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Influence of a topographic gradient on the occurrence, abundance and composition of nine species of palms (Arecaceae) in the Central Amazon

Influência de um gradiente topográfico nas mudanças na ocorrência, abundância e composição de nove espécies de palmeiras (Arecaceae) na Amazônia Central

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ABSTRACT

The study was conducted at the Adolpho Ducke Forest Reserve. The occurrence and abundance of the adult palms *Attalea attaleoides* (Barb. Rodr.) W Boer*, A. microcarpa* Mart.*, Euterpe precatoria* Mart.*, Geonoma aspidiifolia* Spruce*, Iriartella setigera* (Mart.) H. Wendl*, Oenocarpus bacaba* Mart.*, O. bataua* Mart.*, O. minor* Mart.*, Socratea exorrhiza* (Mart.) H. Wendl were observed in 40 50 x 50 m plots and the seedlings in two 50 x 2 m plots located inside the 40 plots demarcated to register the adults. The topographical gradient was divided into swamp valley, slope and plateau based on the altitudes and characteristics of these environments. Occurrence and abundance data were used as dependent variables in the models of Analysis of Variance to verify differences in the topographical gradient. Changes in species composition were evaluated using multivariate analysis of ordination. The distribution and abundance of the seedling and adult phases varied with the topographical gradient. The variation in species composition in different topographic levels probably occurs due to the different responses of the species to the variation in forest heterogeneity, produced by the spatial variation of the structural components of the forest.

Key words: palms, Central Amazon, topography, distribution, "Terra Firme" forest.

RESUMO

O trabalho foi realizado na Reserva Florestal Adolpho Ducke na Amazônia Central. Os dados sobre ocorrência e abundância de adultos das palmeiras *Attalea attaleoides* (Barb. Rodr.) W Boer*, A. microcarpa* Mart.*, Euterpe precatoria* Mart.*, Geonoma aspidiifolia* Spruce*, Iriartella setigera* (Mart.) H. Wendl *, Oenocarpus bacaba* Mart.*, O. bataua* Mart.*, O. minor* Mart.*, Socratea exorrhiza* (Mart.) H. Wendl foram coletados em 40 parcelas de 50 x 50 m e os de plântulas em duas parcelas de 50 x 2 m localizadas dentro das 40 parcelas utilizadas para os indivíduos adultos. O gradiente topográfico foi categorizado em baixio, vertente e platô baseado nas altitudes e características destes ambientes. Os dados de ocorrência e abundância foram usados como variáveis dependentes em modelos de Análise de Variância para verificar diferenças com relação ao gradiente topográfico. As mudanças nas variações na composição das espécies foram avaliadas usando análise multivariada de ordenação. A distribuição e abundância das palmeiras nas fases de plântula e adulto variaram com o gradiente topográfico. A variação na composição das espécies nos diferentes níveis topográficos provavelmente ocorre devido a

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diferentes respostas das espécies à variação na heterogeneidade ambiental da floresta, produzida pela variação espacial nos componentes estruturais da floresta.

Palavras-chave: palmeiras, Amazônia Central, topografia, distribuição, floresta de terra firme.

Introduction

Studies of changes in population and community composition are of great importance to the comprehension of interactions among species and how these species are influenced by ecological factors, determining the local and regional biodiversity (Ricklefs and Schluter, 1993). In the tropical forest, these factors are essential to management actions and conservation politics.

Population ecology studies conducted with palms show that this is one of the most abundant and diverse group of plants in tropical forests (Scariot *et al.*, 1989; Lima-Filho *et al*., 2002), it being found in all forest levels and relief types, and exhibiting a wide variety of growth forms (Kahn and Castro, 1985). The study of populations can reveal more clear distribution patterns in relation to the niche occupied by species than the more complex studies performed to the community.

Palms distribution in Terra Firme forest has been related to the topography because it can influence soil patterns, hydrology, drainage, and forest architecture (Kahn, 1986; Moraes, 1996; Vormisto *et al*., 2004). In the Central Amazon, Kahn and Castro (1985) observed three general types of soil conditions of Terra Firme forest: (i) well-drained soils (plateau), (ii) poorly-drained soils (slope), and (iii) water-logged soils (valley). The authors relate that these three types of environment were favorable to the development of typical palm species, with few species common to two types of soils.

