



Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation

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Abstract

Tree species distribution has been investigated along 45 km of line transects in the tropical rain forest of the Dja Fauna Reserve in Cameroon. The spatial patterns were expressed by the probabilities that two trees are conspecific according to the distance separating them, providing information on the degree of species clumping as well as on alpha- and beta-diversity. Our objective was to assess the relative importance of habitat heterogeneity and limited dispersal in determining these patterns by: (1) comparing the patterns observed within and across major habitats; (2) comparing the patterns with the ones expected under a neutral hypothesis where limited dispersal is the sole factor. Although, habitat heterogeneity affected the distribution of many species, our results suggest that limited dispersal was the major factor affecting the degree of species clumping. The pattern observed was similar to the one found in Amazonia by Condit et al. [Science 295 (2002) 666]. We discuss the relevance of neutral models of tree communities to study the dispersal abilities of tree species.

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1. Introduction

The organization of species assemblages in communities may be viewed as resulting from two main kind of processes: niche-assembly rules and dispersal-assembly rules (Hubbell, 2001). By niche-assembly it is meant that species adaptation to particular ecological niches determines the particular species composition and organization of a community, following deterministic processes. On the contrary, the organi-

zation of a dispersal-assembled community results from localized dispersal events and local demographic stochasticity, following stochastic processes (Hubbell, 1979, 2001). Deterministic and stochastic processes are both at work in nature, but their relative importance in explaining patterns observed in community ecology is still unresolved (e.g. Hubbell, 2001; Condit et al., 2002; Duivenvoorden et al., 2002; Tuomisto et al., 2003) and should depend on: (1) the type of community investigated; (2) the particular property of the pattern observed; (3) the scale of observation.

The mainstream approach in community ecology has been to search for deterministic processes explaining the organization of species assemblages, for

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example by looking for the particular adaptations of each species to abiotic factors or the complexity of species interactions. In this way, community ecologists have been successful to demonstrate that each species is restricted to a more or less wide range of habitats, so that habitat heterogeneity is a main factor determining the geographical distribution of species. However, even within an apparently homogenous habitat, species spatial distribution is often non-random. This may result from our inability to detect finer details of habitat heterogeneity, but also from the fact that individuals tend to aggregate under limited dispersal (dispersal-assembly).

On the basis of spatial inventories of species distributions, two kinds of approach can be used to assess the relative importance of limited dispersal and niche differentiation in the spatial organization of a community: (1) searching for associations between the distribution of species and environmental factors, or (2) assessing if the observed distribution conforms to expectations under dispersal-assembly rules. Statistical tools to apply the former approach are well-developed and commonly used in community ecology (e.g. canonical correspondence analyses; Legendre and Legendre, 1998; Duivenvoorden et al., 2002; Tuomisto et al., 2003; Couteron et al., 2003). On the contrary, the second approach has received much less attention. A notable exception is the recent work by Hubbell (2001) who devised a neutral theory of species distribution that seems successful in explaining some properties of community organization patterns such as species–area relationship or species relative abundance (Bell, 2001). Hubbell's theory may be seen as an equivalent of the neutral theory in population genetics (Kimura, 1983). It postulates that all individuals are equivalent, in the sense that their fate is independent of the species to which they belong. Clearly, such a hypothesis is untrue in reality, but it may provide a good enough approximation in some communities to explain some properties of their organization. This might be the case for some ecological guilds, defined as communities of species exploiting the same trophic resources (e.g. a community of tree species), where most interactions between individuals are competitive, and the result of the competition might be little dependent upon the particular species in interaction. According to Hubbell (2001), communities of tree species in tropical forests might behave

approximately in such a neutral fashion. In these forests, characterized by a high diversity and a low density for most tree species, recruitment is a major limitation (Hubbell et al., 1999), so that empty space (e.g. under gaps) might be colonized essentially following a lottery system (the first arrived establish), reducing the opportunities of establishment of the best locally adapted species.

The analogy of concepts and processes occurring in the field of population genetics and community ecology can be exploited to explore the way species tend to cluster spatially under limited dispersal. This process is called “isolation by distance” by population geneticists and has been well-characterized on theoretical grounds since the early work of Malécot (1948). In essence, limited dispersal causes local genetic drift (“local demographic drift” in the case of a community of species), so that allele (species) frequencies fluctuate among locations, the frequencies among nearby locations being positively correlated. The theory of isolation by distance predicts that the probability of two genes bearing the same allele decreases approximately linearly with distance in a one-dimensional space, and with the logarithm of the distance in a two-dimensional space (Rousset, 1997). Transposing this theory to a neutral community of species under limited dispersal, we can expect that the same pattern occurs when considering the probability that two individuals belong to the same species (Condit et al., 2002; Chave and Leigh, 2002).

Tropical forests have been the focus of much debate regarding the processes maintaining their high diversity and determining their organization. In the present study, our goal is to investigate the spatial organization of tree species in a tropical rain forest of Cameroon in the framework of the theory of isolation by distance. We will investigate: (1) how the probability that two individuals are conspecific, varies according to spatial distances and habitats; (2) what is the impact of habitat heterogeneity on the degree of spatial clustering of each species. The results will be compared with those obtained in neotropical forests (Condit et al., 2002) and used to evaluate the relative role of limited dispersal and niche differentiation on the observed patterns, showing that stochastic processes seem to be more determinant than deterministic ones. We will then discuss the relevance of neutral models for inferring dispersal distances.

2. Material and methods

2.1. Study site and sampling

The Dja Fauna Reserve (DFR) covers an area of 5260 km² situated at 2°50'–3°30'N and 12°20'–13°40'E in the south-eastern corner of Cameroon (Fig. 1), within the area known as the southern plateau (Letouzey, 1968). Most of the DFR is situated at 600–700 m above the sea level and, except for the presence of a few inselbergs, most of DFR is fairly flat. The monthly average temperature lies between 23.5 and 24.5 °C and the annual rainfall between 1180 and 2350 mm with a mean of 1626 mm (Sonké and Lejoly, 1998). According to Köppens' system (Köppen, 1936), this zone belongs to the AW3 climatic type (Bultot, 1950).

