



An assessment of distance decay within woody forest layers in Central African's semi-deciduous forests

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Abstract

In the Central Congo Basin, semi-deciduous forests often express edaphic heterogeneity in their physical characteristics marked by contrasting sandy and clayey habitats, mainly due to microtopographic features. The fact that almost identical substrates are located in separated sites may give rise to local floristic differentiations because of dispersal limitation due to distance and ecological barriers. It is also notable that species composition differs according to forest layers and there could be different soil and distance effects on plant communities when these forest layers are considered.

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Introduction

The coexistence of species within communities is a result of many factors and theories have been developed by ecologists in their search of patterns shaping plant communities. According to the niche differentiation hypothesis, plant species that are specialized for certain sets of environmental conditions can coexist because each is a slightly better competitor in its own niche, provided that there is sufficient environmental variation in time and space (Yamada *et al.*, 2007).

It is also mentioned that if patterns of biodiversity are studied over space and time across environmental gradients, this can lead to a better understanding of its origin, function and maintenance (Venugopal, 2008). Moreover, recording floristic and structural data of the vegetation through spatial scales is sorely needed to understand species and their environmental features (Couteron *et al.*, 2003) as well as to map forest types (Condit, 1996).

Many studies focusing on data collection through spatial scales evidenced cases of decline in the similarity of species composition as a function of distance, a phenomenon generally called distance decay and which is considered to be widespread in natural communities with no exception for tropical forests (Palmer, 2005). According to Hans *et al.* (2001), decay of similarity with distance can be due to species turnover along local and regional environmental gradients or among habitats. In this latter case, spatial variations in species composition are believed to reflect the spatial distribution of suitable environmental conditions for growth and survival of the species. Poulin (2003) mentions that the rate at which biological similarity decays with increasing distance can shed light on some of the processes acting on it.

Explanations for distance decay were suggested by many authors but generally three mechanisms are pointed out (Soininen *et al.*, 2007). First, distance decay can result from decreasing similarity in

environmental features due to niche-based community processes, with species differing in their ability to perform under different environmental conditions. The second emphasizes the role of spatial configuration and the nature of landscape and their respective impacts on dispersal limitation. And as mentioned by the neutral theory, community similarity decreases with distance even if the environment is completely homogeneous, due to organisms' limited dispersal (Hubbell, 2001).

While topography and soil are regarded as the two major interconnecting factors influencing the finer details of vegetation variation (e.g. structure, species composition) in tropical rainforest ecosystems (Thenkabail *et al.*, 2003), it remains important to question the role of spatial distance to account for the importance of ecological factors that control species distributions and the impact of this distance on species functional traits, such their dispersal capabilities.

This study was intended to analyze the effects of soil properties on vegetation features as well as the role of spatial distance on species composition. We then asked the following questions: 1) Does distance decay exist in the Congolese semi-deciduous forests, under a similar climatic range? What is the strength of this distance decay? 2) Does spatial distance affect communities on similar soils? In other words, is there any soil effect on these plant communities?

We hypothesized that: 1) Distance decay exists in our plant communities as an expression of the "first law of geography" (Nekola and White, 1999) which stipulates that the similarity between two observations often decreases or decays as the distance between them increases, and that this decay of similarity with distance results from species turnover along local and regional environmental gradients or among habitats (Hans *et al.*, 2001). 2) Edaphic variables differently affect plant communities in forest layers in accordance with the "resource-use efficiency hypothesis" (Baltzer *et al.*, 2005) which

stipulates that species differ in their ability to withstand conditions of limiting resource availability that vary among soil types.

Materials and Methods

Study sites and data collection

We established sampling vegetation plots in 3 different sites in the Central Congo Basin: Yoko (0°17'34.9" N; 25°18'27.4" E), Biaro (0°14'47" N; 25°19'44.05" E) and Yangambi (0°51'01.62" N; 24°31'43.53" E). The choice of these sites was guided by their low rates of disturbance from human activities (primary forests). They are both located around the city of Kisangani (Eastern Democratic Republic of Congo) and are harbor semi-deciduous forests mainly characterized by the dominance of two *Fabaceae* species, *Scorodophloeus zenkeri* and *Prioria oxyphylla* in the overstorey. Ten kilometers separate Yoko from Biaro (southwards) and Yangambi is located at more than 100 kilometers, further west. The mean elevation of the region is 435 m asl and the annual rainfall ranges from 1417 mm to 1915 mm (mean: 1728 mm) with mean monthly temperatures varying from 23.7°C to 26.2 °C. The dominant rainy season is interrupted by two short dry seasons, from December to January and from June to August. Ferralitic soils are the dominant soil group in the region (van Engelen *et al.*, 2006) and are particularly marked by xanthic ferralsols (Beernaert, 1999).

