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Species Assemblages within Forest Layers in Semi-Deciduous Forests from the Congo Basin: An Analysis of Species Phylogenetic Relationships

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Abstract: *Understanding the phylogenetic structures of plant communities is being developed in community ecology. Based on the species coexistence, we analyzed phylogenetic signals within forest layers, using species abundance data as well as their occurrences (presence/absence) within plots. We found that plant communities in the different forest layers express various phylogenetic structures. While the pattern of abundance phylogenetic structure vary among forest layers, all forest layers showed a pattern of spatial phylogenetic clustering (meaning that species cohabiting within a same plot are much related), with some significant values driven by substrate differentiation.*

Keywords: *plant community, phylogenetic clustering, phylogenetic overdisperion, species coexistence*

1. INTRODUCTION

In their large understanding, ecological communities are considered to be assemblages of co-occurring species with potential interactions among themselves. Furthermore, they are the result of different and complementary processes, present ecological processes as well as past and continuing evolutionary processes (McPeek and Miller 1996). Following this view, phylogenetic information in ecological communities can help reveal the extent to which organisms have a shared evolutionary history and, moreover, provide interesting information about the relative timing of historical events occurring between species (Cavender-Bares and Wilkzek 2003). A phylogenetic signal is viewed as the tendency for taxa that share a common ancestor to resemble each other in how they look, behave and with whom they interact (Kembel et al. 2010; Blomberg et al. 2003). Webb et al. (2002) mention the importance of incorporating phylogenetic information into ecology in the sense that it allows ecological questions to be addressed in an evolutionary context, which leads to a deeper understanding of the processes giving rise to patterns of biological diversity. Apart from their importance to understand ecological interactions between species, phylogenetic structure of communities can help build a link between community ecology and biogeography as well as the study of character evolutionary (Vamosi et al. 2009).

Helmus et al. (2007) define phylogenetic attraction as the pattern in which the species in a community are likely to contain greater phylogenetic relatedness than expected by chance, and phylogenetic repulsion as the opposite pattern. These concepts are termed "phylogenetic clustering" and "phylogenetic overdispersion" by many other authors (e.g. Webb et al. 2002; Swenson et al. 2006; Hardy and Senterre 2007; Vamosi and Vamosi 2007; Swenson et al. 2007; Parmentier and Hardy 2009).

At a general point of view, competitive interactions between species and environmental filtering are considered to be the major cause for the origin of phylogenetic patterns by most community phylogenetists (Johnson and Stinchcombe 2007). Considering these two mechanisms, an agreement exists that phylogenetic clustering is generated by environmental filtering (where related species live in the same habitat because they share ecologically important traits) whereas evidence for phylogenetic overdisperion considers competition to be the main cause for the structure of communities (Johnson and Stinchcombe 2007).

Phylogenetic perspectives are being developed worldwide to study plant communities (Graves and Gotelli 1993; Kelly 1999; Webb 2000; Tofts and Silvertown 2000; Silvertown et al 2001; Chadzon et al. 2003; Cavander-Bares et al. 2004; Cavender-Bares et al. 2006; Lovette and Hochachka 2006; Hardy and Senterre 2007; Swenson et al. 2007; Parmentier and Hardy 2009), but within the Congo Basin they are very scarce and have not yet been undertaken for the Congolese forests, in particular.

Among the Congolese forests, semi-deciduous ecosystems often consist in isolated communities due to diverse ecological barriers. Moreover in some areas, these communities are established on contrasting habitats due to their physical soil patterns, particularly driven by local topography. Some species therefore express preferences for a given soil than another whereas many other species are substrate-indifferent. It is not impossible that within a common genus, pairwise species express contrasted habitat preferences and this within the forest layers.

Considering these facts, we assumed that habitat differentiation (driven by substrate heterogeneity) and isolation through distance effects would lead to changes in phylogenetic structures (expressed by different phylogenetic signals) within plant communities in the forest layers shaping the semi-deciduous forests in the Congo Basin. We therefore addressed the following questions: 1) Do species in different forest layers express different phylogenetic signals? 2) What is the relative importance of spatial distance and edaphic contrast on species phylogenetic turnover?