Ecological studies in DFR were initiated in 1993 to examine, with permanent data monitoring, species diversity, growth, mortality and regeneration of the trees (Sonké, 1998; Sonké and Lejoly, 1998). DFR was chosen as the field of investigation because it is probably a mature to old growth forest. To study the vegetation, line transects covering the heterogeneity of

the DFR system were established (Fig. 1). Along nine transects, each 5 km long, tree species were mapped and identified following two sample schemes: (1) all trees with a diameter at breast height (DBH) above 10 cm over a 5 m wide band, totalling 22.5 ha inventoried; (2) all trees with a DBH above 70 cm over a 50 m wide band, totalling 225 ha inventoried. For buttressed trees, DBH was measured at 10 cm above buttress. Trees with DBH \geq 10 cm include understory trees as well as canopy trees, whereas all trees with DBH \geq 70 cm are canopy or emergent trees. The maximum distance between trees (all transects included) is 110 km. Trees were fully identified up to species level using floras and by comparison with other collection of reference available in the Cameroon national herbarium, and in the National Botanic Garden of Belgium. Voucher specimens were collected and in case of any doubt, supplementary material was collected for further identifications. The 5 m wide transects (trees with DBH \geq 10 cm) contained 11,538 individuals (density = 513 tree/ha) belonging to 375 identified species (178 individuals not identified) among which 90 species were represented by at least 30 individuals. The 50 m wide

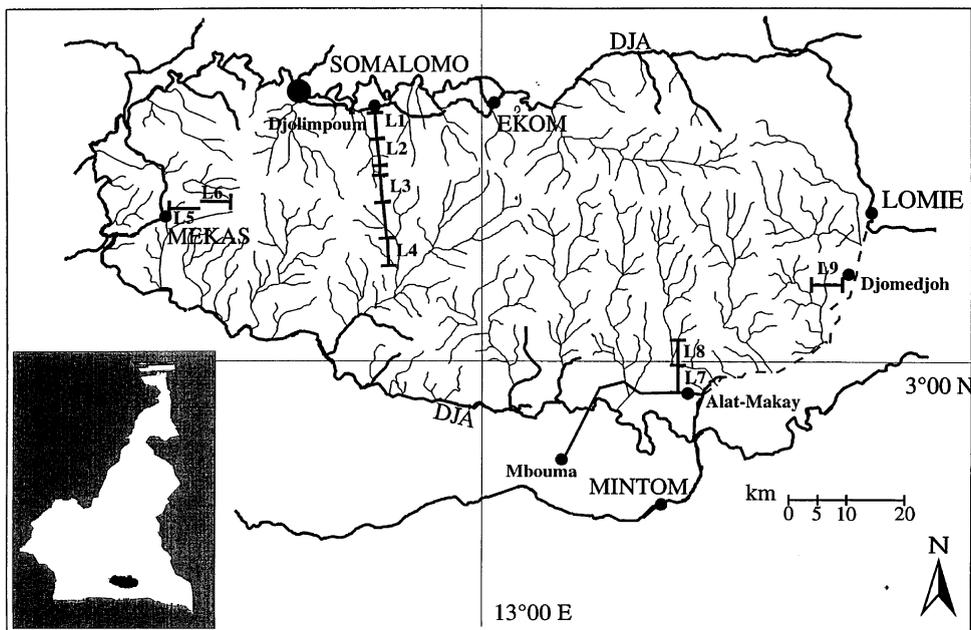


Fig. 1. Map of the Dja Fauna Reserve (DFR) showing the study transects (L1–L9), and map of Cameroon (bottom, left) showing the position of the DFR.

transects (trees with DBH ≥ 70 cm) contained 2947 individuals (density = 13.1 tree/ha) belonging to 178 identified species (69 individuals not identified to the species level) among which only 24 species were represented by at least 30 individuals. A list of the most common species with the number of trees is given in Appendix A.

During the inventory, the DBH per tree was recorded as well as the type of habitat found along the transects. The habitats crossed by the nine transects could be subdivided into three main types on basis of soil hydromorphy, vegetation structure and indicator species (Lebrun and Gilbert, 1954): (1) dryland primary forest (DPF); (2) swamp forest (SwF); (3) secondary forest (SeF), which constituted respectively, 74%, 12% and 14% respectively of the transects total length. DPF and SwF are mature and undisturbed forest, SwF being permanently or periodically inundated. SeF was in majority human disturbed, but also included transect stretches of significant size recently perturbed by natural factors (e.g. large gaps) and showing obvious signs of early successional stages (non-mature forest). This elementary habitat characterization permitted us to investigate the impact of two major ecological determinants of species distribution in lowland dense forests: the drainage conditions and the cover perturbations.

2.2. Data analysis

The pattern of species diversity was analyzed in the framework of isolation by distance theory. We investigated in particular species turnover by estimating the probability that two random individuals belong to the same species according to the distance separating them, $F(d)$. If species are aggregated, $F(d)$ is a decreasing function of d , and can thus reveal the degree of species clustering. Moreover, $F(d)$ can be predicted for neutral models when limited dispersal and speciation are the sole factors determining $F(d)$ (Condit et al., 2002; Chave and Leigh, 2002). $F(d)$ was estimated for a set of mutually exclusive distance intervals, k , as $F(k) = \sum_{i,j} w_{ij}(k) F_{ij} / \sum_{i,j} w_{ij}(k)$, where the sums apply over all pairs of individuals (i, j) sampled, $F_{ij} = 1$ if individuals i and j belong to the same species, otherwise $F_{ij} = 0$, and $w_{ij}(k) = 1$ if the distance separating i and j , d_{ij} , is included in k ,

otherwise $w_{ij}(k) = 0$. $F(k)$ is thus the frequency of conspecific individuals among the pairs separated by a given distance interval. A plot of $F(k)$ values according to distance bears two kinds of information: (1) the level of species diversity (low average $F(k)$ values indicate high diversity); (2) the level of spatial structuring ($F(k)$ values decreasing quickly with distance indicate strong species clustering). Note that looking on a local scale (e.g. at distance inferior to 100 m), $1 - F(k)$ corresponds to Simpson diversity index (Legendre and Legendre, 1998), expressing the alpha-diversity. The way $F(k)$ decreases with distance indicates species turnover rate, expressing thus the beta-diversity at different scales.