Plant inventories and data collection were performed within 1-ha plots. Investigations were carried out on the three woody forest layers, defining the overstorey (layers A and Ad) and the understorey (layers ar). By layer A, we consider all the canopy dominant trees and emergent species (above 20 m in height) whereas the layer Ad refers to the canopy dominated trees (ranging between six meters and 20 meters). In the shrub layer, we considered all species ranging between 1.5 and six meters in height. The sampling efforts varied from a stratum to another. Trees belonging to the stratum A were inventoried within one-hectare plots (200 m by 50 m).

For stratum Ad, inventories were performed within a 2000 m² surface (200 m by 10 m), whereas for stratum ar plants were counted within a 500 m² surface (i.e. 200 m by 2.5 m).

To account for edaphic features, we collected soil samples at a depth of 0-10 cm. They were passed successively through 20- and 2-mm sieves for textural analyses. Percentages of sand, clay and silt were measured by classic granulometric analyses using sedimentation columns in accordance with the Stokes' law. We also determined soil organic matter, pH, phosphorus concentration and soil electrical conductivity. The percentage of organic matter was measured by weighing a soil sample from a drying oven (105°C) as well as before and after calcinations in a muffle furnace (450°C), and then by measuring the masses difference. Phosphorus concentration (µg/ml) was measured using the Ølsen method (Ølsen *et al.*, 1954). Initially, 1 g of soil was weighed to which 20 ml of bicarbonate (extractor) were added. pH and conductivity (µSiemens/cm) were determined following the saturated paste method.

Data analysis

To consider the similarity between plant communities, we used both the Morisita-Horn (M-H) index which was computed using BiodivR 1.0 (Hardy 2005):

$$MH_{ij} = \left[\frac{\sum_s P_{is} P_{js}}{\left(\sum_s P_{is}^2 + \sum_s P_{js}^2 \right) / 2} \right]$$

where p_{is} and p_{js} are frequencies of species S in samples i and j respectively.

We performed Mantel tests to account for the correlations between the floristic composition (based on the matrix of floristic similarity) and spatial (geographic) distance as well as between species composition and ecological distance, estimated through an ordinal scale (0: same substrate and 1: different substrate). Mantel tests were run using Vegan's R package.

We used Correspondence Analysis (CA) to examine the unconstrained variability in species composition and differences between samples. We also computed a Principal Component Analysis (PCA) to visualize community responses to edaphic variables. Prior to these canonical analyses, we performed a cluster analysis to account for any trend in the dataset.

We referred to the Ward’s hierarchical clustering method and the Bray-Curtis similarity distance applied to the matrix of species abundances within plots.

Results

Main floristic features in relation with soil and distance

The PCA clearly distinguishes sandy and clay plots (Fig. 1) with particularities for sandy plots located in Yangambi which clearly distinguish themselves from the others established in Yoko and Biaro.

These differences are surely due to the respective edaphic properties of the sites.

Table 1. Correlations between the matrix of floristic similarity and spatial distance (distance effect) as well as between the matrix of floristic similarity and ecological distance (soil effect). Only data from Yoko and Biaro are taken into account. Note that these correlations are based on the entire dataset and not on particularities of each soil, as expressed in Fig. 3. Pearson’s coefficients are shown for each case. Observations are based on 999 permutations. NS: no significant test.

Forest layers	Distance effect	Soil effect
Layer A	-0.593 (NS)	-0.451 (NS)
Layer Ad	-0.468 (NS)	-0.296 (NS)
Layer ar	-0.404 (NS)	-0.017 (NS)

Species composition in these forests varied according to forest layers and soil types. In the upper arborescent layer (A), 110 species were inventoried whereas the lower arborescent layer (Ad) accounted for 163 species.

