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Impact of fine-scale edaphic heterogeneity on tree species assembly in a central African rainforest

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Keywords
Canopy; Edaphic heterogeneity; Floristic variability; Habitat differentiation; Habitat preference; Subcanopy; Torus-translation

Abbreviations
AL = exchangeable aluminium content; CA = correspondence analysis; CCA = canonical correspondence analysis; CS = clayey soil; EC = electrical conductivity in water; OM = percentage of organic matter; P = available phosphorus concentration; PCA = principal components analysis; SS = sandy soil.

Nomenclature
Lebrun & Stork (2008)

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Abstract

Questions: Soil properties have been shown to partially explain tree species distribution in tropical forests. Locally, species turnover across space can result not only from edaphic heterogeneities but also from limited seed dispersal. To characterize the contribution of each process, contact areas between contrasted soil types offer ideal settings. In the present study, we aimed to test species and species assemblage responses to a sharp edaphic discontinuity in a tropical forest tree community.

Location: Yoko forest reserve (6975 ha), Democratic Republic of the Congo.

Methods: We set up four 500–600-m long parallel transects crossing two contrasted edaphic habitats, one lying on clayey soil and the other on sandy soil. The canopy and subcanopy trees were identified and geo-referenced along the transects over a width of 50 m and 5 m, respectively, and soil samples were collected every 50 m to characterize each habitat.

Results: Correspondence analyses indicated a clear differentiation of tree communities between sandy and clayey soils. Using a torus-translation method combined with Chi-squared non-parametric tests, we observed that ca. 40% and 18% of the species represented by at least 12 individuals displayed significant density differences according to habitat in the canopy and subcanopy, respectively, although very few species displayed significant differences in their relative abundance. Nevertheless, whole community tests of differentiation (in species relative abundances) between soil types were significant in both strata, even after removing individual species or families displaying a significant habitat preference.

Conclusion: While only a minority of species displayed a clear habitat preference, we still observed a community-wide impact of the edaphic discontinuity on species assemblages at a local scale. Our results provide further evidence for the major contribution of environmental heterogeneity in maintaining biodiversity in tropical forests.

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Introduction

The spatial organization of species within tropical tree communities can be viewed as the result of deterministic and stochastic factors (Chase 2014). Deterministic processes are niche-related and tend to distribute species in their optimal habitat (habitat filtering effect) while avoiding their co-existence when substantial niche overlap occurs (competitive exclusion effect), thereby generating floristic turnovers that are well explained by ecological gradients. However, even in the absence of habitat heterogeneity, non-random spatial distributions of species may arise because of dispersal limitation (Hubbell 2001; Hardy & Sonké 2004; Réjou-Méchain & Hardy 2011). Hence, free space will not necessarily be occupied by the most competitive species but rather by those established in the vicinity, leading to stochastic variation in floristic composition.

While understanding the relative contributions of niche-related vs stochastic processes is a long-standing issue in community ecology, most studies have been interested in searching for deterministic factors influencing tree community assemblages. Numerous papers have demonstrated the role of environmental heterogeneity (e.g. Newbery & Proctor 1984; Harms et al. 2001; Phillips et al. 2003; John et al. 2007; Lan et al. 2011; Condit et al. 2013), using essentially topographic and edaphic variables, notably soil texture, which is particularly informative because it reflects many physical and chemical properties of the substrate. This parameter has therefore been widely used to characterize rainforest habitats, and its impact on tree community structure has been demonstrated on different continents (Newbery et al. 1986; Fine et al. 2005; Sukri et al. 2012).

Although environmental determinism on tree species assemblages is well established in the Neotropics and South-East Asia, it remains poorly documented in Central African forests, especially in the Congo Basin; apart from the study of Réjou-Méchain et al. (2008), who detected floristic turnovers explained by soil texture gradients in the northern edge of the basin. In western Central Africa, Newbery et al. (1986) demonstrated the existence of tree species associated with sandy soil and others with clayey soil, while Gartlan et al. (1986) emphasized the major contribution of phosphorus limitation in structuring tree communities. Interestingly, the eastern part of the Congo Basin, near the city of Kisangani (Democratic Republic of the Congo), is composed of a mosaic of sandy plateaus dissected by a hydrographic network revealing clayey soils. The resulting sharp boundary between soil types provides an opportunity to study the effects of habitat filtering on species assemblages at a very local scale.

Our ability to detect the contribution of habitat heterogeneity on tree species distribution depends on multiple factors, notably (1) the scale of observation (Hardy & Sonké 2004); (2) the degree of environmental heterogeneity; (3) the spatial resolution of our environmental data set (Chase 2014) and (4) the life stage investigated (Jiangshan et al. 2009). The latter factor has rarely been taken into account in species–habitat association studies, and deserves further investigation, as ecological needs and the strength of habitat associations may change during plant ontogeny (Webb & Peart 2000; Comita et al. 2007; Jiangshan et al. 2009). For example, the cumulative impact of environmental filtering may increase with age (Webb & Peart 2000). In this case, we could expect stronger habitat associations among canopy species than among subcanopy ones, at least if a substantial portion of the latter contains juveniles regenerating the canopy. Negative density-dependent processes (Janzen 1971; Connell et al. 1984; Harms et al. 2000) may, however, reduce species–habitat associations at later life stages (Jiangshan et al. 2009).