To pick up only the information on species aggregation (species turnover rate), a standardized measure can be defined as $R_{ij} = (F_{ij} - \bar{F}) / (1 - \bar{F})$, where $\bar{F} = \bar{F}_{ij}$ is the probability that two random individuals from the sample are conspecific, irrespectively of the distance separating them. $R(k)$, the average R_{ij} values over distance class k , can be interpreted as an autocorrelation coefficient of species identity. $R(k) > 0$ if two individuals separated by distance class k are more likely to be of the same species than two random individuals in the sample. To make the link with population genetics, if alleles within a population were considered rather than species within a community, $R(k)$ would estimate a “conditional” kinship coefficient among individuals; $R(k)$ (as well as $F(k)$) being expected to decrease approximately linearly with the logarithm of the distance under an isolation by distance process in a two-dimensional space (Hardy and Vekemans, 1999). Hence, the slope of the correlogram, b regressing R_{ij} values on $\ln(d_{ij})$, can be used to quantify more synthetically the degree of species aggregation, or the species turnover rate.

Isolation by distance models can predict the rate of decrease of $F(d)$ under neutrality, so that dispersal parameters can potentially be inferred from the pattern of species distribution. A simple way to estimate dispersal distances can be derived from procedures originally used to infer gene dispersal (Rousset, 1997; Hardy and Vekemans, 1999): the ratio $(F_0 - 1)/b$ provides an estimate of $2\pi D\sigma^2$, where F_0 refers to the F between neighboring trees, b is the regression slope of $F(d)$ on $\ln(d)$ (which should be computed for $d \geq \sigma$), D is the effective density of reproducing trees (i.e. accounting for the variance of reproductive

success), and σ^2 is half the mean square dispersal distance from parent to surviving offspring.

$F(k)$ was computed separately on the sample collected on the 5 m wide transects ($\text{DBH} \geq 10$ cm) and the sample collected on the 50 m wide transects ($\text{DBH} \geq 70$ cm). A common geographical reference was used for all nine transects to attribute spatial coordinates for each individual, so that analyses were performed on the combined samples of all transects. To investigate the impact of habitat heterogeneity, $F(k)$ were computed considering: (1) the whole sample irrespectively of habitat; (2) sub-samples within each habitat (DPF, SeF, SwF).

$F(k)$ and $R(k)$ curves provide global descriptions of species clustering but do not account for the differences of patterns among species. Therefore, to characterize the spatial clustering of a given species S , we computed R_{ij} values considering all species different from S as an alternative species, giving $R_{ij|s}$, that were averaged over distance intervals, $R_S(k)$. Then, to get a synthetic measure of the degree of spatial clustering for each species, we used the regression slopes of $R_{ij|s}$

on $\ln(d_{ij})$, denoted b_S . Slopes were computed considering pairs of individuals separated by 100 m to 10 km, to catch the degree of clustering on a “mesoscale”. Only species with at least 30 individuals sampled were analyzed in this way to avoid excessive sampling variance.

To check, whether species frequencies varied among habitats, we used a χ^2 -test of independence for the number of trees found in DPF, SwF and SeF for each species (considering only the species with at least 30 individuals sampled in the 5 m wide transects).

3. Results

The probability that two random trees are conspecific decreases with spatial distance, indicating species clustering (Fig. 2). At equal distance, this probability is somewhat higher when the individuals compared are located within the same habitat than in different habitat (Fig. 2), reflecting the impact of niche differentiation. Nevertheless, $F(d)$ curves are nearly

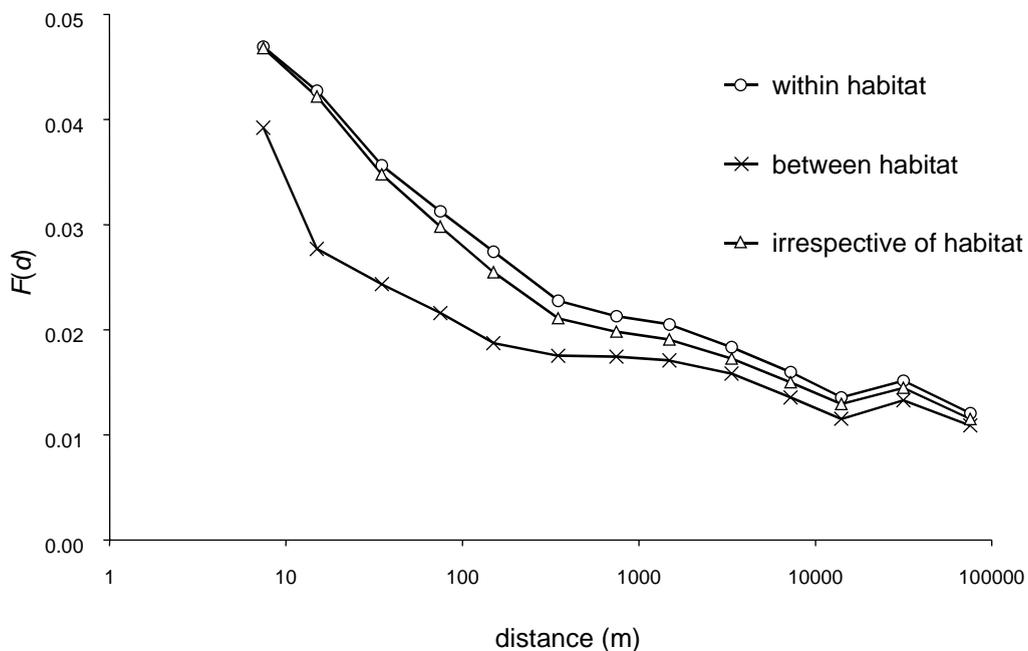


Fig. 2. Effect of habitat heterogeneity on species turnover. The probabilities that two trees are conspecific according to the distance, $F(d)$, are given for different ways pairs of trees were sampled: (1) all pairs of trees, irrespectively of habitats (triangles); (2) all pairs of trees found within a same type of habitat (circles); (3) all pairs of trees found in different habitats (crosses). Based on the sample of trees with $\text{DBH} \geq 10$ cm (11360 individuals, 375 species).