In the understorey (layer ar), 133 species were surveyed. Overall sandy soils were much favorable to species like *Scorodophloeus zenkeri* and other Fabaceae species (*Cynometra hankei*, *Prioria balsamiferum*, *Prioria oxyphylla*) while on clayey soils this forest layer was rather dominated by *Petersianthus macrocarpus*, *Pericopsis elata* and *Trilepisium madagascariens*. For the lower arborescent layer (Ad), clayey substrates distinguished themselves with species such as *Diospyros boala*, *Aidia micrantha* and *Staudtia kamerunensis*. On sandy substrates, this forest layer was most dominated by *Grossera multinervis* and *Anonidium mannii*.

From the cluster analyses (Fig. 2), one observes a clear partition, following floristic features, between sandy and clayey plots. This is much evident in the upper arborescent layer, exception for the plots established in Biaro where there seems to be no soil effect on species distributions. Though some notable differences in the vegetation were observed when sites were taken into consideration, the CA analyses (Fig. 3) show that for the upper arborescent layer the first axis clearly separates sandy and clayey plots, with a slight exception for the sandy plots located in Biaro which appear to be closer to clayey plots in their species compositions. The lower arborescent layer and the shrub layer somewhat express the same trends but the separation between clay and sandy plots along the first axis becomes less evident as long as lower forest layers are considered.

Table 2. Correlations between the matrix of floristic similarity and spatial distance. Analysis based on the entire dataset given the presence of sandy soils in all the 3 sites (Yoko, Biaro, Yangambi). Observations are based on 999 permutations. NS: no significant test.

Forest layers	Mantel statistic-r	p-value
Layer A	-0.151	0.964 (NS)
Layer Ad	-0.576	0.981 (NS)
Layer ar	0.137	0.097 (NS)

Distance decay analysis

Impact of ecological distance: sandy and clayey soils

It was observed that all the forest layers expressed a decrease in the similarity of their vegetation (Fig. 4). When substrates are compared among themselves, the decrease in the similarity of species composition

was much more evident in the upper arborescent layer (Fig. 4A; $R^2 = 0.89$). This is particularly evidenced by the absence in Biaro of some species (e.g. *Scorodophloeus zenkeri*, *Cynometra hankei*, etc.) which appeared be linked to sandy soils in Yoko (and even in the Yangambi).

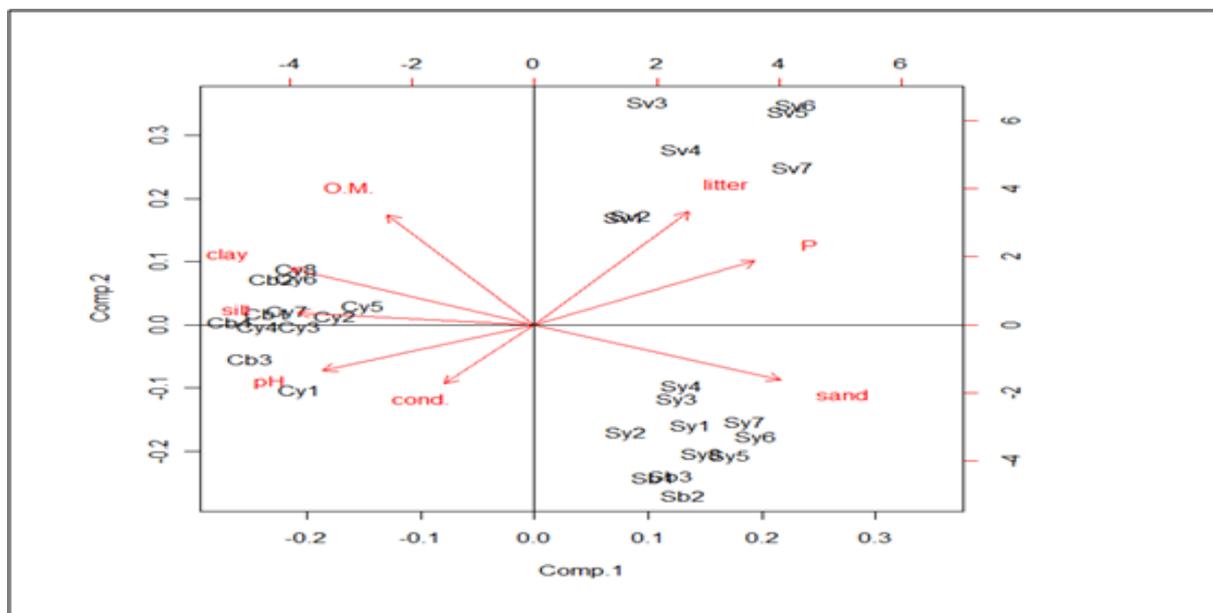


Fig. 1. Principal Component Analysis expressing the edaphic variables effect on plant communities. The first and second axes account for 79.5 of the total variability (Cy: plots on clayey soils in Yoko; Cb: plots on clayey soils in Biaro; Sy: plots on sandy soils in Yoko; Sb: plots on sandy soils in Biaro; Sv: plots on sandy soils in Yangambi).

