala & Levin, 1997; Silvertown, 2004).

We expected to find an aggregation of adult and juvenile trees among species in the Fabaceae. *Tetraberlinia bifoliolata* and *Amanoa strobilacea* showed aggregation as small inter-tree distances, but generally, the size classes were segregated with no interaction between young and adult trees of *Lophira alata*. The spatial segregation between young trees and adults is likely due to Janzen–Connell effects (Clark & Clark, 1984; Janzen, 1970). The segregation could additionally be explained by negative density dependence acting independently of Janzen–Connell effects (Clark & Clark, 1984; Hao, Zhang, Song, Ye, & Li, 2007). Other studies in this region suggest the prevalence of negative density dependence (Engone Obiang et al., 2010).

5 | CONCLUSION

This study showed that the salient feature of the spatial pattern of the majority of the canopy species at Rabi was aggregation. Seed dispersal limitation mainly explained the observed aggregation pattern while habitat filtering as evidenced by the influence of topographic variables on niche occupancy also marginally, yet significantly, explained this pattern. The distribution of *Lophira alata* was not correlated with topography, and its spatial distribution pattern was random and showed no niche preference. Most canopy species showed spatial repulsion between species, likely due to



their close phylogenetic relationships (Pei et al., 2011), leading to strong competition (Weiher & Keddy, 1995). Surprisingly, species in the family Fabaceae did not show aggregation between adults and juveniles. Their spatial segregation highlights the potentially strong activity of seed-specific predators and pathogens. Spatial repulsion among canopy species appears to be driven by niche segregation, with coexistence facilitated by the avoidance effect (Wright, 2002). These processes will likely continue to maintain canopy species diversity and may suggest that the large-diameter cohort (and hence carbon sequestration) of the Rabi forest will be resilient.

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AUTHORS CONTRIBUTION

The bulk of data analysis was performed by NLEO during the ForestGEO analytical workshops, with the contribution of DK, JAL, and NP. All the authors contributed to the writing of the manuscript. DK, HRM, PB and AA participated in the design of the project, data collection and data management.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

The data used in this paper are a subset of the first census of the 25-ha Rabi plot, available upon request at the ForestGEO website (<http://ctfs.si.edu/datarequest/index.php/main/region/tree/africa>).

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REFERENCES

Adam, J.-G. (1971). Quelques utilisations de plantes par les Manon du Libéria (Monts Nimba). *Journal d'agriculture tropicale et de botanique appliquée*, 18, 372–378. <https://doi.org/10.3406/jatba.1971.6870>

Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Joseph Wright, S., ... Zimmerman, J. (2015). CTFs-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21, 528–549. <https://doi.org/10.1111/gcb.12712>

Baddeley, A., Rubak, E., & Turner, R. (2015). *Spatial point patterns: methodology and applications with R*. New York, NY: CRC Press.

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., ... Dalling, J. W. (2013). Soil resources and topography shape local tree community structure in tropical forests. *Proceedings of the Royal Society B Biological Sciences*, 280, 20122532. <https://doi.org/10.1098/rspb.2012.2532>

Bastin, J.-F., Barbier, N., Couteron, P., Adams, B., Shapiro, A., Bogaert, J., & De Cannière, C. (2014). Aboveground biomass mapping of African forest mosaics using canopy texture analysis: toward a regional approach. *Ecological Applications*, 24, 1984–2001. <https://doi.org/10.1890/13-1574.1>

Berman, M. (1986). Testing for spatial association between a point process and another stochastic process. *Journal of the Royal Statistical Society Series C (Applied Statistics)*, 35, 54–62. <https://doi.org/10.2307/2347865>

Biwolé, A. (2015). *Origine et dynamique des populations d'arbres des forêts denses humides d'Afrique Centrale, le cas de Lophira alata Banks ex Gaertn. C.F. (Ochnaceae)*. Doctoral dissertation. Liège, Belgique: Université de Liège.