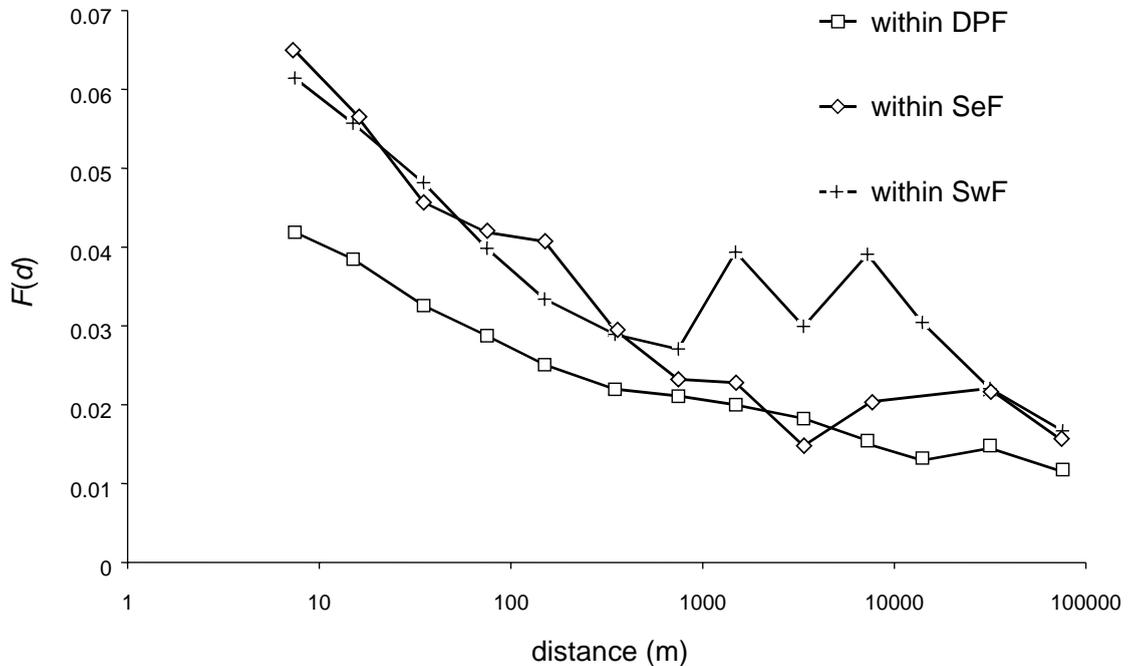


Fig. 3. Difference among habitats on species turnover. The probabilities that two trees sampled within an habitat are conspecific according to the distance, $F(d)$, are given for the following habitat types: (1) DPF—dryland primary forest (squares, 8441 trees); (2) SeF—secondary forest (diamonds, 1624 trees); (3) SwF—swamp forest (plus, 1295 trees). Based on the sample of trees with $\text{DBH} \geq 10$ cm.

unchanged when analyzing the whole data set (i.e. across all habitats) or restricting the analysis within habitat (Fig. 2), so that habitat heterogeneity does not affect strongly $F(d)$.

When $F(d)$ is computed over trees sampled within each type of habitat, $F(d)$ values are higher within SeF and SwF than within DPF (Fig. 3), indicating that the later habitat supports higher diversity of tree species. Up to a distance of 1 km, $F(d)$ declines somewhat faster with distance in SeF and SwF than in DPF (Fig. 3), species turnover is thus slower in DPF.

The patterns illustrated for the sample of trees with $\text{DBH} \geq 10$ cm (Figs. 2 and 3) also hold for the sample of large trees ($\text{DBH} \geq 70$ cm; results not shown). There are, however differences between the two samples. First, diversity is higher in the sample of small trees than large trees (lower average $F(d)$ values, Fig. 4), which is easily explained by the fact that many tree species (e.g. understory trees) do not reach large diameters, reducing the diversity observed in the sample of large trees. Secondly, up to a distance of about 500 m, $F(d)$ decreases faster with distance for the sample of large trees than small

trees (Fig. 4). The later observation suggests a higher tendency towards species clumping on a local scale for large trees than small ones. This is also observed to some extent when $F(d)$ is computed over the subsample of trees with $\text{DBH} \geq 30$ cm in the 5 m wide transects (Fig. 4).

At first sight, $F(d)$ decreases approximately linearly with the logarithm of the distance (Figs. 2–4), as predicted by neutral theory, and suggesting that limited dispersal might be the primary factor determining species clumping. A closer examination shows that $F(d)$ declines faster at short distance (up to about 500 m) than at larger distance, this phenomenon being particularly pronounced for large trees (Fig. 4). For example, the regression slope of $F(d)$ on $\ln(d)$ is $b = -0.0068$ ($\text{DBH} \geq 10$ cm) and $b = -0.0185$ ($\text{DBH} \geq 70$ cm) for $d < 500$ m, and $b = -0.0018$ ($\text{DBH} \geq 10$ cm) and $b = -0.0026$ ($\text{DBH} \geq 70$ cm) for $d \geq 500$ m.