Different complementary approaches have been developed to test environmental filtering on tree species assemblages. Direct ordination methods, like canonical correspondence analysis (ter Braak 1986), have become standard tools to filter out the proportion of floristic inertia explained by environmental heterogeneity. Another approach consists of testing the null hypothesis of independence between species distribution and habitat. To deal with the spatial autocorrelation problem when comparing nearby sample points taken following a grid, an appropriate method consists of randomizing the observed spatial distribution of individuals or habitats while maintaining the autocorrelation patterns using a torus-translation process (Harms et al. 2001). Torus-translation has the advantage of conserving most of the observed spatial patterns while de-correlating species distribution and habitat. This technique has proved to be useful in detecting significant species–habitat associations in rainforest tree communities from the Neotropics (Harms et al. 2001), Central Africa (Chuyong et al. 2011) and South-East Asia (Noguchi et al. 2007; Itoh et al. 2010).

Following a torus-translation approach similar to that used in Noguchi et al. (2007), the objective of the present study was to assess the impact of a sharp soil texture discontinuity on tree species turnover in a tropical forest of the Congo Basin. Using georeferenced inventories of canopy and subcanopy trees (separately) along parallel transects crossing an ecotone between sandy soil (SS) and clayey soil (CS), we addressed the following questions: (1) which soil properties distinguish SS from CS; (2) at the community level, does floristic differentiation occur between these two habitats, and which species respond to edaphic heterogeneity in terms of stem densities and relative abundances; and (3) does the strength

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of species–habitat association vary according to forest strata (canopy vs subcanopy trees)?

Methods

Study area

The present study was carried out in a lowland, semi-evergreen tropical forest of the eastern Congo Basin. We prospected an unlogged area of the Yoko forest reserve (6975 ha), located about 30 km southeast of the city of Kisangani (0°31′N, 25°11′E). The region is dominated by Ferralsols (IUSS Working Group WRB 2006), with a topography characterized by a main sandy plateau at *ca.* 400 m a.s.l., dissected (10- to 20-m deep) by a hydrographic network revealing CS on which topography is consequently more rugged than on SS. The climate is equatorial, with two maximum rainfall seasons (from March–June and August–December) separated by two relatively less humid periods, but monthly rainfall always exceeds 100 mm. Mean annual rainfall reaches *ca.* 1700 mm (Léonard 1996).

We prospected the forest in search of a sharp transition zone between SS and CS. Soil type was first visually characterized by determining the texture based on a simplified protocol adapted from Coche & Laughlin (1985). More precisely, we wetted a soil sample and kneaded it by hand to make a compact structure. If the structure broke or disintegrated, the soil was considered 'sandy' (SS), while if the structure remained compact we qualified it as 'clayey' (CS). The chosen area (00°18′N, 25°18′E) was characterized by a relatively flat plateau on the SS side (east), while the CS side (west) had a more rugged topography, with slopes of up to 20%. These two habitats were separated by a 100–200-m wide hydromorphic ecotone where a stream of *ca.* 1–5 m width meandered in a general south–north direction. This ecotone displayed a highly heterogeneous patchwork of sandy and clayey soils.

Field sampling

We set up four parallel transects across the transition zone (Fig. 1). A transect was composed of a pair of 200-m long plots, one on each soil type (SS and CS), separated by a 100-m to 188-m long plot on the ecotone. Each plot on CS and SS was subdivided into four 50-m long subplots, while plots on the ecotone were subdivided into three or four 43-m to 47-m long subplots according to their length in the corresponding transect. For transect number 4, however, the ecotone could not be inventoried because of impenetrable marsh vegetation and time limitation in the field.

We collected a soil sample (5 cm of upper soil layer below the litter) at the centre of each subplot located on SS and CS. No soil samples were collected in the ecotone because the very high edaphic heterogeneity observed within each ecotone subplot (important variation of soil texture at a very fine scale and hydromorphic conditions due to presence of a stream) prevented us from collecting any representative sample in this area.

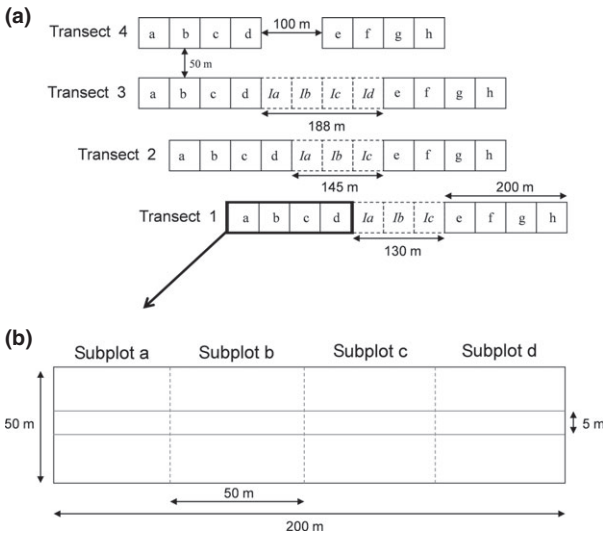

Fig. 1. (**a**) Schematic disposition of the four transects. Each transect is composed of two plots separated by an ecotone of variable length. (**b**) A plot is 200-m long and is composed of four subplots: **a**, **b**, **c** and **d** are located on clayey soil while **e**, **f**, **g** and **h** are located on sandy soil. The ecotone is composed of three or four subplots: Ia, Ib, Ic and Id (the ecotone could not be inventoried in transect 4). Along each transect, all canopy trees were inventoried over a width of 50 m, while all subcanopy trees were inventoried over a width of 5 m to compensate for the lower density of canopy trees.