2. METHODS

2.1. Study Area and Data Collection

Data were collected into 3 different sites within the Congo Basin (appendices 22-24): 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). Ten kilometers separate Yoko from Biaro (southwards) and Yangambi is located at more than 100 kilometers, further west. Many species found in these sites are semi-deciduous plants which lose the majority of their leaves during the small dry season. The mean elevation of the region is 435 masl and climate is of the kind Af in the Köppen classification. The annual rainfall ranges from 1417 mm to 1915 mm (mean: 1728.4 mm) with mean monthly temperatures varying from 23.7°C to 26.2 °C. Throughout the year, the region is marked by a long rainy season interrupted by two small dry seasons, the first going from December to January whereas the second one extends from June to August (Nshimba 2008). Soils in the region are mainly ferralitic with small rates in exchangeable bases (< 3 meq/100 g). They are acidic soils (pH < 6) and appear to be red or yellow in colors (Kombele 2004). Ferralitic soils are the dominant group in the region (van Engelen et al. 2006) and are particularly marked by xanthicferralsols (Beernaert 1999).

Plant inventories were performed according to forest layers, defined following Senterre (2005). By forest layer A, we considered the upper arborescent layer including canopy and emergent trees (over 20 m in height). The lower arborescent layer was defined as Ad and includes dominated trees, ranging from 6 to 20 m. Within the understorey, stratum ar represents the shrub layer with species varying from 1.5 to 6 m in height. Finally, the herbaceous layer (H) is represented by all herbaceous species. Sampling efforts varied among strata. Trees belonging to the stratum A were

inventoried in a 50 × 200 sqm area (1 ha). For stratum Ad, inventories were performed within a 10 × 200 m² area (2000 m²), whereas for stratum ar plants were counted within a 2.5 × 200 m² area (500 m²). Species belonging to stratum H were inventoried in two 10 × 10 m² areas, each subdivided in 2 × 2 m² subplots, which were chosen at each end of the 1-ha main plot, in areas considered to be the most representative of the herbaceous flora. We only considered species occurrences in the herbaceous layer whereas for the woody layers (A, Ad and ar), abundance data (based on the number of individuals) were taken into account. Furthermore, species were associated to the forest layer they actually belong to.

In each plot, soil samples were collected every 50 m at a depth of 0-10 cm. They were air-dried, cleaned of stones and roots fragments, and then passed successively through 20- and 2-mm sieves for textural analyses, based on the percentages of sand, clay and silt. Percentages of sand, clay and silt were measured by classic granulometric analyses using sedimentation columns in accordance with the Stokes' law.

2.2. Measures of Phylogenetic Structure

An ultrametric phylogenetic tree (with branch lengths given in Newick format) representing the species pool is an important component to assess the phylogenetic analyses of community structure. It is used to compute phylogenetic distances between species as well as to operate (partial) phylogenetic tree randomizations for testing the phylogenetic structure of the community or of species traits. This ultrametric tree was generated using Phylomatic and is based on the Angiosperm consensus tree from Davies et al. (2004). Phylomatic represents an online phylogenetic query tool to which a list of taxa (written as "family/genus/species")is submitted (Webb and Donoghue 2005; Hardy 2008) and which gives back a phylogenetic hypothesis for the relationships among taxa. The Nexus file obtained from Phylomatic was then imported into the community phylogenetic software SPACoDi 0.6 (Hardy 2008). Phylogenetic signals can be viewed at two levels: the plot level and following species abundance data. The analysis of phylogenetic signal in global species abundances characterizes the "abundance phylogenetic structure" given by the "phylogenetic abundance deviation" (PAD) index (Hardy 2008). Its formula is $PAD = 1 - Db^*/DELTA_p$, where $DELTA_p$ stands for the mean phylogenetic distance between all sampled species and Db* is the mean phylogenetic distance between distinct species weighted by the product of their global abundances. PAD describes how species abundances are distributed across the phylogenetic tree: PAD > 0 in case of phylogenetic clustering of species abundances, PAD < 0 in case of phylogenetic overdispersion of species abundances. Phylogenetic analyses at plot level are based on the Global statistics which include (Hardy 2008):

a) I-statistics (given when abundances rather than just presence/absence data are provided in the species-plot matrix) are based on probabilities of species identity for pairs of individuals (they partition Gini-Simpson diversity into alpha and beta components (Hardy and Senterre 2007). The formula for I-statistics is Ist= (Dia-Diw)/Dia, where Diw representsthe probability that two individuals from a plot belong to distinct species and Diaisthe probability that two individuals from different plots belong to distinct species.