Bonnefille, R. (2011). Rainforest responses to past climatic changes in tropical Africa. In M. Bush, J. Flenley, W. Gosling (Eds), *Tropical rainforest responses to climatic change* (pp. 125–184). Berlin, Germany: Springer Praxis Books. https://doi.org/10.1007/978-3-642-05383-2_5

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, 73, 1045–1055. <https://doi.org/10.2307/1940179>

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27, 325–349. <https://doi.org/10.2307/1942268>

Caballé, G. (1978). Essai sur la géographie forestière du Gabon. *Adansonia*, 17, 425–440.

Chesson, P. (2000). General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, 58, 211–237. <https://doi.org/10.1006/tpbi.2000.1486>

Clark, D. A., & Clark, D. B. (1984). Spacing dynamics of a tropical rain forest tree: Evaluation of the Janzen-Connell model. *American Naturalist*, 124, 769–788. <https://doi.org/10.1086/284316>

Condit, R. (1998). *Tropical forest census plots: Methods and results from Barro Colorado Island, Panama and a comparison with other plots*. New York, NY: Springer.

Condit, R., Ashton, P. S., Baker, P., Bunyavechewin, S., Gunatilleke, S., Gunatilleke, N., ... Yamakura, T. (2000). Spatial patterns in the

- distribution of tropical tree species. *Science*, 288, 1414–1418. <https://doi.org/10.1126/science.288.5470.1414>
- Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 5064–5068. <https://doi.org/10.1073/pnas.1218042110>
- Connell, J. (1970). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P. J. den Boer & G. R. Gradwell (Eds), *Dynamics of populations: Proceedings of the advanced study institute on dynamics of numbers in populations* (pp. 298–312). Wageningen, Netherlands: Centre for Agricultural Publishing and Documentation.
- Cressie, N. A. C. (1993). *Statistics for spatial data: Wiley Series in Probability and Mathematical Statistics*. New York, NY: Wiley-Interscience. <https://doi.org/10.1002/9781119115151>
- Detto, M., & Muller-Landau, H. C. (2016). Rates of formation and dissipation of clumping reveal lagged responses in tropical tree populations. *Ecology*, 97, 1170–1181. <https://doi.org/10.1890/15-1505.1>
- de Wasseige, C., Devers, D., de Marcken, R., Eba'a Atyi, R., Nasi, R., & Mayaux, P. (2009). *Les forêts du bassin du Congo: état des Forêts 2008*. Luxembourg: Office des publications de l'Union européenne.
- Doucet, J.-L. (2003). *L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon*. Thèse de Doctorat. Gembloux, Belgium: Faculté universitaire des sciences agronomiques de Gembloux.
- Engone Obiang, N. L., Ngomanda, A., Mboma, R., Nzabi, T., Ngoye, A., Atsima, L. & Picard, N. (2010). Spatial pattern of central African rainforests can be predicted from average tree size. *Oikos*, 119, 1643–1653. <https://doi.org/10.1111/j.1600-0706.2010.18440.x>
- Engone Obiang, N. L., Ngomanda, A., White, L., Jeffery, K. J., Chézeaux, E., & Picard, N. (2012). A growth model for azobé, *Lophira alata*, in Gabon. *Bois et Forêts des Tropiques*, 314, 65–72.
- Fangliang, H., Legendre, P., & LaFrankie, J. V. (1997). Distribution patterns of tree species in a Malaysian tropical rain forest. *Journal of Vegetation Science*, 8, 105–114. <https://doi.org/10.2307/3237248>
- Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L., & Freycon, V. (2010). Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, 98, 106–116. <https://doi.org/10.1111/j.1365-2745.2009.01604.x>
- Furniss, T. J., Larson, A. J., & Lutz, J. A. (2017). Reconciling niches and neutrality in a subalpine temperate forest. *Ecosphere*, 8, e01847. <https://doi.org/10.1002/ecs2.1847>
- Grinnell, J. (1917). The niche-relationships of the California Thrasher. *The Auk*, 34, 427–433.
- Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Esufali, S., Harms, K. E., Ashton, P. M. S., Burslem, D. F. R. P., & Ashton, P. S. (2006). Species-habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology*, 22, 371–384. <https://doi.org/10.1017/s0266467406003282>
- Hao, Z., Zhang, J., Song, B., Ye, J., & Li, B. (2007). Vertical structure and spatial associations of dominant tree species in an old-growth temperate forest. *Forest Ecology and Management*, 252, 1–11.
- Hardy, O. J., & Sonké, B. (2004). Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation. *Forest Ecology and Management*, 197, 191–202. <https://doi.org/10.1016/j.foreco.2004.05.014>