Environmental variables

We measured ten soil variables: pH-H_2O, pH-KCl, ΔpH, electrical conductivity in water (EC), exchangeable aluminium content (Al), available phosphorus content (P) and percentage of organic matter (OM), clay, silt and sand. Soil pH-H_2O and EC were measured using glass electrodes and a conductivity meter in a 1:5 v/v soil:water ratio. Soil pH-KCl and exchangeable Al were determined in 1 M KCl extract of the same soil:extractant ratio using derivative titration curves. ΔpH was calculated as the difference between pH-KCl and pH-H_2O. Available P was extracted with Na bicarbonate and determined colorimetrically (Olsen & Sommers 1982). Organic matter content was measured by loss on ignition at 550 °C. Soil texture (percentage of clay, silt and sand) was determined using wet sieving and the pipette method after OM destruction and Na citrate dispersion of the samples. All measurements were performed using conventional soil analysis protocols (Pansu & Gautheyrou 2006). For each subplot, we also

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estimated the slope with an ordinal variable scaled from 1 to 3: 1 = slope < 3°, 2 = 3° < slope < 10°. 3 = slope >10°. For each soil type, we computed the mean and SD (at the subplot level) of each environmental variable, and tested differences between SS and CS with (1) a non-parametric Wilcoxon signed-rank test (using R *stats* package; R Foundation for Statistical Computing, Vienna, AT), as well as (2) an intra-class correlation coefficient between soil type and each environmental variable, tested with a torus-translation procedure taking spatial autocorrelation into account. The latter analysis was performed using the software TOROCOR (TOROCOR 1.0, http://ebe.ulb.ac.be/ebe/TOROCOR.html). We also verified whether SS and CS subplots segregated on the ordination axes of a principal components analysis (PCA) performed with all environmental variables, using the R *vegan* package (Dixon 2003). Subplot values for all environmental variables are provided in Appendix S1.

Floristic inventories

We used the diameter at breast height (DBH) as a practical criterion to identify two different vegetation strata (Senterre 2005): canopy trees were identified as all the individuals with a DBH ≥30 cm, while we defined subcanopy trees as all individuals with a DBH ≥5 cm and <30 cm. In some cases, however, when small-diameter trees (<30 cm) were visually similar in height to surrounding canopy trees, they were classified in the latter group (4% of total individuals and 11% of canopy trees).

Each tree was geo-referenced with an *x* coordinate indicating its position along the transect. The width of each plot varied according to the stratum investigated: 50 m and 5 m for canopy and subcanopy trees, respectively (Fig. 1); this ensured comparable sampling effort (in terms of number of individuals) between the two strata.

Species identification

We identified trees by examining leaves, shape of the trunk, surface patterns of the bark and by cutting the bark and analysing different features of the slice and/or the gash: colour of wood, texture (fibrous or granular), presence and colour of latex. About 80–85% of the trees of both strata could be identified reliably in the field with the help of local botanists and a renowned field identification guide (Wilks & Issembé 2000). Further identification was carried out on collected herbarium material and by comparing specimens with those of the Herbarium of the Université Libre de Bruxelles (BRLU). Nomenclature follows Lebrun & Stork (2008) except for families that follow APG III (Angiosperm Phylogeny Group 2009).

Floristic differentiation between edaphic habitats

We compared floristic differences between habitats (separately for canopy and subcanopy) in terms of stem densities and species diversity. The latter was quantified (using the R *vegan* package) as (i) the effective number of species computed as the reciprocal of Simpson concentration (Jost 2006), and (ii) the expected number of species for a random sample of 100 individuals. These are two measures giving relatively more weight to abundant and rare species, respectively. Correspondence analysis (CA) was performed on species densities data to characterize floristic variation among subplots for each stratum, while canonical correspondence analysis (CCA) was used to explain this variation in relation to environmental variables. Ordinations were performed using the R *vegan* package (Dixon 2003). Significant environmental variables in the CCA were selected using an Akaike information criterion (Akaike 1974) in the same R package. Species densities data in the canopy and subcanopy are available in Appendices S2 and S3, respectively.

Testing floristic differences between habitats while accounting for spatial autocorrelation

As most ecological variables are spatially autocorrelated, and tree species are subject to dispersal limitation, environmental and floristic data of nearby subplots cannot be considered as independent observations, invalidating classical association tests such as the chi-squared test. To overcome this problem, we applied constrained randomizations, similar to torus-translation randomizations (Harms et al. 2001), which break down the spatial associations between variables while minimizing the loss of their spatial structure. Following the method applied in Noguchi et al. (2007), we generated randomized data sets where species distribution and edaphic habitats were uncorrelated. To this end, each transect was considered as a ring (as if opposite ends were adjacent) along which all individuals were translated in parallel using a random value (ranging from 1 m to the length of the corresponding transect), while the orientation of the transect could also be reversed, with a probability of 0.5. This is equivalent to translating the habitat map, as the whole community structure is preserved within transects. To generate a new randomized data set, this procedure was performed independently for each of transects 1, 2 and 3 (transect 4 was not taken into account since its ecotone could not be inventoried). Translating tree coordinates along a continuous axis allowed more possible rearrangements than the discrete translation approach of Harms et al. (2001).