b) P-statistics (given when a phylogenetic tree and abundances data are provided in the species-plot matrix) are based on mean phylogenetic distances between individuals (Hardy and Senterre 2007). P-statistics are computed as Pst= (Dpa-Dpw)/Dpa where Dpw stands forthe mean phylogenetic distance between individuals from the same plot whereas Dpaisthe mean phylogenetic distance between individuals from different plots.

c) B-statistics (given when a phylogenetic tree and abundances data are provided in the species-plot matrix) are based on mean phylogenetic distances between individuals of distinct species (Hardy and Jost 2008) and are computed using the formula: Bst= (Dba-Dbw)/Dba in which Dbw isthe mean phylogenetic distance between individuals of distinct species from the same plot and Dbaisthe mean phylogenetic distance between individuals of distinct species from different plots.

d) PI-statistics (given when a phylogenetic tree and a species-plot matrix are provided) are based on mean phylogenetic distances between species, not accounting for species abundances (Hardy and Senterre 2007). Their calculation is based on the formula: PIst= (DELTApa-DELTApw)/DELTApa, where DELTApw isthe mean phylogenetic distance between species

from the same plot and DELTAparepresentsthe mean phylogenetic distance between species from different plots.

Based on these Global statistics, spatial phylogenetic clustering (i.e. species within plots are more related on average than species from distinct plots) occurs when Pst>Ist,Bst> 0, or PIst> 0. Conversely, spatial phylogenetic overdispersion (i.e. species within plots are less related on average than species from distinct plots) is expected when Pst<Ist,Bst< 0, or PIst< 0.

3. RESULTS

3.1. Floristic Composition and Phylogenetic Diversity/Distinctness

In each of the forest layers, 30 plots were inventoried. The upper arborescent stratum (layer A) was represented by 25 plant families subdivided into 81 genera, 111 species and 3126 individuals. The most important families are respectively *Fabaceae* (38 species), *Meliaceae* (13), *Sapotaceae* (9) and *Olacaceae* (6). In the lower arborescent stratum (layer Ad), 4153 individuals belonging to 169 species, 113 genera and 37 families were inventoried. *Rubiaceae* and *Annonaceae* are the dominant families in the lower arborescent layer with 40 and 13 species. The other important families are *Euphorbiaceae* (13), *Malvaceae* (12), *Ebenaceae* (9*), Clusiaceae* (7) and *Apocynaceae* (7). Eight families rank ahead in the shrub layer: *Rubiaceae* (29 species), *Malvaceae* (10), *Euphorbiaceae* (9), *Phyllanthaceae* (8), *Anacardiaceae* (8), *Annonaceae* (7), *Ochnaceae* (6) and *Salicaceae* (6). Herbs are particularly represented by 5 families: *Marantaceae* (12 species), *Commelinaceae* (9), *Araceae* (6), *Convolvulaceae* (6) and *Rubiaceae* (6).

Within a plot, on clay soils, the probability that two individuals belong to different species is Diw = 0.93 for the upper arborescent layer, the mean divergence time between individuals is Dpw = 96.93 Myr, and the mean divergence time between species is DELTApw = 101.9 Myr (Table 1). Overall, these values are higher than those observed on sandy soils within the same forest layer. Compared to the other woody forest layers, species encountered in the lower arborescent layer appear to be more phylogenetically distant, both on sandy and clay soils. This is also the more diversified layer as shown by the Diw index.