- Harms, K. E., Condit, R., Hubbell, S. P., & Foster, R. B. (2001). Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, 89, 947–959. <https://doi.org/10.1111/j.1365-2745.2001.00615.x>
- Hawthorne, W. (1998). *Amanoa strobilacea*. The IUCN Red List of threatened species 1998. <https://doi.org/10.2305/iucn.uk.1998.rlts.t34645a9881025.en>
- Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203, 1299–1309. <https://doi.org/10.1126/science.203.4387.1299>
- Hutchinson, G. E. (1957). The multivariate niche. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–421.
- Jalilian, A., Guan, Y., & Waagepetersen, R. (2013). Decomposition of variance for spatial Cox processes. *Scandinavian Journal of Statistics*, 40, 119–137. <https://doi.org/10.1111/j.1467-9469.2012.00795.x>
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104, 501–528. <https://doi.org/10.1086/282687>
- John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., ... Foster, R. B. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 864–869. <https://doi.org/10.1073/pnas.0604666104>
- Kenfack, D., Thomas, D. W., Chuyong, G., & Condit, R. (2007). Rarity and abundance in a diverse African forest. *Biodiversity and Conservation*, 16, 2045–2074. <https://doi.org/10.1007/s10531-006-9065-2>
- Kenkel, N. C. (1988). Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology*, 69, 1017–1024. <https://doi.org/10.2307/1941257>
- LaManna, J. A., Mangan, S. A., Alonso, A., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., ... Myers, J. A. (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, 356, 1389–1392. <https://doi.org/10.1126/science.aam5678>
- Law, R., Illian, J., Burslem, D. F. R. P., Gratzner, G., Gunatilleke, C. V. S., & Gunatilleke, I. A. U. N. (2009). Ecological information from spatial patterns of plants: Insights from point process theory. *Journal of Ecology*, 97, 616–628. <https://doi.org/10.1111/j.1365-2745.2009.01510.x>
- Lee, M. E., Alonso, A., Dallmeier, F., Campbell, P., & Pauwels, O. S. G. (2006). The Gamba complex of protected areas: An illustration of Gabon's biodiversity. *Bulletin of the Biological Society of Washington*, 12, 229–241.
- Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.-F., & He, F. (2009). Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology*, 90, 663–674. <https://doi.org/10.1890/07-1880.1>
- Letouzey, R. (1957). La forêt à *Lophira alata* de la zone littorale camerounaise. *Bois et Forêts des Tropiques*, 53, 9–20.
- Letouzey, R. (1968). *Etude phytogéographique du Cameroun*. Paris, France: Lechevalier.
- Lin, G., Stralberg, D., Gong, G., Huang, Z., Ye, W., & Wu, L. (2013). Separating the effects of environment and space on tree species distribution: From population to community. *PLoS ONE*, 8, e56171. <https://doi.org/10.1371/journal.pone.0056171>
- Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., ... Zimmerman, J. K. (2018). Global importance of large-diameter trees. *Global Ecology and Biogeography*, 27, 849–864. <https://doi.org/10.1111/geb.12747>
- Lutz, J. A., Larson, A. J., Freund, J. A., Swanson, M. E., & Bible, K. J. (2013). The importance of large-diameter trees to forest structural heterogeneity. *PLoS ONE*, 8, e82784. <https://doi.org/10.1371/journal.pone.0082784>
- Lutz, J. A., Larson, A. J., Furniss, T. J., Donato, D. C., Freund, J. A., Swanson, M. E., ... Franklin, J. F. (2014). Spatially nonrandom tree mortality and ingrowth maintain equilibrium pattern in an old-growth *Pseudotsuga-Tsuga* forest. *Ecology*, 95, 2047–2054.
- Lutz, J. A., Larson, A. J., Swanson, M. E., & Freund, J. A. (2012). Ecological importance of large-diameter trees in a temperate mixed-conifer forest. *PLoS ONE*, 7, e36131. <https://doi.org/10.1371/journal.pone.0036131>
- Memighe, H. R., Lutz, J. A., Korte, L., Alonso, A., & Kenfack, D. (2016). Ecological importance of small-diameter trees to the structure, diversity and biomass of a tropical evergreen forest at Rabi, Gabon. *PLoS ONE*, 11, e0154988. <https://doi.org/10.1371/journal.pone.0154988>
- Newbery, D. M., Van Der Burgt, X. M., & Newbery, D. M. (2004). Structure and inferred dynamics of a large grove of *Microberlinia bisulcata* trees in central African rain forest: The possible role of periods of multiple