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The number of individuals and the relative abundance of each species occurring on each edaphic habitat (SS, CS and ecotone) were computed for the original data set and for each randomized data set. Three types of Chi-square-related statistics were then computed to test (i) stem density difference among edaphic habitats for each species (i.e. species habitat preference), and (ii) species relative abundance difference among these habitats (i.e. species differentiation in habitat preferences). First, single species statistics were computed in the canopy and subcanopy separately, as follows:

$$S = \sum\nolimits_h [(O_{ih} - E_{ih})^2 / E_{ih}] \quad (1)$$

$$s = \sum\nolimits_h [(o_{ih} - e_{ih})^2 / e_{ih}] \quad (2)$$

with

$$E_{ih} = P_h O_i \quad (3)$$

$$e_{ih} = \sum [o_{ih}]/n \quad (4)$$

The equations are taken over the $n = 3$ habitat types h. O_{ih} is the observed abundance (i.e. number of individuals) of species i found in habitat h, while E_{ih} is the expected abundance in the absence of habitat preferences (i.e. tree density expected to be constant in each habitat), i.e. the product between P_h, the proportion of the sampled area occupied by habitat h, and O_i, the total number of individuals of species i. Similarly, o_{ih} is the observed relative abundance of species i found in habitat h, while e_{ih} is the expected relative abundance under the assumption that the relative dominance of a species does not vary among habitats. These two statistics are complementary because the abundance of a species is statistically independent from other species, while its relative abundance depends on the other species abundances.

Second, we quantified the overall habitat differentiation among all species for each stratum, using the following equation:

$$D = \sum\nolimits_i \sum\nolimits_h [(O_{ih} - E'_{ih})^2 / E'_{ih}] \quad (5)$$

where E'_{ih} is the expected abundance of species i found in habitat h in the absence of niche differentiation among species. E'_{ih} is computed as:

$$E'_{ih} = (O_{\cdot h}\, O_{i\cdot})/O_{\cdot\cdot} \quad (6)$$

where $O_{\cdot h}$, $O_{i\cdot}$ and $O_{\cdot\cdot}$ are, respectively, the total number of individuals (all species) sampled in habitat h, the abundance of species i (across all habitats) and the total number of individuals in the data set. Note that, compared to a series of single-species tests, the D test has higher power when different species show similar but weak trends, and it is less prone to type I error due to the potentially very high number of species–habitat tests used.

The S, s and D statistics, computed with the original data set (observed values), were then compared to their null distribution obtained with 4999 randomized data sets, and a P-value was obtained as the proportion of simulated values higher than the observed value. Thanks to this technique, we tested for each stratum whether: (1) there was a significant difference in tree density between habitats for each species (S tests), (2) the relative abundance of each species differed among habitats (s tests) and (3) habitat differentiation occurred among them (D test). We also tested S, s and D statistics on family abundance data to check whether habitat preference and habitat differentiation occurred at a higher taxonomic level. Finally, the S test was also performed after aggregating all the species to assess whether overall stem density in each stratum varied according to soil type. Continuous torus-translation tests were performed in R v 2.13.2. The R code and the data set used for these tests are available in Appendices S4 and S5, respectively.

Results

Edaphic heterogeneity

Despite the limited size of our soil data set, we detected highly significant difference between SS and CS for each environmental variable, except EC and pH-KCl, (Table 1). Segregation of the subplots on the first PC axis confirmed the presence of two distinct habitats (Appendix S6). All variables except pH-KCl and EC were significantly correlated with this first axis using permutation tests (not shown). Environmental heterogeneity was higher on CS than on SS, as shown by the higher SD of edaphic variables (Table 1) and the dispersion of subplots on the PC axes (Appendix S6).

Floristic patterns

In both the canopy and subcanopy, species diversity was higher on CS than on SS (Appendix S7), while the number of subcanopy trees per canopy tree was higher on CS and ecotone (ca. 21) than on SS (ca. 16). Using torus-translation tests, we found that stem densities were significantly different between soil types in the canopy and subcanopy ($P = 0.02$ in both strata, using data from transects 1 to 3 only, see Methods). The proportion of identified species reached about 95% in both strata. *Julbernardia seretii* (Fabaceae) was the most abundant species in the canopy, while

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Table 1. Mean subplot values (±SD) of 11 environmental variables on sandy soil and clayey soil. The two last columns indicate the statistical significance of difference between soil types, according to a Wilcoxon test (W) and a torus-translation test of the intra-class correlation coefficient between soil type and each environmental variable (T).

	Sandy soil	Clayey soil	W	T
pH-H_2O	3.88 (±0.08)	4.29 (±0.38)	***	**
pH-KCl	3.85 (±0.14)	3.79 (±0.18)	n.s.	n.s.
ΔpH	−0.03 (±0.12)	−0.50 (±0.27)	***	***
Percentage of organic matter	1.88 (±0.48)	4.54 (±2.09)	***	**
Electrical conductivity ($\mu S \cdot cm^{-1}$)	54.75 (±9.14)	57.89 (±54.74)	n.s.	n.s.
Exchangeable Al ($cmolc \cdot kg^{-1}$)	0.55 (±0.33)	6.80 (±4.15)	***	***
Slope category	1.25 (±0.58)	2.44 (±0.73)	***	*
Available P ($\mu g \cdot g^{-1}$)	64.70 (±45.45)	13.40 (±9.41)	***	***
Percentage of clay	10.65 (±2.67)	39.96 (±15.53)	***	***
Percentage of silt	1.72 (±1.65)	11.52 (±9.30)	***	***
Percentage of sand	87.63 (±2.41)	48.53 (±20.28)	***	***

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; n.s. = not significant.