Using these regression slopes for $d \geq 500$ m and the observed density of trees, the estimated dispersal distances according to the predictions of isolation by distance models are equal to $\sigma = 41.6, 76.2$, and

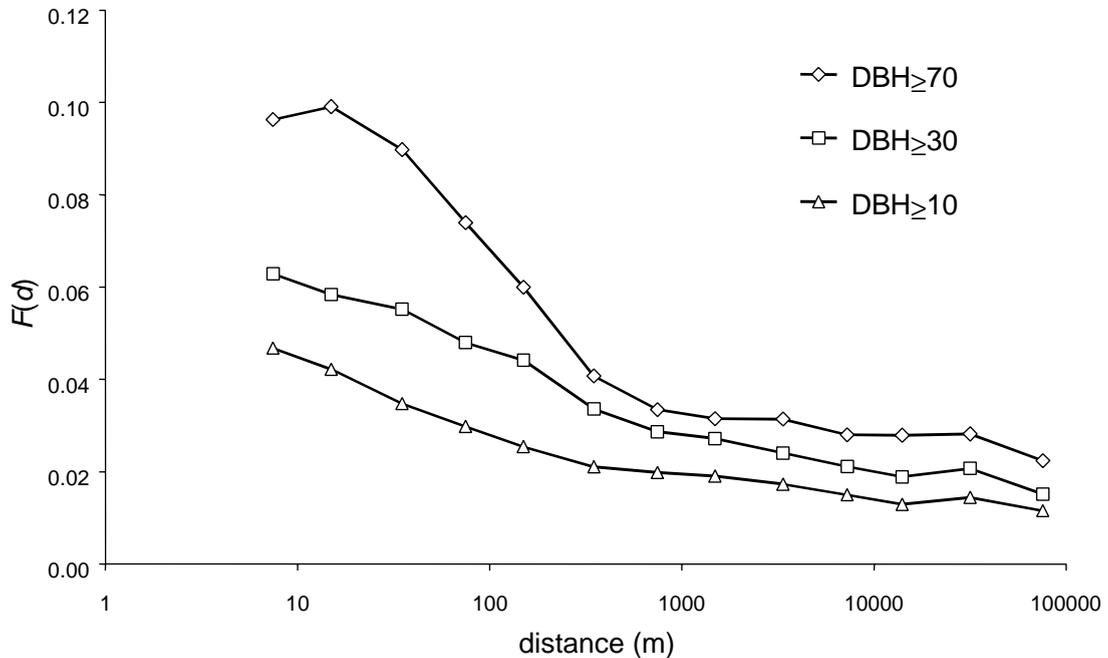


Fig. 4. Effect of tree size on species turnover. The probabilities that two trees are conspecific according to the distance, $F(d)$, are given for different tree size limits (diameter at breast height, DBH): (1) $\text{DBH} \geq 10$ cm (triangles); (2) $\text{DBH} \geq 30$ cm (squares); (3) $\text{DBH} \geq 70$ cm (diamonds). Trees were sampled along a total of 45 km of line transects over a 50 m wide band for trees with $\text{DBH} \geq 70$ cm (6521 trees), and over a 5 m wide band for trees with $\text{DBH} \geq 10$ cm (11360 trees) and $\text{DBH} \geq 30$ cm (2248 trees).

217 m using data on trees with $\text{DBH} \geq 10$, 30, and 70 cm, respectively.

The b_S values, quantifying the degree of clustering of each species on a mesoscale (trees separated by 100 m to 10 km), were computed over the total sample (all habitats confounded, values were given in Appendix A), and over the sub-sample of trees occurring in DPF. The b_S values varied widely among species (Fig. 5). For most species, b_S values were very similar within DPF and across habitats (Fig. 5), suggesting again that habitat differentiation is not a major determinant of spatial clustering. However, *Musanga cecropioides* (Moraceae) constitutes a notable exception, appearing much more clumped when seen across habitats than within DPF (Fig. 5). This is actually a typical pioneer species, strongly associated with disturbed habitat, so that habitat specificity appears to be a major determinant of the degree of spatial clumping for this species.

Over 90 species, χ^2 -tests of independence with respect to habitat were significant at a 1% level for 39 species (43% of the species). Habitat preference

cannot necessarily be concluded for these species because spatial autocorrelation of both habitat and species distributions cause the test to be liberal (i.e. it rejects the null hypothesis too often, Legendre, 1993). However, over a subset of 18 species showing essentially no spatial autocorrelation (flat $R_S(d)$ correlograms), the test was significant for eight species (44% of the species). Hence, for most species, spatial autocorrelation is unlikely to be responsible for the significant tests.

4. Discussion

4.1. Dispersal limitation versus niche differentiation

In a community of trees from a tropical rain forest of Cameroon, we found that the probability that two individuals are conspecific decreases approximately linearly with the logarithm of the spatial distance. According to the theory of isolation by distance, this is the pattern expected if species clustering is caused

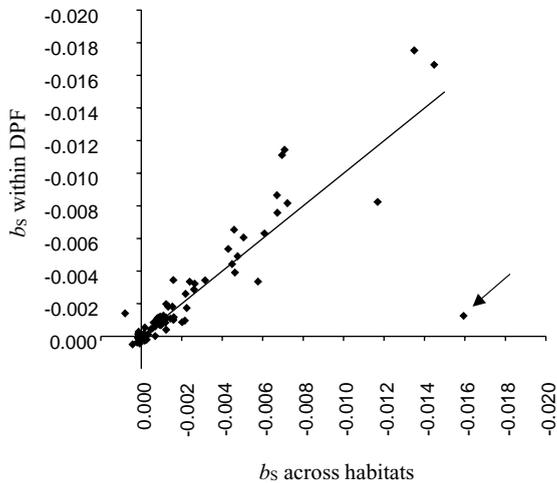


Fig. 5. Impact of habitat heterogeneity on the degree of spatial clustering of each species. The degree of spatial clustering was evaluated by the slope of each species specific autocorrelogram (b_s , see text) in the 100 m–10 km range. For 70 species with at least 40 individuals, the b_s values computed within the dominant habitat (dryland primary forest, DPF) are compared with those computed over the whole sample (across habitats), and subject to the impact of habitat heterogeneity. The line shows the expected relationship in the absence of habitat effect, and the arrows points to the case of *Musanga cecropioides*.

by limited dispersal and ecological drift. Interestingly, the slope of $F(d)$ was steeper at short distances (<200 m), as was also found in Ecuador by Condit et al. (2002) who interpreted this result as evidence of a significant departure from neutral expectations. However, Condit et al. (2002) assumed that dispersal followed a Gaussian distribution when fitting their data on isolation by distance models. As shown by simulations (Heuertz et al., 2003), very leptokurtic dispersal distributions could also explain the steeper $F(d)$ slope at short distance.