Palms able to establish in a certain habitat present a more restricted distribution and higher density than rare species (Castilho *et al.*, 1998, De Souza *et al.*, 1999). Most of the studies conducted at Ducke Reserve, near Manaus, are about communities (Tello, 1997; Zuquim *et al.* 2007). In the same area, the species composition of the palm community varied significantly in relation to environmental and geographical gradients (Costa *et al*., 2009). The distribution of populations of more abundant palm species can be influenced by several components of the forest structure, like litter quantity, canopy opening, tree density, soil types, etc (Cintra *et al.,* 2005). However, in most of these studies, only adults were considered. This study differs from previous studies performed at Ducke Reserve because it evaluates the distribution and abundance of palms, including some less abundant, considering seedling and adult phases. Furthermore, we analyzed the populations at only one micro basin of the reserve, separating *a priori* the potential effect in a spatial mesoscale that different micro basins can produce in palm distribution and abundance.

Since palms are relatively abundant and distributed all over the Reserve, our prediction is that community composition is relatively homogeneous along the variation of the topographical gradient (plateau, slope, valley). Nevertheless, palm species differ in the capacity to occupy more complex environments and some more direct relations are expected, for example, changes in species composition with concomitant changes in soil type or topographical gradients.

Material and methods

Study area

The study was conducted at Adolpho Ducke Forest Reserve (02°55, 59°59'W), in Terra Firme forest, which is not seasonally inundated by the river flood (Ribeiro *et al*., 1999).

Ducke Reserve has a system of regularly spaced trails each with an extension of 8 km in north-south and east-west directions, separated to each other by 1 km. The path system forms a grid and cover an area of 64 km^2, of which, 12 km^2 correspond to one of the five hydrographic micro basins of the Reserve (Barro Branco stream "igarapé"), located in the northwest region of the reserve considered in this study (Figure 1).

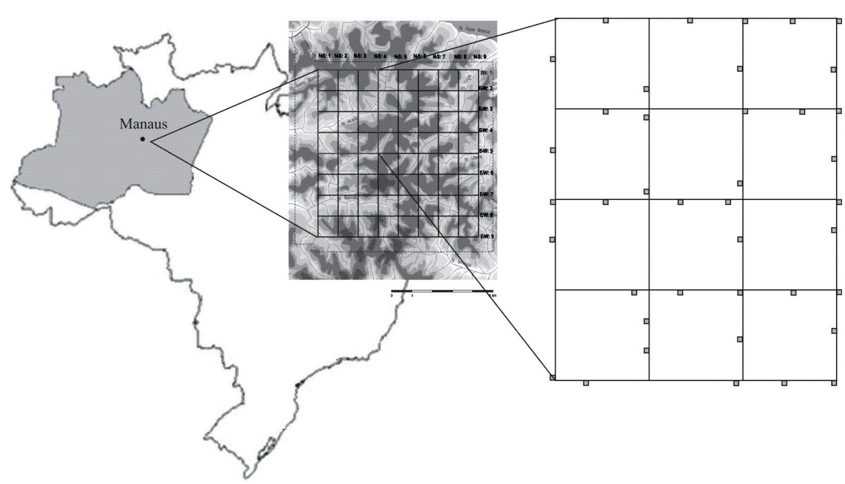

Figure 1. Map with the location of Adolfo Ducke Forestal Reserve and the grid with plots location.

Data collection

Information on relief was collected in the field, observing plot location, categorized in valley, slope, and plateau, based on the altitudes and characteristics of these environments according to Ribeiro *et al.* (1999).

Richness and abundance data of palm seedlings were collected in June 2007 in two subplots of 50 x 2 m, distant twenty meters from each other. All the seedlings found in the subplots were recorded. The two subplots were distributed inside each of the 40 50 X 50 m plots, demarcated for the adults survey (see below). Each group of two subplots was considered a sample unity. Seedlings of nine palm species were sampled: *Attalea attaleoides* (Barb. Rodr.) W Boer*, A. microcarpa* Mart.*, Euterpe precatoria* Mart.*, Geonoma aspidiifolia* Spruce*, Iriartella setigera* (Mart.) H. Wendl*, Oenocarpus bacaba* Mart.*, O. bataua* Mart.*, O. minor* Mart.*,* and *Socratea exorrhiza* (Mart.) H. Wendl. *Oenocarpus minor* and *Euterpe precatoria* seedlings were differentiated by the colour on the abaxial surface which is white in *E. precatoria* and green in *O.minor*, *Attalea attaleoides* and *Syagrus inajai* seedlings were differentiated by the pilose abaxial surface and green abaxial surface in the leaves of *S. inajai* which is whiter in *A. attaleoides*. *Socratea exorrhiza* can be distinguished from *Iriatella setigera* by its spiny stilt roots.