Aidia micrantha (Rubiaceae) was the most abundant one in the subcanopy. The most important family within both strata was the Fabaceae (46 and 14% of all individuals in the canopy and subcanopy, respectively). We also observed that canopy and subcanopy shared 37, 32 and 40% of all species found on CS, ecotone and SS, respectively.

Floristic differentiation among habitats at the community level

The two-first axes of the CA separated most of the subplots on SS from those on CS in the canopy, while substantial overlap was observed for subcanopy subplots (Fig. 2). Subplots from the ecotone were highly dispersed among SS and CS subplots. In the canopy, separation was still observed when CA was performed after removing *Scorodophloeus zenkeri* (Fabaceae) from the species pool, a species that is particularly dominant on SS while almost absent on CS (Appendix S8a). After removing all Fabaceae species (significantly more abundant on SS, see below), separation was still observed although less clearly (Appendix S8b). We did not observe any major change in the ordination after removing any other individual species or family (one-by-one) in the subcanopy (not shown).

Habitat association and differentiation

The power of *S* and *s* tests should depend on sample size and on the degree of species spatial aggregation, but as the minimum sample size leading to a significant test was 12 individuals, hereafter we report results only for species or

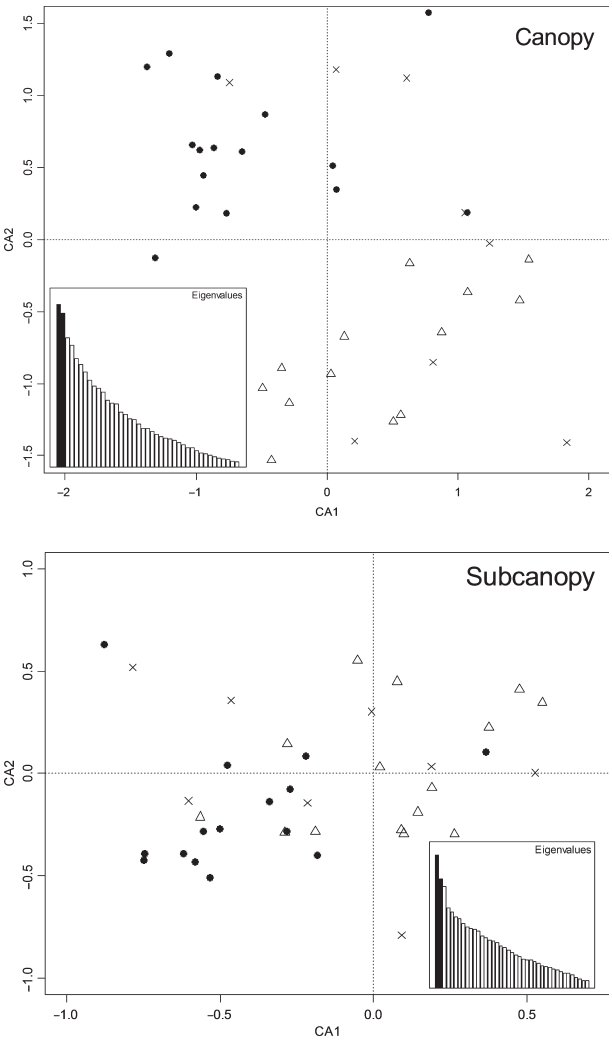

Fig. 2. Ordination of the subplots on the two-first axes of a correspondence analysis performed on species densities in the canopy (above) or the subcanopy (below). Each symbol represents a soil type: sandy soil (black dots), clayey soil (triangles) and ecotone (crosses). Histograms represent eigenvalues for the first axes.

families represented by at least 12 individuals. In the canopy, seven out of the 18 testable species (39%) showed habitat preference according to the *S* test, which is more than expected by chance (5%). Five of them preferred SS while two preferred CS (Table 2). The strongest habitat preference was found for *Scorodophloeus zenkeri* (Fabaceae), which was highly abundant on SS but almost absent on CS. *Gilbertiodendron dewevrei* (Fabaceae) and *Pseudospondias microcarpa* (Anacardiaceae) were the only species displaying a significant difference in relative abundance (*s* test). Among subcanopy trees, seven of the 40 testable species (18%) showed habitat preference using the *S* test (five for CS and two for SS), while the *s* test was only significant for *Strombosiopsis tetrandra* (Olacaceae), which was also the

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Table 2. Density (number of stems per ha) and relative abundance (%, in italics) of each testable species (≥ 12 individuals) of the canopy (n = 18) and subcanopy (n = 40) on each soil type (using data from transects 1 to 3 only, see Methods). For each stratum, species are listed in decreasing order of total abundance. Species in bold were only observed in the subcanopy.