The same trend is observed in the shrub layer (Fig. 4C; $R^2 = 0.78$). But the impact of the geographic distance is less strong in the lower arborescent layer (Fig. 4B; $R^2 = 0.49$). Plant communities on clayey soils appear to be almost stable compared to those established on sandy soils, particularly in the overstorey, though the decrease in similarity becomes more and more evident as distance increases. In the shrub layer, the geographic distance does not appear to induce any change in species composition (Fig. 4C; $R^2 = 0.0004$).

Overall, there much more species turnover in the overstorey when soils are considered separately compared to the general trend displayed when one accounts for inter-substrate similarity.

In either woody forest layer, a negative correlation exists between the matrix of species features and ecological distance, on one hand, and between species data and the matrix of spatial distance, on the other hand, as evidenced by the Mantel tests (Table 1).

Spatial distance on sandy soils

Since sandy soils were found in both the 3 sites, an analysis of similarity in vegetation features versus spatial distance was possible. We observed that, for the sole case of the overstorey, there is very little change in species composition in the upper arborescent layer attributable to spatial distance (Fig. 5; $R^2 = 0.01$) in comparison to the situation in the lower arborescent layer (Fig. 5; $R^2 = 0.36$). Though this distance effect is not significant in both cases (table 2), communities in the lower arborescent layer appear to be prone to a high species turnover.

Discussion

Factors shaping plant communities in tropical ecosystems

Many factors are believed to play a key role in the location and distribution of species in biological communities and understanding these processes has triggered a large number of interesting studies. At a general point of view, ten major factors are considered to limit tree species distributions (Veenendaal and Swaine, 1998).

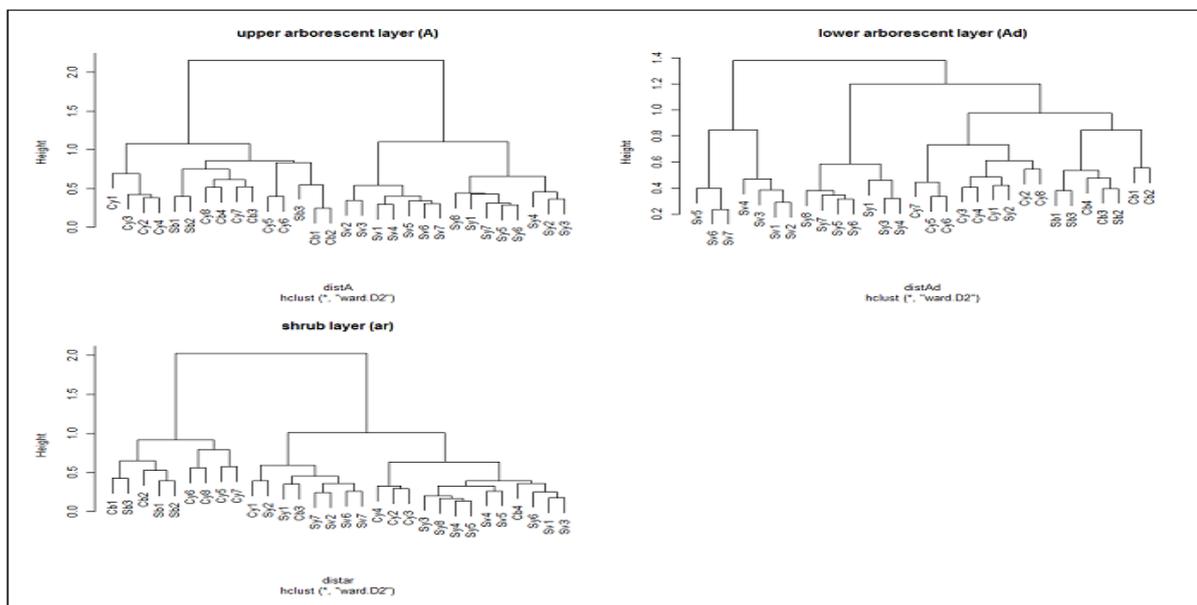


Fig. 2. Species partitioning following forest layers and soil types. Overall, soil appears to be an important parameter segregating plant communities, particularly in the upper arborescent layer (Cy: plots on clayey soils in Yoko; Cb: plots on clayey soils in Biaro; Sy: plots on sandy soils in Yoko; Sb: plots on sandy soils in Biaro; Sv: plots on sandy soils in Yangambi).