All the adult individuals were registered in the 40 50 x 50 m plots. Each was considered a sample unit and was demarcated with a minimum distance of 200 m from each other.

Palms were identified according to Ribeiro *et al.* (1999). Individuals considered adults were those with evident signs of earlier reproduction or with remains of inflorescences or presence of mark of fruit production. In multiple-stemmed species (*Geonoma aspidiifolia* and *Oenocarpus minor*) each stem was considered an individual.

Statistical Analyses

Abundance data of seedlings and adults were used as dependent variables in Analyzes of variance models (ANOVA) in order to verify differences of palm species abundance in relation to the relief (valley, slope, and plateau).

Changes in composition variation of palm species were evaluated using non-metric multidimensional scaling ordination (NMDS), available in PCORD program (McCune and Mefford, 1979). From the data matrix (species/plot), dissimilarity matrices were constructed using the Bray Curtis index. Ordination analyses were performed on qualitative (presence / absence) and quantitative (abundance) matrices of seedlings and adults. The vectors resultant from ordination analyses were used as dependent variables in the Multivariate analysis of variance models (MANOVA), available in the SYSTAT program (Wilkinson, 1998), to evaluate differences in palm species composition in relation to the topographical gradient (valley, slope, plateau). Two NMDS axes captured most of the variance in the original variables for both qualitative and quantitative data in the seedling and adult palm species matrices (Cumulative proportion of total variance (CPV) ranging from 0.60 to 0.80). Therefore, two axes were used as dependent variable in the MANOVAs.

Analysis of variance (ANOVA) was used to verify differences in seedlings and adults abundance in relation to the topographical gradient. To use analyses of variance ANOVA and MANOVA, quantitative data were normalized, performing first the 0.5 sum, and then the square root of the data.

Results and discussion

The pattern of occurrence and distribution of species found in this study corroborates results found in the community in general, in the Amazon Forest (Figures 2 and 3), confirming that palms distribution and abundance are related to the topographic gradient (Kahn and Castro, 1985; Kahn, 1987; Vormisto *et al.,* 2004).

Some of the palms found, like *Attalea attaleoides*, *Oenocarpus bataua*, *Euterpe precatoria*, *Socratea exorhiza* and some others, are relatively well distributed in the Amazon region (Henderson 1995). The wide distribution of these species suggests that they can tolerate a great variation of light intensity, soil, nutrient, humidity and topography of the environmental gradient.

Seedlings and adults of *Oenocarpus bacaba* and adults of *Oenocarpus minor* and *Geonoma aspidiifolia* were less frequent, and seedlings and adults of *Attalea microcarpa* and adults of *Oenocarpus bataua* were more frequent in valleys (Table 2). These

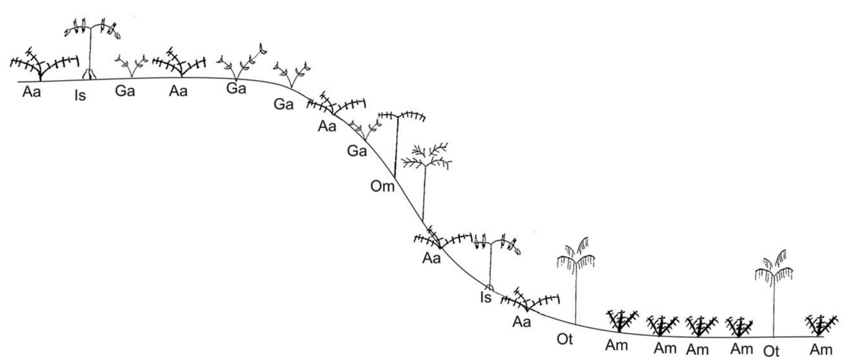

Figure 2. Species distribution of the more abundant adult palms along the topographic gradient at Ducke Reserve. Aa= *Attalea attaleoides*, Am= *Attalea microcarpa*, Is= *Iriartella setigera*, Ga= *Geonoma aspidiiflolia*, Om=*Oenocarpus minor*, Ot=*Oencarpus bataua*.