	Clay		Ecotone		Sand		S test	s test
Canopy								
Scorodophloeus zenkeri	0.67	*0.63*	9.94	*13.45*	24.67	*20.67*	***	n.s.
Julbernardia seretii	10.00	*9.40*	3.02	*4.09*	17.00	*14.25*	*	n.s.
Gilbertiodendron dewevrei	7.00	*6.58*	18.57	*25.15*	4.67	*3.91*	n.s.	*
Greenwayodendron suaveolens	3.33	*3.13*	2.59	*3.51*	10.33	*8.66*	*	n.s.
Guarea cedrata	5.67	*5.33*	1.30	*1.75*	4.67	*3.91*	n.s.	n.s.
Anonidium mannii	2.67	*2.51*	2.59	*3.51*	4.67	*3.91*	n.s.	n.s.
Celtis tessmannii	4.00	*3.76*	1.73	*2.34*	1.67	*1.40*	n.s.	n.s.
Cynometra hankei	1.00	*0.94*	1.30	*1.75*	4.00	*3.35*	*	n.s.
Strombosiopsis tetrandra	3.00	*2.82*	0.86	*1.17*	2.00	*1.68*	n.s.	n.s.
Pterocarpus soyauxii	3.33	*3.13*	0.86	*1.17*	1.33	*1.12*	*	n.s.
Musanga cecropioides	3.00	*2.82*	2.16	*2.92*	0.67	*0.56*	n.s.	n.s.
Blighia welwitschii	2.67	*2.51*	1.30	*1.75*	1.67	*1.40*	n.s.	n.s.
Trilepisium madagascariense	3.33	*3.13*	0.43	*0.58*	1.33	*1.12*	n.s.	n.s.
Prioria oxyphylla	0.00	*0.00*	2.59	*3.51*	3.00	*2.51*	**	n.s.
Panda oleosa	1.00	*0.94*	0.00	*0.00*	4.00	*3.35*	n.s.	n.s.
Staudtia stipitata	1.67	*1.57*	1.30	*1.75*	1.67	*1.40*	n.s.	n.s.
Pseudospondias microcarpa	4.00	*3.76*	0.00	*0.00*	0.00	*0.00*	*	*
Petersianthus macrocarpus	1.67	*1.57*	0.86	*1.17*	1.67	*1.40*	n.s.	n.s.
Subcanopy								
Aidia micrantha	180.00	*7.98*	116.63	*7.46*	110.00	*5.69*	n.s.	n.s.
Staudtia stipitata	90.00	*3.99*	69.11	*4.42*	116.67	*6.03*	n.s.	n.s.
Guarea cedrata	123.33	*5.47*	21.60	*1.38*	76.67	*3.97*	n.s.	n.s.
Gilbertiodendron dewevrei	76.67	*3.40*	56.16	*3.59*	43.33	*2.24*	n.s.	n.s.
Anonidium mannii	36.67	*1.62*	12.96	*0.83*	106.67	*5.52*	n.s.	n.s.
Drypetes sp.	56.67	*2.51*	56.16	*3.59*	50.00	*2.59*	n.s.	n.s.
Cola griseiflora	10.00	*0.44*	43.20	*2.76*	96.67	*5.00*	*	n.s.
Grossera multinervis	46.67	*2.07*	43.20	*2.76*	56.67	*2.93*	n.s.	n.s.
Cleistanthus mildbraedii	26.67	*1.18*	51.84	*3.31*	63.33	*3.28*	n.s.	n.s.
Pancovia harmsiana	36.67	*1.62*	38.88	*2.49*	60.00	*3.10*	n.s.	n.s.
Diospyros boala	80.00	*3.55*	56.16	*3.59*	3.33	*0.17*	*	n.s.
Scaphopetalum thonneri	40.00	*1.77*	38.88	*2.49*	53.33	*2.76*	n.s.	n.s.
Guarea thompsonii	43.33	*1.92*	34.56	*2.21*	50.00	*2.59*	n.s.	n.s.
Julbernardia seretii	40.00	*1.77*	34.56	*2.21*	43.33	*2.24*	n.s.	n.s.
Pycnanthus angolensis	40.00	*1.77*	21.60	*1.38*	50.00	*2.59*	n.s.	n.s.
Carapa procera	30.00	*1.33*	43.20	*2.76*	40.00	*2.07*	n.s.	n.s.
Strombosiopsis tetrandra	16.67	*0.74*	51.84	*3.31*	40.00	*2.07*	*	*
Ochthocosmus africanus	36.67	*1.62*	47.52	*3.04*	16.67	*0.86*	n.s.	n.s.
Scorodophloeus zenkeri	3.33	*0.15*	43.20	*2.76*	46.67	*2.41*	n.s.	n.s.
Greenwayodendron suaveolens	33.33	*1.48*	12.96	*0.83*	40.00	*2.07*	n.s.	n.s.
Strombosia pustulata	40.00	*1.77*	12.96	*0.83*	26.67	*1.38*	n.s.	n.s.
Grewia pinnatifida	36.67	*1.62*	17.28	*1.10*	20.00	*1.03*	n.s.	n.s.
Dialium pachyphyllum	13.33	*0.59*	17.28	*1.10*	40.00	*2.07*	n.s.	n.s.
Celtis mildbraedii	26.67	*1.18*	12.96	*0.83*	30.00	*1.55*	n.s.	n.s.
Chrysophyllum africanum	40.00	*1.77*	17.28	*1.10*	6.67	*0.34*	**	n.s.
Rinorea oblongifolia	26.67	*1.18*	8.64	*0.55*	23.33	*1.21*	n.s.	n.s.
Myrianthus preussii	43.33	*1.92*	4.32	*0.28*	10.00	*0.52*	*	n.s.
Massularia acuminata	23.33	*1.03*	8.64	*0.55*	26.67	*1.38*	n.s.	n.s.
Dacryodes yangambiensis	30.00	*1.33*	34.56	*2.21*	0.00	*0.00*	n.s.	n.s.
Coelocaryon preussii	40.00	*1.77*	12.96	*0.83*	6.67	*0.34*	n.s.	n.s.
Trichilia gilgiana	36.67	*1.62*	8.64	*0.55*	10.00	*0.52*	n.s.	n.s.
Strombosia grandifolia	40.00	*1.77*	4.32	*0.28*	6.67	*0.34*	**	n.s.
Diospyros crassiflora	33.33	*1.48*	0.00	*0.00*	16.67	*0.86*	*	n.s.
Anthonotha fragrans	23.33	*1.03*	4.32	*0.28*	23.33	*1.21*	n.s.	n.s.