Table 1. *Phylogenetic diversity and distinctness of species between forest layers*

Indices	Clay soils				Sandy soils			
	Layer A	Layer Ad	Layer ar	Layer H	Layer A	Layer Ad	Layer ar	Layer H
DELTAp	97.79	111.16	107.28	123.14	98.42	111.21	108.50	124.00
D*p	104.48	113.60	103.17	120.47	97.26	113.36	100.42	120.57
Diw	0.93	0.96	0.78	-	0.87	0.95	0.67	-
Dia	0.97	0.97	0.87	-	0.91	0.97	0.72	-
Dpw	96.93	109.03	79.92	-	84.96	107.09	67.53	-
Dpa	101	110.51	89.72	-	88.78	109.83	72.70	-
Dp*w	104	113.54	102.74	-	97.22	113.33	101.07	-
Dp*a	104.6	113.61	103.91	-	97.13	113.36	100.23	-
DELTApw	101.9	110.99	105.68	119.62	101.98	111.57	106.10	119.67
DELTApa	102.3	111.08	105.71	120.49	102.04	111.66	106.29	120.57

However, the mean phylogenetic distances between species are particularly much higher when one considers the herbaceous layers (119.62 Myr on clay soils and 119.67 on sandy substrates).

3.2. Changes in Phylogenetic Structure among Forest Layers

Phylogenetic signals changed according to the considered forest layers (table 2). In the overstorey (layers A and Ad), there is a pattern of phylogenetic overdispersion of species abundances though the signals are not significant. However, within the shrub layer (ar), there is a pattern of phylogenetic clustering of species abundances. When testing for the spatial phylogenetic structures, both indices show a pattern of phylogenetic clustering within all the forest layers, with a significant signal in the upper arborescent layer (p = 0.011).

Table 2. *Community phylogenetic structuring in forest layers. Based on species abundances, differences appear within forest layers but both the overstorey and the understorey express a spatial phylogenetic clustering.*

	Layer A	Layer Ad	Layer ar	Layer H
PAD	-0.022	-0.019	0.062	-
Ist	0.06	0.023	0.099	-
Pst	0.07	0.024	0.100	-
P*st	0.006	0.0008	0.0002	-
PIst	0.004*	0.0009	0.001	0.0067

The general trend shows that Ist and Pst indices were increasing with distance whereas values of P*st and PIst decreased with increasing distance, as shown in figure 1.

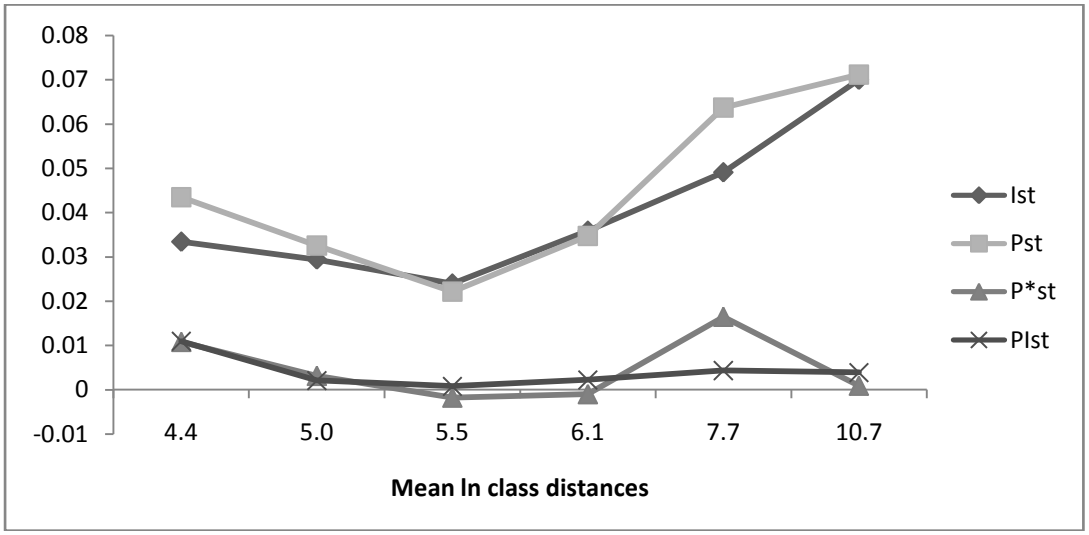

Fig. 1a. *Spatial phylogenetic indices and their general trend through distance (layer A). PIst index shows that species cohabiting in the same plot are more related but this relatedness decreases when plots are separated.*