Our analysis also shows that looking within or across habitats does not affect strongly the pattern of $F(d)$, although habitat differentiation occurs, and the clustering of one characteristic pioneer species could be attributed mostly to its affinity for disturbed habitats. These results suggest that the degree of species aggregation is mostly determined by dispersal-assembly rules rather than niche-assembly rules, at least for the common species, as the sample size was too limited for other species to assess their spatial patterns of distribution. This is important because common species might be more habitat generalists

than rare species. We must also acknowledge that our characterization of habitats may have missed some crucial dimensions of niche differentiation. Actually, niche differentiation explains some properties of the patterns observed, such as the increased diversity (lower $F(d)$ values) observed over pairs of trees sampled in different habitats. This is in line with the fact that the frequencies of many species were not uniform with respect to habitat according to χ^2 -tests of independence.

Many studies have reported significant effect of edaphic factors on floristic composition of trees in tropical forests (e.g. Clark et al., 1999; Sabatier et al., 1997; Coueron et al., 2003; Duivenvoorden et al., 2002). However, the percentage of variance in floristic composition that could be attributed to edaphic factors on a mesoscale (ca. 1–100 km²) was typically low. Hence, although niche differentiation is likely commonplace in tropical forest trees so that habitat heterogeneity might influence substantially the distribution of various species, the pattern of species aggregation, when expressed by the probabilities of finding two conspecific individuals according to the distance, may be more dependent upon dispersal limitation than habitat heterogeneity.

4.2. African versus neotropical forests

Our results are similar to those found in neotropical forests by Condit et al. (2002), where $F(d)$ was computed over trees with DBH ≥ 10 cm sampled in plots from Panama, Peru and Ecuador. For example, in the Ecuadorian plot on *terra firme* (the equivalent of what we called DPF), $F(d)$ declined linearly with $\ln(d)$ for distances comprised between 200 m and 100 km, with a slope $b = -0.0015$, very similar to the one we obtained ($b = -0.0018$ for trees with DBH ≥ 10 cm). In the Panamanian plots, where soil and climate heterogeneity is higher than in the western Amazonian plots, Condit et al. (2002) found much steeper slopes on a mesoscale, suggesting that the greater habitat heterogeneity in Panama was responsible for this difference. Given the relative homogeneity of environmental conditions in the DFR, our results should better compare with the studies carried out in Amazonia. African forests are known to be less species rich than neotropical forests and, because the vegetation cover was probably more affected by past climatic

fluctuations, they might also contain more generalist, wide-ranging species with better dispersal abilities (Richards, 1973). The lower local species diversity (alpha-diversity) in Africa is confirmed by comparing the average $1-F(d=100\text{ m})$ values in Cameroon (0.972) and in Ecuador (0.982; Condit et al., 2002). However, species turnover rates are similar in Cameroon and Ecuador, so that there is no evidence that dispersal limitation was lower in the African forest.

4.3. Estimating dispersal parameters from neutral models

When limited dispersal and speciation are the main factors determining the rate of decrease of $F(d)$, neutral models may potentially be used to estimate these parameters from the patterns of species distribution. Condit et al. (2002) fitted their data of $F(d)$ with neutral expectations to estimate dispersal distances (σ^2 , half the mean square dispersal distance from parent to surviving offspring) and speciation rate (ν), getting estimates of σ ranging from 40 to 73 m, and ν ranging from 5×10^{-8} to 2×10^{-14} per tree birth, according to plots, using tree with $\text{DBH} \geq 10$ cm. Our estimate of σ using the same DBH class is very similar $\sigma = 41.6$ m. However, even when habitat heterogeneity is not affecting the observed patterns, the reliability of such inferences is questionable for at least three major reasons: (1) the timescale needed to get $F(d)$ curves at equilibrium is very long; (2) the neutral model used to make these inferences assumes that all species share equal dispersal capabilities (σ) and life cycles, which is clearly unrealistic; (3) the minimal DBH considered in the sample plots is set arbitrarily and affects strongly the estimates of σ (see results).

Regarding the first problem, $F(d)$ values depend on a balance between speciation, dispersal and ecological drift, reaching equilibrium on a timescale of the order of $2/\nu$ generations (Chave and Leigh, 2002), an enormous time, so that ν estimates are probably little reliable. However, the rate of decrease of $F(d)$ is essentially a balance between dispersal and ecological drift (not speciation), reaching equilibrium on a time-scale dependent on the ratio between the geographical scale of observation and σ , which can be reasonably short on a small spatial scale (Hardy and Vekemans, 1999). Hence, σ might be more reliably estimated when a rather small geographical scale is considered,

which should also limit the impact of habitat heterogeneity.

To address the second and third problems, more theoretical work is required to investigate how $F(d)$ curves are affected when species differ regarding their life cycles and dispersal distances, and when growth is implemented. Such work is essential for interpreting $F(d)$ curves correctly. Models implementing differences among species would not be neutral in the strict sense (the behavior of an individual is no more independent of the species) but could still assume the absence of habitat differentiation. Preliminary simulations suggest that such models keep most of the properties of strict neutral models, potentially allowing the development of methods to estimate σ for each species from their own pattern of spatial distribution (O.J. Hardy, unpublished).