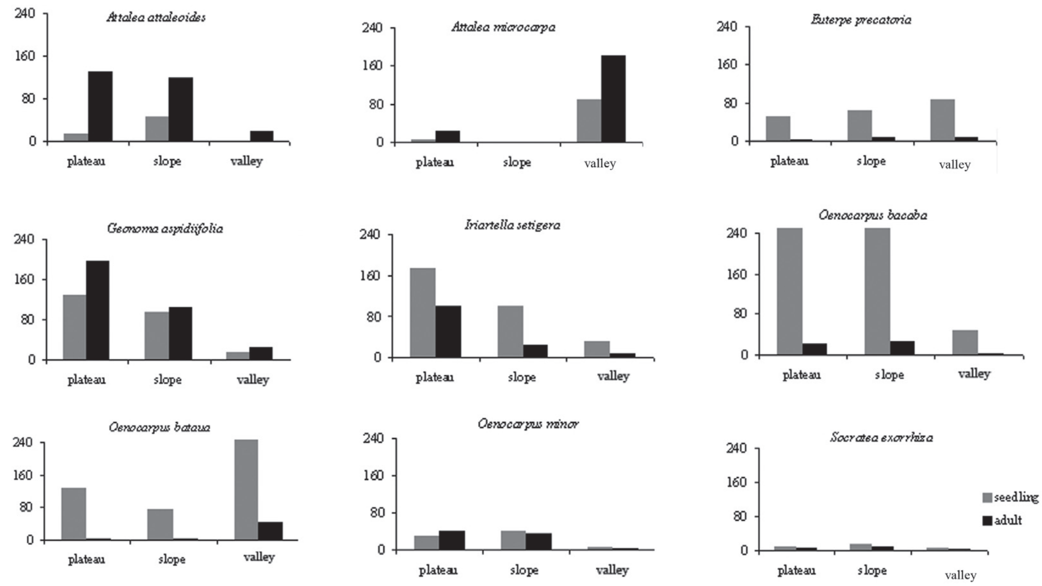

Figure 3. Abundance of the nine palm species in seedling and adult phases in the topographic gradient (plateau, slope, and valley) of Adolpho Ducke Forest Reserve.

Table 1. Analyses of variance (ANOVA) results of abundance data of the nine studied species in relation to the relief gradient. v = valley, s= slope and p= plateau.

	r^2		F		P	
	seedlings	**adults**	**seedlings**	**adults**	**seedlings**	**adults**
Attalea attaleoides (Barb. Rodr.) W Boer	0.167	0.185	3.705	4.1890	**0.0340**	**0.0230**
Attalea microcarpa Mart.	0.364	0.488	10.585	17.6380	**0.0001**	**0.0001**
Euterpe precatória Mart.	0.078	0.074	1.559	1.4730	0.2240	0.2420
Geonoma aspidiifolia Spruce	0.187	0.211	4.246	4.9440	**0.0220**	**0.0130**
Iriartella setigera (Mart.) H. Wendl.	0.069	0.161	1.365	3.5490	0.2680	**0.0390**
Oenocarpus bacaba Mart.	0.246	0.123	6.038	2.6000	**0.0050**	0.0880
Oenocarpus bataua Mart.	0.507	0.540	19.061	21.7450	**0.0001**	**0.0001**
Oenocarpus minor Mart.	0.148	0.186	3.201	4.2210	**0.0520**	**0.0220**
Socratea hexohriza (Mart.) H. Wendl.	0.031	0.025	0.587	0.4800	0.5610	0.6230

Tabela 2. Distribution in relation to relief of seedlings and adults of palms in “floresta de terra firme” in the Central Amazon.

Species	Phase	Plateau	Slope	Valley	Total
Attalea	seedlings	14	45	0	59
attaleoides	adults	130	120	18	268
Attalea	seedlings	6	0	89	95
microcarpa	adults	23	0	182	205
Euterpe	seedlings	50	65	88	203
precatoria	adults	3	8	8	19
Geonoma	seedlings	130	97	14	241
aspidiifolia	adults	196	105	23	324
Iriartella	seedlings	173	101	30	304
setigera	adults	101	24	8	133
Oenocarpus	seedlings	563	456	48	1067
bacaba	adults	21	25	2	48
Oenocarpus	seedlings	127	74	247	448
bataua	adults	4	2	43	49
Oenocarpus	seedlings	30	39	5	74
minor	adults	40	34	3	77
Socratea	seedlings	10	14	7	31
exorrhiza	adults	5	10	3	18

results probably indicate a distribution pattern in which physiological characteristics that favor the establishment and development in flooded areas are enable the establishment of species in the valley. The presence of water is the main factor in the variation of plant species recruitment, inhibiting growth of species that do not present physiological adaptations to deal with the hydric stress (Joly and Crawford, 1982).