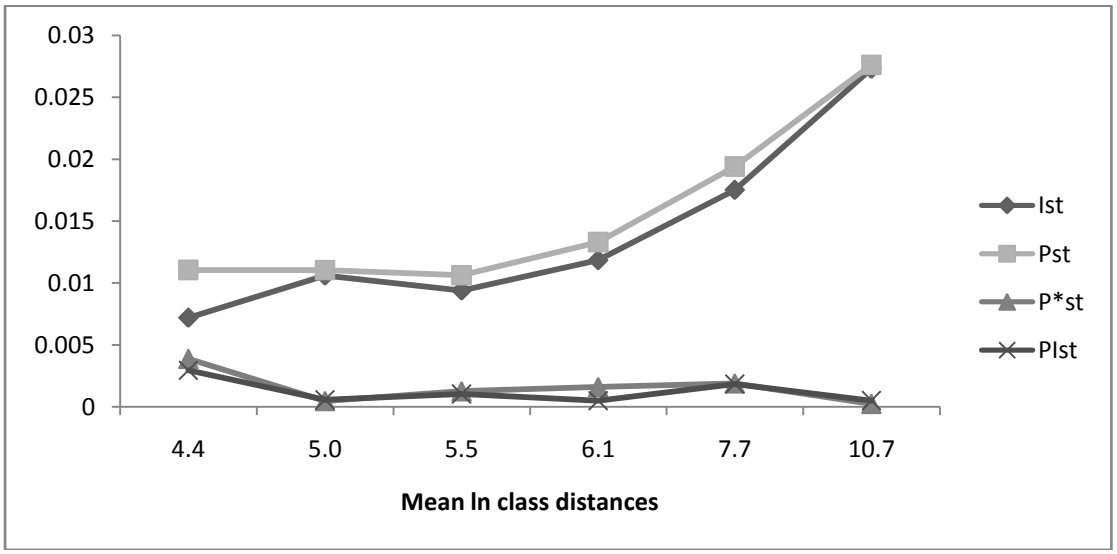

Fig. 1b. *Spatial phylogenetic indices and their general trend through distance (layer Ad). PIst index shows that species cohabiting in the same plot are more related but this relatedness decreases when plots are separated.*

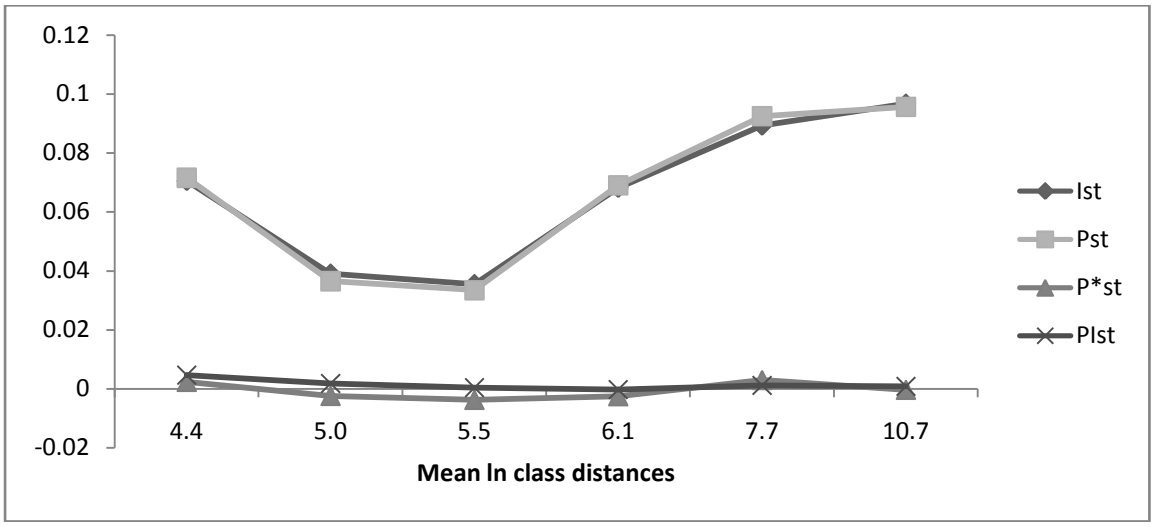

Fig. 1c. *Spatial phylogenetic indices and their general trend through distance (layer ar). PIst index shows that species cohabiting in the same plot are more related but this relatedness decreases when plots are separated.*