These are: 1) temperature, 2) rainfall too little or soil too wet, 3) nutrient supply inadequate or cation toxicity, 4) mycorrhizal inoculums not present, 5) pathogen pressure, 6) dispersal ineffective or phenology mistimed, 7) large-scale disturbance, 8) past climate fluctuations: species slow to spread from refugia, 9) geographic limitations: species unable to transgress a natural boundary, 10) competition with existing species. For lowland tropical rainforests, in particular, Veenendaal and Swaine (1998) argue that water and nutrient availability are the most ubiquitously variable factors and thus likely to limit the distributions of many species.

However, since rainfall and soil fertility tend to covary (due to leaching under high rainfall) it is difficult to segregate their effects on individual species and an experimental approach is strongly indicated (Swaine, 1996).

The forest ecosystems that drove the interest of this study are located in the same geographic region (the Central Congo Basin) and, logically, it can be considered to be less variations in the expression of climatic patterns affecting them. The fact that both the considered sites are home to the same forest

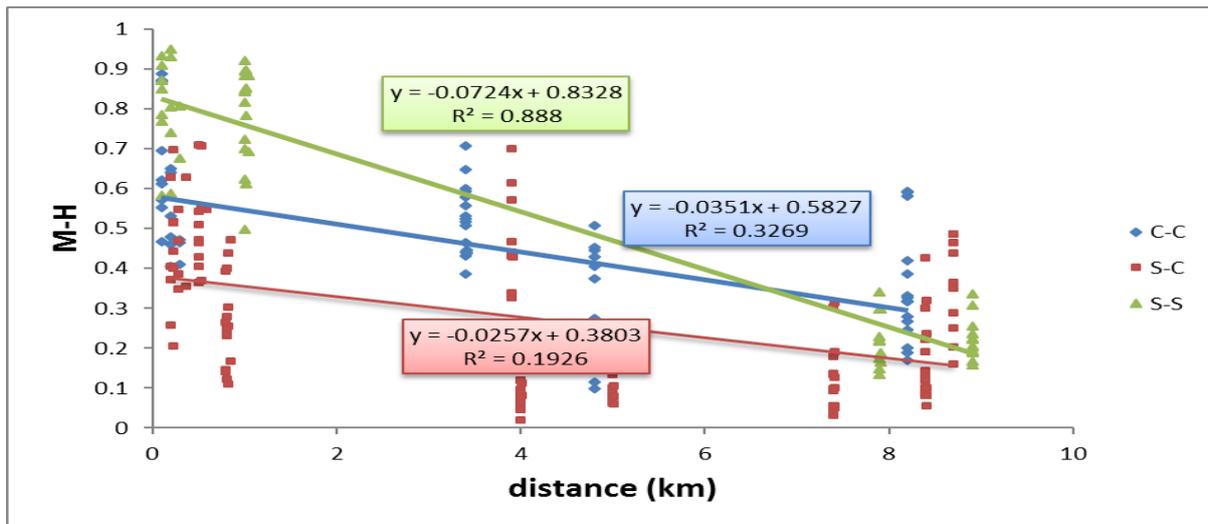


Fig. 4A. Variation of the species composition between substrates and among substrates in the upper arborescent layer. C-C: comparison between two plots on clay substrate; C-S: comparison between two plots on different substrates; S-S: comparison between two plots on sandy substrate. Only data from Yoko and Biaro were considered.

This can be considered as an evidence of edaphic determinism in these communities. As stated above, in the upper arborescent layer, species tend to be aggregated in their distributions, with some abundant species expressing substrate preferences. Palmiotto *et al.* (2004) confirm that many authors (e.g. Hubbell, 1979; Condit *et al.*, 2000) recognize that the spatial patterns of species distributions within tropical rainforests, which is particularly marked by

aggregation of many species, can be explained by both neutral and niche-based theories. Proponents of the niche-assembly processes establish a link between this spatial aggregation with a high degree of species habitat specialization (Ashton, 1998; Clark *et al.*, 1999; Hubbell, 2001) whereas neutral models point out the effects of limitations to seed dispersal (Bell, 2000; Hubbell, 2001).