4.4. Characterising the spatial patterns of species distribution

Spatial statistics based on point processes, such as Ripley's K -function (e.g. Ripley, 1981), have often been used to describe the spatial distribution of trees (e.g. Pélissier and Goreaud, 2001), and they could be applied on each species separately. In this paper, we proposed a spatial autocorrelation approach, considering one focal species and grouping the other ones into a single alternative class. Although both approaches are closely related (Shimatani and Takahashi, 2003) and essentially indicate the extent to which individuals are spatially clustered at different scales, the analysis of clustering is relative to a continuous space using Ripley's K -function, whereas it is relative to a set of discrete positions (the positions of all sampled trees irrespective of species) using the spatial autocorrelation approach. Consequently, local variations in tree densities (all species included), such as due to gaps of tree cover following the presence of a river, would affect Ripley's K -function (but see Pélissier and Goreaud, 2001), whereas not the spatial autocorrelation approach, which is also unaffected by the overdispersion of large trees due to local competition. Hence, the spatial autocorrelation approach is well-suited in the framework of the neutral theory, where all species are assumed substitutable, and isolation by distance models can provide quantitative expectations under null hypotheses.

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Appendix A

The following table lists species with at least 50 individuals in the 5 m wide transects (DBH \geq 10 cm) or the 50 m wide transects (DBH \geq 70 cm), ordered by families. The number of individuals found (N) and the intensity of their spatial aggregation at a mesoscale (expressed by $-10^3 b_S$ values within 100 m to 10 km, see text) are given for each species and sampling scheme when $N \geq 30$.

Family	Species	DBH \geq 10 cm, 22.5 ha		DBH \geq 70 cm, 225 ha	
		N	$-10^3 b_S$	N	$-10^3 b_S$
Anacardiaceae	<i>Sorindeia grandifolia</i> Engl.	96	-0.20	0	
	<i>Trichoscypha acuminata</i> Engl.	125	-0.13	2	
Annonaceae	<i>Anonidium mannii</i> (Oliv.) Engl. and Diels	179	2.20	4	
	<i>Enantia chlorantha</i> Oliv.	88	0.35	0	
	<i>Polyalthia suaveolens</i> Engl. and Diels	332	1.02	0	
	<i>Xylopia quintasii</i> Engl. and Diels	57	-0.42	1	
Apocynaceae	<i>Alstonia boonei</i> De wild.	45	0.13	212	3.61
	<i>Funtumia elastica</i> (Preuss) Stapf	63	-0.80	0	
	<i>Tabernaemontana crassa</i> Benth.	627	5.77	0	
Arecaceae	<i>Raphia monbuttorum</i> Drude	68	2.16	0	
Burseraceae	<i>Dacryodes edulis</i> (G. Don) H.J. Lam	60	1.02	2	
	<i>Santiria trimera</i> (Oliv.) Aubrév.	341	0.87	2	
Caesalpiniaceae	<i>Anthonotha macrophylla</i> Pal. Beauv.	124	0.56	0	
	<i>Dialium zenkeri</i> Harms	62	0.89	0	
	<i>Distemonanthus benthamianus</i> Baill.	42	1.23	86	0.96
	<i>Erythrophleum suaveolens</i> (Guil. and Perr.) Brenan	36	0.08	96	-0.07
	<i>Gilbertiodendron dewevrei</i> (De wild.) Léonard	53	13.49	50	50.75
	<i>Hylodendron gabunense</i> Taubert	77	0.79	50	6.19
Clusiaceae	<i>Allanblackia floribunda</i> Oliv.	58	1.10	12	
Combretaceae	<i>Terminalia superba</i> Engl. and Diels	27		72	5.56
Euphorbiaceae	<i>Antidesma laciniatum</i> Müll. Arg.	119	1.60	0	
	<i>Dichostemma glaucescens</i> Pierre	200	6.09	1	
	<i>Klaineanthus gaboniae</i> Pierre ex Prain	58	1.33	0	
	<i>Macaranga spinosa</i> Müll. Arg.	52	1.23	0	
	<i>Mareyopsis longifolia</i> (Pax) Pax and Hoffm.	100	4.30	0	
	<i>Plagiostyles africana</i> (Müll. Arg.) Prain	231	4.63	0	

Appendix A. (Continued)