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Table 2. *(Continued).*

	Clay		Ecotone		Sand		S test	s test
Trilepisium madagascariense	30.00	*1.33*	8.64	*0.55*	10.00	*0.52*	n.s.	n.s.
Pterocarpus soyauxii	23.33	*1.03*	4.32	*0.28*	16.67	*0.86*	n.s.	n.s.
***Campylospermum* sp.**	36.67	*1.62*	4.32	*0.28*	3.33	*0.17*	n.s.	n.s.
Sterculia sp.	23.33	*1.03*	12.96	*0.83*	6.67	*0.34*	n.s.	n.s.
Petersianthus macrocarpus	13.33	*0.59*	12.96	*0.83*	16.67	*0.86*	n.s.	n.s.
Diospyros deltoidea	23.33	*1.03*	8.64	*0.55*	10.00	*0.52*	n.s.	n.s.

The significance of S and s tests is denoted by the symbol * (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) or "n.s." (not significant).

only species for which both *S* and *s* tests were significant. Note that stem density on the ecotone was not always intermediate between densities found on SS and CS (Table 2). Among the 40 testable subcanopy species, 11 were observed in this layer only (28%), while the 29 others occurred in both strata. Three out of the 11 subcanopy-restricted species (27%) and four out of the 29 other species (14%) displayed significant habitat association (*S* test only; Table 2).

In the canopy, two out of the 15 testable families (13%), Fabaceae (more abundant on sand) and Anacardiaceae (more abundant on clay), displayed significant habitat preference only with the *S* test ($P = 0.015$ and $P = 0.012$, respectively; Appendix S9), while the same test was significant for two out of the 23 (9%) testable families in the subcanopy: Ebenaceae (more abundant on clay) and Chrysobalanaceae (more abundant on sand, $P = 0.046$ for both families).

The *D* test of habitat differentiation between all species was highly significant for both canopy and subcanopy species ($P = 0.003$ in both strata). In the canopy, significance slightly decreased when *Scorodophloeus zenkeri* ($P = 0.019$) was removed, and disappeared when all species in the Fabaceae ($P = 0.103$) were removed. We also found that habitat differentiation between all families was significant within the canopy ($P = 0.017$) but not after removing the Fabaceae ($P = 0.124$). In the subcanopy, habitat differentiation among families was weakly significant ($P = 0.041$).

In the CCA, environmental variables clearly differentiated subplots on SS from those on CS; all canonical axes explaining 41.1% and 36.35% of the whole floristic inertia in the canopy and subcanopy, respectively (Appendix S10). Based on the AIC, pH-H_2O, ΔpH, OM, Al and slope significantly explained the variation in floristic density in the canopy, while in the subcanopy the only significant variables were the slope and the percentage of sand.

Discussion

This study sheds light on the role of edaphic heterogeneity in rainforest tree communities, a subject poorly documented in the Congo Basin. We used a modification of the torus-translation test on floristic data from multiple transects crossing a contact zone between contrasted edaphic habitats, distinguishing the canopy and subcanopy strata. This protocol allows testing for species–habitat association without the considerable investment required to establish a fully mapped forest plot. At a local scale, our results highlight a clear floristic differentiation between edaphic habitats across a contact zone between sandy and clayey soil types, and a highly heterogeneous, partly hydromorphic, ecotone (CA and *D* tests). Nevertheless, only a minority of canopy (39%) or subcanopy (18%) species tested displayed significant change in density with respect to habitat (*S* tests), and the number of species with significant relative abundance differences (three significant *s* tests over 58 tests performed) was not higher than expected by chance (expected number of significant tests under the null hypothesis = 0.05*58 ≈ 3). Hence, weak patterns at the species level, if manifested in many species, can still produce significant floristic variation across soil habitats. The fact that we observed more significant *S* tests than *s* tests suggests that part of the differences in species density among habitats resulted from differences in carrying capacity among habitats rather than species differentiation in habitat preferences, as stem densities differed significantly between soil types. Interestingly, at the family level, the abundant Fabaceae displayed significantly higher abundance on sandy soils in the canopy, suggesting niche conservatism within this family. Finally, we found that floristic differentiation was more marked in the canopy than in the subcanopy, despite lower sample size in the former.