Based on the abundance data, the index of phylogenetic abundance deviation (PAD) also expresses different values within the woody forest layers, according to the divergence class intervals (fig. 2). When considering the highest divergence class interval (143.8 Myr), this index express negative values in the overstorey (PAD = -0.022 for the upper arborescent layer and PAD = -0.019 in the lower arborescent layer). However, it is positive in the shrub layer (PAD = 0.062) though a negative value was observed at class interval 90 Myr, expressing a pattern of phylogenetic overdispersion of species abundances (PAD = -0.025). A signal of phylogenetic clustering is also observed at that distance interval in the upper arborescent layer (0.071).

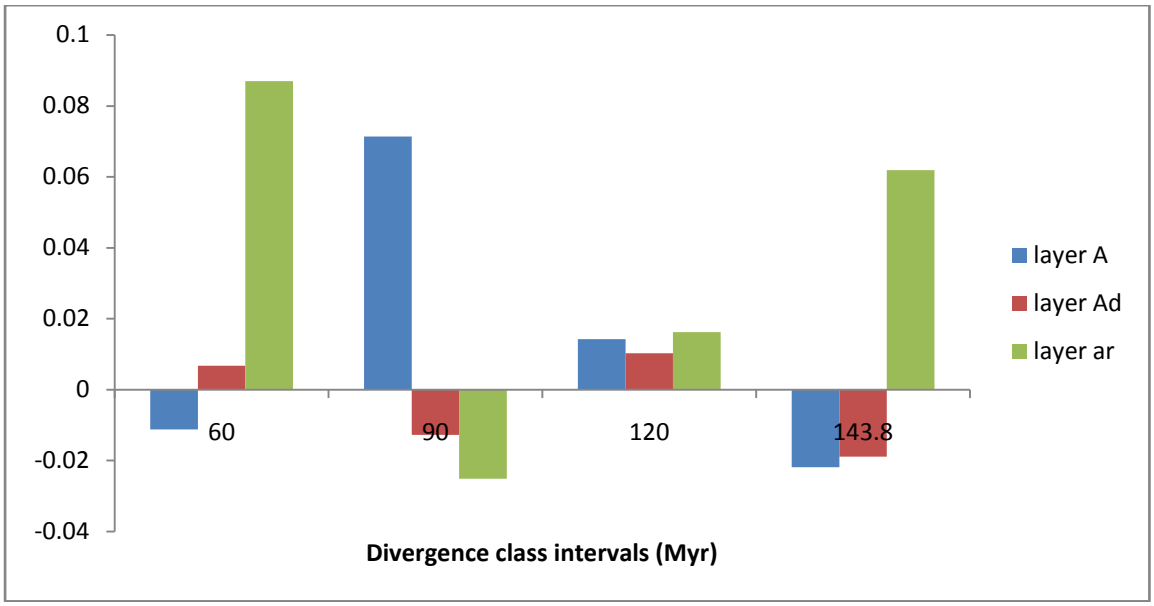

Fig. 2. *Patterns of the abundance phylogenetic structure (PAD) in woody forest layers. The index of Phylogenetic Abundance Deviation reflects different values according to forest layers and divergence class intervals. This index (PAD) also varies within the same forest layer.*

4. Impact of Edaphic Heterogeneity on Community Phylogenetic Structuring

Different phylogenetic patterns are observed when forest layers are compared among themselves and it is obvious that phylogenetic signals change according to the considered substrate. In the upper arborescent layer, a pattern of phylogenetic overdispersion of species abundances exist on clay soils (PAD = -0.068) whereas sandy soils are marked by a positive PAD (0.012), giving rise to a pattern of phylogenetic clustering (table 3).