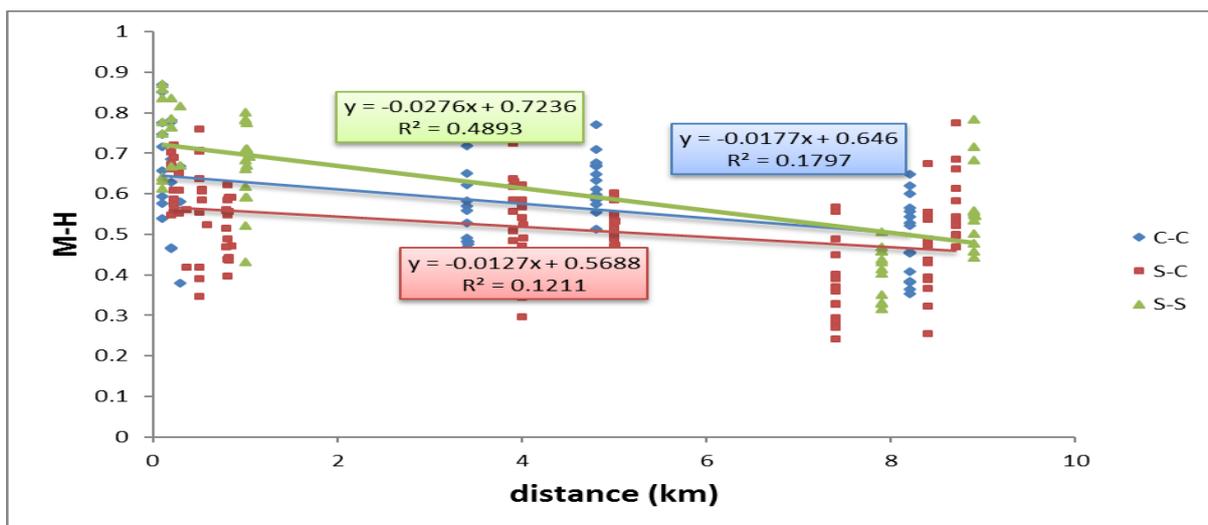


Fig. 4B. Variation of the species composition between substrates and among substrates in the lower arborescent layer. C-C: comparison between two plots on clay substrate; C-S: comparison between two plots on different substrates; S-S: comparison between two plots on sandy substrate. Only data from Yoko and Biaro were considered.

Among plant communities established on sandy plots, slight differences appear between Yoko and Yangambi. If both sites are, for instance, marked by the presence of *Scorodophloeus zenkeri*, *Cynometra hankei* and *Polyalthia suaveolens* in the upper arborescent layer, some species oppose the two sites. This is the case of *Prioria balsamiferum* and *Prioria oxyphylla* which are abundant on sandy soils in Yoko whereas they become very scarce in Yangambi. But

the real clear-cut difference between the two sites comes from *Petersianthus macrocarpus*. This species is among the most frequent trees on sandy soils in Yangambi, yet none of the sandy plots located in Yoko harbored it. Furthermore, a species like *Strombosiopsis tetrandra* (very common on sandy plots in Yangambi) was rather found in lower arborescent layer in Yoko, and particularly on clayey substrates.