Habitats characteristics

Despite the limited size of our environmental data set, we demonstrated a clear contrast in soil properties between SS and CS (Table 1), with higher heterogeneity of edaphic variables on CS. Higher soil pH-H_2O and organic matter content on CS indicated increased availability of essential base cations (Sollins 1998), which might thus be more limiting on the more acidic SS. Higher ΔpH on SS reflected higher anion exchange capacity (or lower cation exchange capacity), which explains the lower Al^{3+} sorption capacity and the higher P retention, as soluble P occurs as anionic

forms (phosphate) and precipitates in unavailable forms when reacting with Al^{3+}. Moreover, multiple regression analyses confirmed that P was most influenced by Al (not shown). Higher P content on SS compared to CS was already observed in Amazonia (Jiménez et al. 2009) and South-East Asia (Kochsiek et al. 2013).

Differences in relief and hydromorphy between habitats could have played important roles in structuring species distribution (Lan et al. 2011) in both strata, and may also explain the lower carrying capacity (stem densities) of the ecotone compared to SS and CS (Duivenvoorden 1996; Webb & Peart 2000), as well as the higher density ratio between canopy trees and subcanopy trees found on SS, where the flat substrate might offer better conditions for the establishment of large trees.

Species distribution pattern and habitat association

At the community level, the CA and *D* tests revealed clear floristic differentiation between soil types in both strata (Fig. 2). Subplots from the ecotone were highly dispersed in the ordination plane of the CA, revealing the absence of a continuous floristic gradient between SS and CS. This is consistent with field observations suggesting a patchwork of SS and CS rather than a progressive textural transition in the ecotone, if we assume that community assembly is mostly structured by habitat heterogeneity. However, lack of knowledge of soil properties for the ecotone limits this interpretation.

Despite community-level floristic differentiation between edaphic habitats, only a few species displayed significant habitat preference according to *S* and *s* tests. This may indicate that only a few species really responded to the edaphic discontinuity, or that single species tests lack statistical power to detect differences with our data set. The latter explanation is consistent with the fact that (i) CA still showed floristic differentiation when species or families displaying clear habitat preference were removed from the data set, and that (ii) the *D* test for overall habitat differentiation among species was significant in both strata, despite little evidence for single-species habitat preference in the subcanopy.

The weaker species–habitat association observed in the subcanopy might result from a lower impact of habitat filtering in this layer due to the presence of juveniles that would still be undergoing competitive exclusion. This interpretation is supported by the fact that the subcanopy shares about 50% of its species with the canopy, suggesting that an important fraction of subcanopy trees are juveniles regenerating the canopy. Moreover, the percentage of species significantly associated with habitat in the subcanopy was higher among the 11 subcanopy-restricted species (27%) than among the 29 subcanopy species also found in the canopy (14%; Table 2), although this trend was not statistically significant, possibly due to the limited size of our data set.

When removing the Fabaceae from the canopy, the significance of the *D* test disappeared, while it remained significant when removing *Scorodophloeus zenkeri* (Fabaceae) only, suggesting that this family largely explains the overall floristic differentiation in response to edaphic habitat. Lower amounts of available N on sand (Doff Sotta et al. 2008) might favour the Fabaceae on SS, although we lack soil N content data to support this hypothesis.

As revealed in the CCA, the floristic contrast between edaphic habitats in the canopy was mostly explained by variation in pH-H_2O, OM, ΔpH, exchangeable Al and slope (CCA). The two-first soil variables are known to be positively correlated with base cation availability (see above), while the next two correlate (positively and negatively, respectively) with P availability, suggesting a role of soil nutrient limitation on species distribution. In the subcanopy, only the slope and the percentage of sand were significant in the CCA. While the sandy texture reflects nutrient depletion (except for P) in the subcanopy, the significant effect of slope variation in both strata may also indicate that species differ in their ability to establish on a steep substrate. Thus it is uncertain whether floristic contrasts between SS and CS are mostly driven by differences in relief or in edaphic conditions.

Conclusion

Our results support previous studies that have emphasized species–habitat associations using torus-shift randomizations (e.g. Harms et al. 2001; Chuyong et al. 2011). More specifically, we demonstrated a floristic differentiation driven by soil texture contrasts, as documented in e.g. Russo et al. (2005) in Borneo, Fine et al. (2005) in a Neotropical forest or Réjou-Méchain et al. (2008) in Central Africa. Finally, while it has been suggested that environmental gradients usually generate broad-scale floristic structures, and thus necessitate carrying out inventories at large spatial scales to efficiently detect species–habitat associations (Borcard et al. 2004; Legendre et al. 2009; Chase 2014), our study highlighted that ecological filtering can also act at very fine spatial scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Subplot values of all environmental variables.

Appendix S2. Subplot density of each canopy species used in the CA and CCA.

Appendix S3. Subplot density of each subcanopy species used in the CA and CCA.

Appendix S4. R code for computing *S*, *s* and *D* statistics.

Appendix S5. List of all canopy and subcanopy individuals used in the R code (Appendix S4).

Appendix S6. PCA performed on environmental variables.

Appendix S7. Summary of stem densities and floristic diversity data on each edaphic habitat, for the canopy and subcanopy strata.

Appendix S8. Ordination of the subplots (CA) after removing the highly dominant species *Scorodophloeus zenkeri* (a) or the Fabaceae (b) in the canopy.

Appendix S9. Densities and relative abundances of each testable family of the canopy and subcanopy on each soil type, and significance of the *S* and *s* tests.

Appendix S10. CCA performed on canopy and subcanopy species densities and environmental data.

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