Table 3. *Patterns of phylogenetic structure driven by edaphic differentiation. Both sandy and clay substrates reflect a pattern of spatial phylogenetic clustering. However the index of Phylogenetic Abundance Deviation (PAD) varies according to soil texture.*

Indices	Clay soils				Sandy soils			
	Layer A	Layer Ad	Layer ar	Layer H	Layer A	Layer Ad	Layer ar	Layer H
PAD	-0.068	-0.022	0.038	-	0.012	-0.019	0.074	-
Ist	0.035	0.013	0.1031	-	0.043	0.003	0.0787	-
Pst	0.040	0.013	0.1092	-	0.043	0.003	0.0711	-
P*st	0.005	0.0005	0.0056	-	-0.0009	-0.0003	-0.0085	-
PIst	0.004*	0.0009	0.0003	0.007	0.0005	0.002	0.0018	0.03*

Conversely, lower arborescent layers express the same phylogenetic pattern (phylogenetic overdispersion of species abundances) on both the two substrates. This is also the case for shrub layers where both the two soils reflect a pattern of phylogenetic clustering of species abundances. However, the pattern of spatial phylogenetic structuring does not differ between the two soils, all the forest layers express a spatial phylogenetic clustering with significant values of the PIst index in the upper arborescent layer ($p = 0.029$) and the herbaceous layer ($p = 0.03$).

5. DISCUSSION

Determining the phylogenetic patterns in plant communities is being developed in modern ecology, the central interest being based on species co-occurrence and their relatedness. Overall, two phylogenetic patterns are expected given that coexisting species may be more related (phylogenetic clustering) or less related (phylogenetic overdispersion). Test of these phylogenetic trends refer either on species spatial distribution (Are species within sites more or less related than species from different sites?) or on their frequency and abundance (Are there clades of mostly abundant species and clades of mostly rare species?), as reported by Hardy and Senterre (2007).

Phylogenetic analyses in our communities showed that species in different forest layers may express different phylogenetic patterns and this was observed when abundance or incidence (presence/absence) data are considered. Taking into account the forest layers without regard to substrate, we observed that species in the overstorey respond to a pattern of phylogenetic overdispersion of their abundances. However when substrate was considered, we observed that species in the upper arborescent layer are overdispered in their abundances on clay soils whereas on sandy soils species are rather clustered. On both the two soils, a pattern of phylogenetic overdispersion is observed in the lower arborescent layer and the contrary (phylogenetic clustering) in the shrub layer. These observations suggest that clades of abundant species and those of rare species are found in each of the woody forest layers. Phylogenetic trees of species are provided in appendices 18-21. Floristic data revealed that some taxa at family level are particularly abundant and on each of the substrate there are species which are dominant, considering the number of their individuals. This is the case of *Scorodophloeus zenkeri* on sandy soils. Some other abundant species, showing no substrate preference, were observed. As an example, we can cite *Scaphopetalumthonneri* which is the most common species in the shrub layer.

Considering the spatial phylogenetic structure, all species coexisting in the different layers express a pattern of spatial phylogenetic clustering. Again this is explained by the fact that many species belong to the same families and families with a small number of species are not numerous. Significant signals were observed in the upper arborescent layer which is particularly dominated by two families: *Fabaceae* and *Meliaceae*. When edaphic features are considered, significant spatial phylogenetic patterns were observed in the upper arborescent layer on clay soil and in the herbaceous layer on sandy soils. Species co-occurring in these two layers particularly belong to much related clades. For example, on the 89 species inventoried in the layer A (clay soils), 31 (ca 35%) belong to the *Fabacea*e family (including subfamilies *Faboideae*, *Mimosoideae* and *Caesalpinioideae*). Likewise, the great majority of the 46 herbaceous species surveyed on sandy substrates are monocots (ca 52%) with 11 species (ca 24%) belonging to the order *Zingiberales*, with the unique family *Marantaceae* accounting for ca 22% (10 species).

Overall, we observed that the spatial phylogenetic structure was decreasing with increasing distance separating plots (fig. 3), except in the herbaceous layer. This means that species cohabiting in the same plot are more related but this relatedness decreases when plots are separated. In other terms, species cohabiting locally are much related.