- disturbance events. *Journal of Tropical Ecology*, 20, 131–143. <https://doi.org/10.1017/s0266467403001111>
- Pacala, S. W., & Levin, S. A. (1997). *Biologically generated spatial pattern and the coexistence of competing species*. In D. Tilman & P. Kareiva (Eds), *Spatial ecology: The role of space in population dynamics and interspecific interactions* (pp. 204–232). Princeton, NJ: Princeton University Press.
- Pachepsky, Y. A., Timlin, D. J., & Rawls, W. J. (2001). Soil water retention as related to topographic variables. *Soil Science Society of America Journal*, 65, 1787–1795. <https://doi.org/10.2136/sssaj2001.1787>
- Palla, F., Louppe, D., & Doumenge, C. (2002). Azobé. *Série Forafri 33*. Montpellier, France: CIRAD-Forêt.
- Paoli, G. D., Curran, L. M., & Slik, J. W. F. (2008). Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*, 155, 287–299. <https://doi.org/10.1007/s00442-007-0906-9>
- Pei, N., Lian, J.-Y., Erickson, D. L., Swenson, N. G., Kress, W. J., Ye, W.-H., & Ge, X.-J. (2011). Exploring tree-habitat associations in a Chinese subtropical forest plot using a molecular phylogeny generated from DNA barcode loci. *PLoS ONE*, 6, e21273. <https://doi.org/10.1371/journal.pone.0021273>
- Pelissier, R. (1998). Tree spatial patterns in three contrasting plots of a southern Indian tropical moist evergreen forest. *Journal of Tropical Ecology*, 14, 1–16. <https://doi.org/10.1017/s0266467498000017>
- Pielou, E. C. (1961). Segregation and symmetry in two-species populations as studied by nearest- neighbour relationships. *Journal of Ecology*, 49, 255–269. <https://doi.org/10.2307/2257260>
- Plotkin, J. B., Potts, M. D., Leslie, N., Manokaran, N., LaFrankie, J., & Ashton, P. S. (2000). Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology*, 207, 81–99. <https://doi.org/10.1006/jtbi.2000.2158>
- Réjou-Méchain, M., Flores, O., Bourland, N., Doucet, J.-L., Fétéké, R. F., Pasquier, A., & Hardy, O. J. (2011). Spatial aggregation of tropical trees at multiple spatial scales. *Journal of Ecology*, 99, 1373–1381. <https://doi.org/10.1111/j.1365-2745.2011.01873.x>
- Richards, P. W. (1996). *The tropical rain forest: an ecological study*. Cambridge, UK: Cambridge University Press.
- Rietkerk, M., Ketner, P., & De Wilde, J. J. F. E. (1995). Caesalpinioideae and the study of forest refuges in Gabon: Preliminary results. *Bulletin du Muséum National d'Histoire Naturelle, 4ème Série - Section B, Adansonia*, 17, 95–105.
- Robert, A., & Moravie, M.-A. (2003). Topographic variation and stand heterogeneity in a wet evergreen forest of India. *Journal of Tropical Ecology*, 19, 697–707. <https://doi.org/10.1017/s0266467403006096>
- Russo, S. E., Davies, S. J., King, D. A., & Tan, S. (2005). Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology*, 93, 879–889. <https://doi.org/10.1111/j.1365-2745.2005.01030.x>
- Satabie, B. (1982). *Le phénomène de vicariance chez deux espèces écophylétiques au Cameroun: Lophira alata Banks ex Gaertn. f. et Lophira lanceolata Van Tiegh. ex Keay (Ochnaceae)*. These. Yaoundé, Cameroon: Univ. Yaounde.
- Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & Evolution*, 19, 605–611. <https://doi.org/10.1016/j.tree.2004.09.003>
- Slik, J. W. F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., ... Zweifel, N. (2013). Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography*, 22, 1261–1271. <https://doi.org/10.1111/geb.12092>