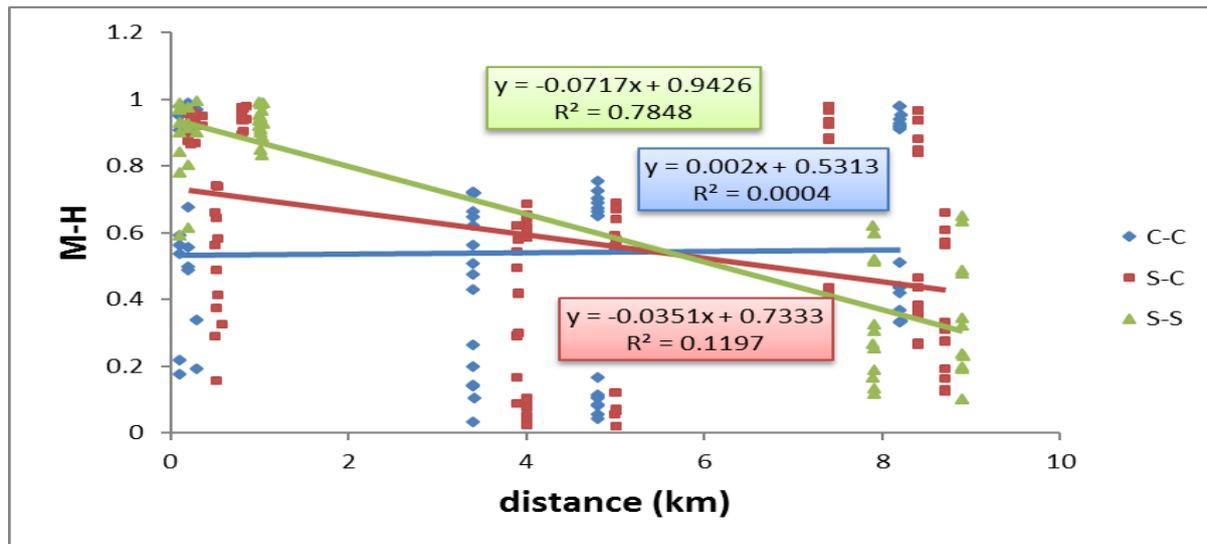


Fig. 4C. Variation of the species composition between substrates and among substrates in the shrub layer. C-C: comparison between two plots on clay substrate; C-S: comparison between two plots on different substrates; S-S: comparison between two plots on sandy substrate. Only data from Yoko and Biaro were considered.

An uneven observation comes when one considers floristic features in Biaro, a site not that very far from Yoko. No major differences were observed in species composition on sandy and clayey soils. We even found similarities between sandy plots in Biaro and clayey plots located in Yoko. For example, species such *Trilepisium madagascariensis* and *Petersianthus macrocarpus* reported to be abundant on clayey soils in Yoko were the important species found on sandy soils in Biaro. It is therefore evident that other environmental factors are to be taken into account, in addition to soil properties.

Species occurrences and distributions across space and time has been among topics of major focus in tropical ecology and seminal studies dealing with species coexistence exist (e.g. Wilson, 1997; Graham,

2000; Wilson and Lee, 2000; Brown *et al.*, 2001; Whittaker *et al.*, 2001; Chave and Leigh, 2002; Terborgh *et al.*, 2002; Wright, 2002; Chase, 2003; Chave, 2004; Turner, 2004; Rangel and Diniz-Filho, 2005; Graham *et al.*, 2006; Hubbell, 2006; Ricklefs, 2006). Relevant explanations were put forward by both the proponents of the niche and neutral theories (Hubbell, 2001; Condit *et al.*, 2002; Whitfield, 2002; Tuomisto *et al.*, 2003; Chave, 2004; Hubbell, 2005; Kembel and Hubbell, 2006; Jabot *et al.*, 2008). As stated by Chave (2004), many ecologists consider the neutral theory to be a radical shift from established niche theories but he notes that instead of being conflicting, niche and neutral theories are rather complementary. While the theory of species coexistence by niche differentiation is based on effects of purely deterministic processes with a small number

of species interacting through fixed rules, the neutral theory seems to be much more suitable for species-rich communities (tropical forests, coral reefs) with many rare species, where the role of stochasticity at the individual scale becomes unavoidable (Chave, 2004). Neutral theories particularly focus on the hypothesis of functional equivalence. Following this hypothesis, trophically similar species are considered to be demographically identical on a per capita basis in terms of their vital rates of birth, death, dispersal and even speciation (Hubbell, 2005).

However, it is considered that if dispersal limitation is an explanatory factor for the assembly of ecological communities, the similarity in species composition should decline across samples as inter-plot distance increases (Condit *et al.*, 2002). Referring to other authors, Jabot *et al.* (2008) raise attention on the fact that the neutral theory of biodiversity disregards the importance of post-dispersal environmental filtering, yet crucial in understanding the processes structuring natural communities.