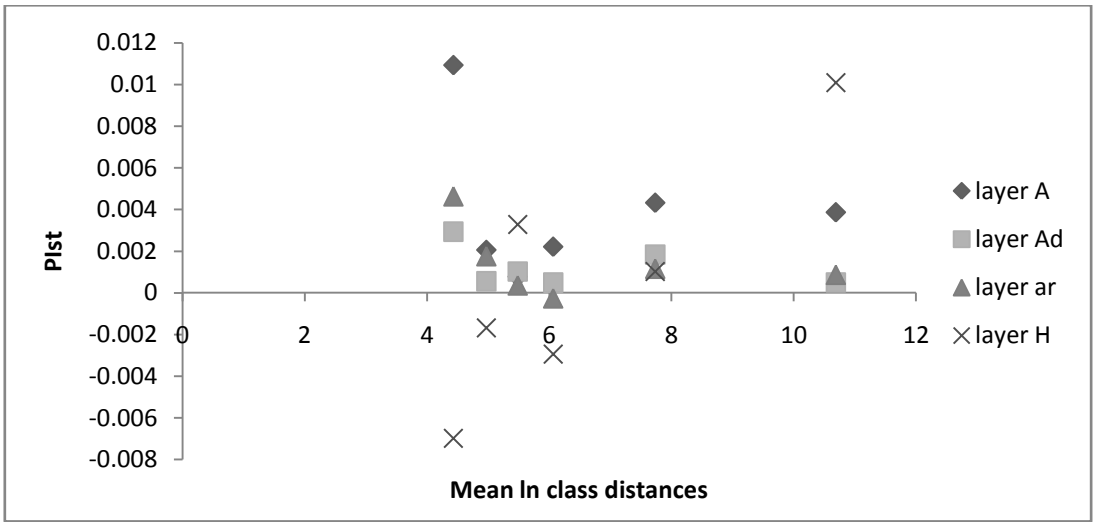

Fig. 3. *Changes in species relatedness (PIst index) with spatial distance in forest layers (layer A: R^2 = 0.032; layer Ad: R^2 = 0.14; layer ar: R^2 = 0.16; layer H: R^2 = 0.73)*

Significant phylogenetic structure in the species abundance was also reported by Parmentier and Hardy (2009) who found that abundant species tended to belong mostly to one or several related clades in plots from humid and mesoxeric grasslands within inselberg's plant communities (western Africa). They also reported a pattern of spatial phylogenetic clustering and showed that it decreased with spatial distance. The same phylogenetic pattern was found in Monte Alén National Park (Equatorial Guinea) by Hardy and Senterre (2007). Studying sunfish communities in Wisconsin (USA), Helmus et al. (2007) simultaneously found phylogenetic clustering driven by environmental filtering and phylogenetic overdispersion possibly caused by competition. As they state, citing other sources (e.g. Lovette&Hochachka 2006), a dichotomy often results from environmental filtering and competitive exclusion that operate differently to generate the two opposed phylogenetic patterns. Environmental factors exert a selection on phylogenetically related species occurring in the same community whereas competitive exclusion cause phylogenetically related species to occur in different communities.

Within plant communities, a pattern of spatial phylogenetic overdisperion was reported by Cavender-Bares et al. (2004) in oak communities (Florida), contrasting with our results and those reported by Hardy and Senterre (2007), as well as Parmentier and Hardy (2009). According to Hardy and Senterre (2007), these contrasting results can originate from the different taxonomic scales separating angiosperms and gymnosperms, represented in this case by the genus *Quercus* (oak communities). They emphasize that processes of competitive exclusion, responsible for the pattern of phylogenetic overdispersion, are more expected to occur in closely related species given that their niche overlap. In the same way, phylogenetic overdispersion of closely related species can result from speciation by habitat specialization (sympatric speciation).

6. CONCLUSION

Studying the phylogenetic patterns of plant communities in semi-deciduous forests within the Congo Basin may help understanding the ecological processes shaping these ecosystems. We found that differences in phylogenetic structures exist within the forest layers and that substrate may play a role in structuring these communities. Overall, upper arborescent layers express various phylogenetic patterns when their species abundances are taken into account. However, all the forest layers expressed a pattern of spatial phylogenetic clustering explaining that co-existing species within a plot are more related.

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