- Tange, T., Yagi, H., Sasaki, S., Niiyama, K., & Kassim, A. R. (1998). Relationship between topography and soil properties in a hill dipterocarp forest dominated by *Shorea curtisii* at Semangkok Forest Reserve, Peninsular Malaysia. *Journal of Tropical Forest Science*, 10, 398–409.
- Thibault, M., Fisher, B. L., & Goodman, S. M. (2004). Description of Monts Doudou, Gabon, and the 2000 biological inventory of the reserve. *Memoirs of the California Academy of Sciences*, 28, 3–15.
- Tilman, D., & Pacala, S. (1993). The maintenance of species richness in plant communities. In R. E. Ricklefs & D. Schluter (Eds), *Species diversity in ecological communities: Historical and Geographical Perspectives* (pp. 13–25). Chicago, IL: University of Chicago Press.
- Valencia, R., Foster, R. B., Villa, G., Condit, R., Svenning, J.-C., Hernández, C., ... Balslev, H. (2004). Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. *Journal of Ecology*, 92, 214–229. <https://doi.org/10.1111/j.0022-0477.2004.00876.x>
- Van Der Burgt, X. M. (1997). Explosive seed dispersal of the rainforest tree *Tetraberlinia moreliana* (Leguminosae-Caesalpinioideae) in Gabon. *Journal of Tropical Ecology*, 13, 145–151. <https://doi.org/10.1017/s0266467400010336>
- Van der Burgt, X. M., Mackinder, B. A., Wieringa, J. J., & de la Estrella, M. (2015). The *Gilbertiodendron ogoouense* species complex (Leguminosae: Caesalpinioideae), Central Africa. *Kew bulletin*, 70, 29. <https://doi.org/10.1007/s12225-015-9579-4>
- Waagepetersen, R., & Guan, Y. (2009). Two-step estimation for inhomogeneous spatial point processes. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 71, 685–702. <https://doi.org/10.1111/j.1467-9868.2008.00702.x>
- Wang, X., Ye, J., Li, B., Zhang, J., Lin, F., & Hao, Z. (2010). Spatial distributions of species in an old-growth temperate forest, northeastern China. *Canadian Journal of Forest Research*, 40, 1011–1019. <https://doi.org/10.1139/x10-056>
- Ward, J. S., Parker, G. R., & Ferrandino, F. J. (1996). Long-term spatial dynamics in an old-growth deciduous forest. *Forest Ecology and Management*, 83, 189–202. [https://doi.org/10.1016/0378-1127\(96\)03722-x](https://doi.org/10.1016/0378-1127(96)03722-x)
- Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74, 159–164. <https://doi.org/10.2307/3545686>
- Whittaker, R. H. (1956). Vegetation of the Great Smoky Mountains. *Ecological Monographs*, 26, 1–80. <https://doi.org/10.2307/1943577>
- Wiegand, T., & Moloney, K. A. (2004). Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, 104, 209–229. <https://doi.org/10.1111/j.0030-1299.2004.12497.x>
- Wieringa, J. J. (1999). *Monopetalanthus* exit: a systematic study of *Aphanocalyx*, *Bikinia*, *Icuria*, *Michelsonia* and *Tetraberlinia* (Leguminosae, Caesalpinioideae). *Wageningen Agricultural University Papers*, 99, 1–320.
- Wright, J. S. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1–14. <https://doi.org/10.1007/s004420100809>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Summary stand characteristics of the 20 main canopy tree species of the 25-ha Rabi plot in Gabon according to their importance value index (IVI)

Appendix S2. Distribution maps of five dominant canopy tree species in the 25-ha plot at Rabi

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