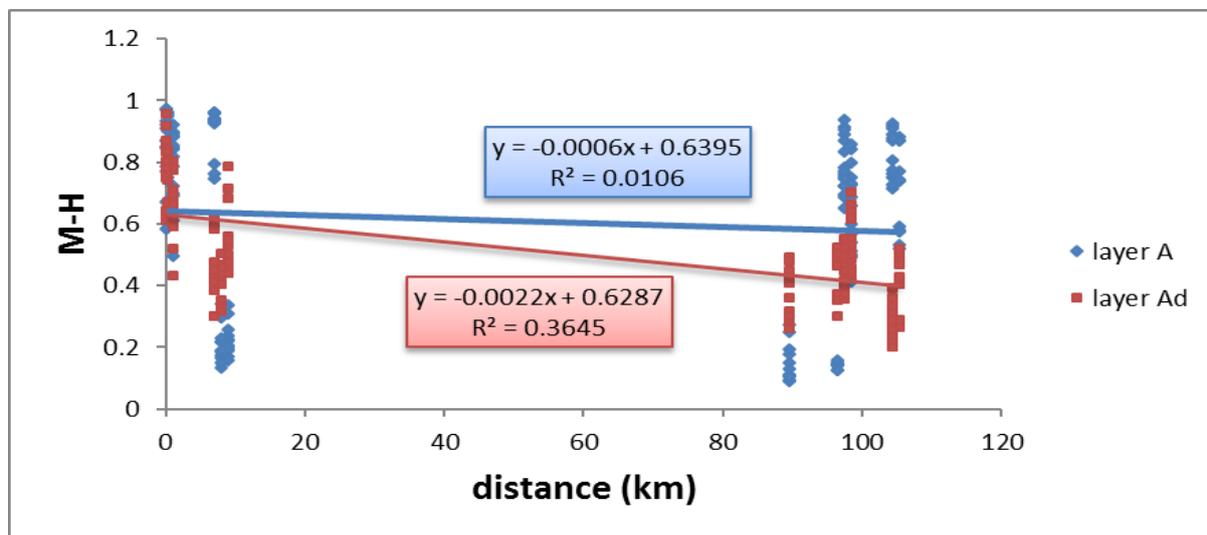


Fig. 5. Variation of the species composition on sandy soils in the overstorey. Communities in the upper arborescent layer express little variation in their composition. Results from the entire dataset (all 3 sites considered).

Decline in similarity in species composition: a measure of the species turnover

As recognized by Condit *et al.* (2002), species turnover can be the consequence of deterministic processes, such as species' adaptations to differences in climate or substrate, or it can result from limited dispersal coupled with speciation, delayed response to climatic change, or other historical effects. Comparing species composition, we observed that plant communities reflected by a decrease in the similarity of species composition, a phenomenon that affected differently the woody forest layers. This results from the spatial separation of the sites with many other environmental factors acting.

According to Palmer (2005), distance decay in plant communities may result from environmental heterogeneity, limited dispersal, mass effect, animal behavior, local disturbances, interspecific interactions and even land management.

Studies comparing the variation of similarity in plant communities have been conducted worldwide. Using large data sets on the plant communities of North American spruce-fir forests, Nekola and White (1999) compared the distance decay of similarity for various categories of plants. Their findings showed that both the decrease in environmental similarity with increasing distances and limits to dispersal affect rates of distance decay in biological similarity.

In his study in Costa Rica, Palmer (2005) observed that trees in the old growth portion of La Selva demonstrate significant distance decay. The probability of encountering a conspecific species declines continuously at least to a distance of 1500 m. Studying the beta-diversity in tropical trees in lowland *terra firme* forests in Panama, Ecuador and Peru, Condit *et al.* (2002) also reported a case of distance decay.

Conclusion

Plant communities in the considered semi-deciduous forests are influenced by substrate heterogeneity, characterized by contrasting habitats particularly marked by the occurrence of sandy and clayey soils.

The fact that these forest ecosystems are found in different parts of our study area aroused our interest to investigate the patterns of floristic similarities among sites, with a particular focus of forest layers which define distinct ecological guilds. The edaphic heterogeneity (marked by the occurrence of sandy and clayey soils) evidenced in these ecosystems allowed us to account for both the soil effect (ecological distance) and spatial distance effect on floristic similarity, and therefore replace the core of our findings in the ecological debates regarding species occurrences and distributions, following environmental factors and species life histories.

Though we were not able to report cases of significant distance decay, it is nonetheless worth mentioning the general trend of the decrease in similarity of species composition observed within the different forest layers.

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