Family	Species	DBH \geq 10 cm, 22.5 ha		DBH \geq 70 cm, 225 ha	
		<i>N</i>	$-10^3 b_S$	<i>N</i>	$-10^3 b_S$
	<i>Uapaca acuminata</i> (Hutch.) Pax and Hoffm.	67	2.25	10	
	<i>Uapaca guineensis</i> Müll. Arg.	327	6.71	1	
	<i>Uapaca paludosa</i> Aubrév. and Léandri	256	6.96	139	14.05
Fabaceae	<i>Angylocalyx pynaertii</i> De wild.	75	1.04	0	
	<i>Pterocarpus soyauxii</i> Taub.	75	-0.15	69	1.14
Irvingiaceae	<i>Irvingia gabonensis</i> (Aurey-Lecomte ex O'Rorke) Baill.	82	0.10	23	
	<i>Desbordesia glaucescens</i> (Engl.) Van Thiegh.	205	1.54	127	2.21
	<i>Klainedoxa gabonensis</i> Pierre	55	-0.07	60	-1.32
Lecythidaceae	<i>Petersianthus macrocarpus</i> (Beauv.) Liben	381	4.59	126	0.75
Lepidobotryaceae	<i>Lepidobotrys staudtii</i> Engl.	83	0.61	0	
Meliaceae	<i>Carapa procera</i> DC.	133	3.15	7	
	<i>Trichilia rubescens</i> Oliv.	206	1.61	0	
	<i>Trichilia tessmannii</i> Harms	50	11.69	0	
Mimosaceae	<i>Calpocalyx dinklagei</i> Harms	88	1.20	0	
	<i>Cylicodiscus gabunensis</i> Harms	20		56	-0.56
	<i>Pentaclethra macrophylla</i> Benth.	235	0.48	195	10.99
	<i>Piptadeniastrum africanum</i> (Hook.f.) Brenan	30	0.54	77	0.88
Moraceae	<i>Musanga cecropioides</i> R.Br.	97	15.93	101	19.01
	<i>Trilepisium madagascariense</i> DC.	87	14.48	1	
Myristicaceae	<i>Coelocaryon preussii</i> Warb.	149	4.49	6	
	<i>Pycnanthus angolensis</i> (Welw.) Exell	50	0.80	49	1.27
	<i>Staudtia kamerunensis</i> Warb.	105	0.69	14	
Olacaceae	<i>Heisteria trillesiana</i> Pierre	154	7.22	23	
	<i>Heisteria zimmereri</i> Engl.	94	2.65	53	-0.17
	<i>Strombosia pustulata</i> Oliv.	169	0.94	0	
	<i>Strombosia scheffleri</i> Engl.	83	2.60	1	
	<i>Strombosiopsis tetrandra</i> Engl.	238	1.44	18	
Pandaceae	<i>Panda oleosa</i> Pierre	57	-0.04	12	
Rubiaceae	<i>Aidia micrantha</i> (K. Schum.) F. White	78	7.09	0	
	<i>Corynanthe pachyceras</i> K. Schum.	131	2.40	0	
Sapindaceae	<i>Blighia sapida</i> König	81	1.10	2	
	<i>Pancovia pedicellaris</i> Radlk. and Gilg.	52	5.06	0	
Tiliaceae	<i>Duboscia macrocarpa</i> Bocq.	74	0.18	93	4.35
Ulmaceae	<i>Celtis tessmannii</i> De wild.	102	0.96	21	
	<i>Celtis zenkeri</i> Engl.	107	6.73	19	
Violaceae	<i>Rinorea oblongifolia</i> (C.H.Wright) Marquand	189	-0.13	0	

References

- Bell, G., 2001. Neutral macroecology. *Science* 293, 2413–2418.
- Bultot, F., 1950. Carte des régions climatiques du Congo belge établie d'après les critères de Köppen. Publ. INEAC, Bureau Climatologique, Communication 2.
- Chave, J., Leigh, E.G., 2002. A spatially-explicit neutral model of beta-diversity in tropical forests. *Theor. Popul. Biol.* 62, 153–168.
- Clark, D.B., Palmer, M.W., Clark, D.A., 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80, 2662–2675.
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., Hubbell, S.P., 2002. Beta-diversity in tropical forest trees. *Science* 295, 666–669.
- Couteron, P., Pélissier, R., Mapaga, D., Molino, J.-F., Teillier, L., 2003. Drawing ecological insights from a management-oriented forest inventory in French Guiana. *For. Ecol. Manage.* 172, 89–108.
- Duivenvoorden, J.F., Svenning, J.-C., Wright, S.J., 2002. Beta diversity in tropical forests. *Science* 295, 636–637.
- Hardy, O.J., Vekemans, X., 1999. Isolation by distance in a continuous population: reconciliation between spatial autocorrelation analysis and population genetics models. *Heredity* 83, 145–154.
- Heuertz, M., Vekemans, X., Hausman, J.F., Palada, M., Hardy, O.J., 2003. Estimating seed versus pollen dispersal from spatial genetic structure in the common ash. *Mol. Ecol.* 12, 2483–2495.
- Hubbell, S.P., 1979. Tree dispersion, abundance and diversity in a dry tropical forest. *Sciences* 203, 1299–1309.
- Hubbell, S.P., 2001. *A Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., Loo de Lao, S., 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283, 554–557.
- Kimura, M., 1983. *The Neutral Theory of Molecular Evolution*. Cambridge University Press.
- Köppen, W., 1936. In: Köppen, W., Geiger, R., (Eds.). *Das geographische system der klimate*. Handbuch der klimatologie, Berlin.
- Lebrun, J., Gilbert, G., 1954. Une classification écologique des forêts du Congo. Publication de l'Institut National pour l'Etude Agronomique du Congo belge 63, 9–89.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier.
- Letouzey, R., 1968. *Etude phytogéographique du Cameroun*. Lechevalier, Paris.
- Malécot, G., 1948. *Les Mathématiques de l'Hérédité*. Masson et Cie.
- Pélissier, R., Goreaud, F., 2001. A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation. *J. Veg. Sci.* 12, 99–108.
- Richards, P., 1973. Africa, the “odd man out”. In: Meggers, B., Ayesu, E., Duckworth, W. (Eds.), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Institution Press, Washington, DC, pp. 21–26.
- Ripley, B.D., 1981. *Spatial Statistics*. Wiley, New York, NY.
- Rousset, F., 1997. Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics* 145, 1219–1228.
- Sabatier, D., Grimaldi, M., Prévost, M.-F., Guillaume, J., Godron, M., Dosso, M., Curmi, P., 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. *Plant Ecol.* 131, 81–108.
- Shimatani, K., Takahashi, M., 2003. On methods of spatial analysis for genotyped individuals. *Heredity* 91, 173–180.
- Sonké, B., 1998. *Etudes floristiques ets tructurales des forêts de la réserve de faune du Dja (Cameroun)*. Ph.D. Thesis, Université Libre de Bruxelles.
- Sonké, B., Lejoly, J., 1998. Biodiversity study in Dja Fauna Reserve (Cameroun): using the transect method. In: Huxley, C.R., Lock, J.M., Cutler, D.F. (Eds.), *Chronoly, Taxonomy and Ecology of the Floras of Africa and Madagascar*. Royal Botanic Garden, Kew, pp. 171–179.
- Tuomisto, H., Ruokolainen, K., Yli-Halla, M., 2003. Dispersal, environment, and floristic variation of Western Amazonian forests. *Science* 299, 241–244.