The presence of water constrains the growth of species that do not present physiological adaptations to deal with the hydric stress, and plants adapted to this condition tend to be dominant in the community (Joly and Crawford, 1982; Losos, 1995; Scarano *et al.*, 1997; Pacheco, 2001). Seedlings of *Attalea microcarpa* and *O. bataua* were more abundant in the valley and seedlings of *O. bacaba* and *Geonoma aspidiifolia* were less abundant (Figure 4). Adults of *Attalea attaleoides*, *Geonoma aspidiifolia,* and *Oenocarpus minor* were less abundant in the valley and *Attalea microcarpa* and *O. bataua* were more abundant. *Iriartella setigera* was more abundant in the plateau (Table 1, Figure 5).

Adults of *Attalea attaleoides* were found in higher abundance with greater slope areas. De Souza *et al.* (1999) found that *Attalea attaleoides* was abundant with greater slopes, probably because it is acaulescent species, and thus more resistant to changes in soil drainage.

The composition of the palm communities of the Oriental, Central and Occidental Amazon Forest were compared, showing that species richness is higher in the Occidental region and in the Terra Firme forest, dominated by understory palm species (Kahn *et al.,* 1988). The authors state that the largest and one of the most diverse palm communities of the world is represented, in most part, by small understory species. Arborescent adult palms occur in low density in the Terra Firme forest and the opposite is found in the seasonally flooded forests. Studies of palms in flooded forests in low Ucayali River valley in Peru, re-

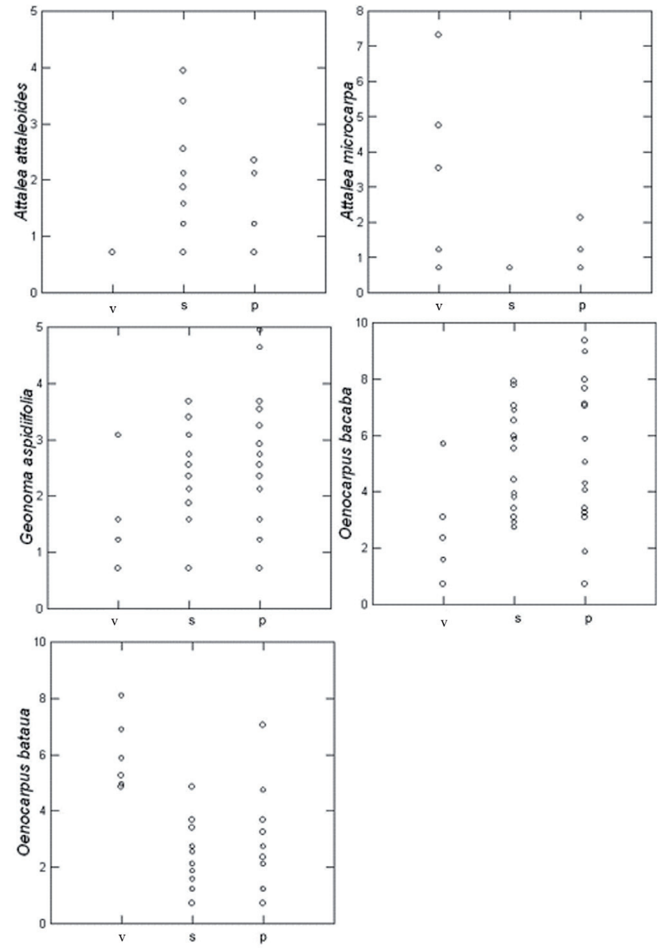

Figure 4. Relationship between seedlings abundance of *Attalea attaleoides, A.microcarpa, Geonoma* aspidiifolia, *Oenocarpus bacaba*, *O. bataua* and the relief. v=valley, s=slope, and p= plateau.

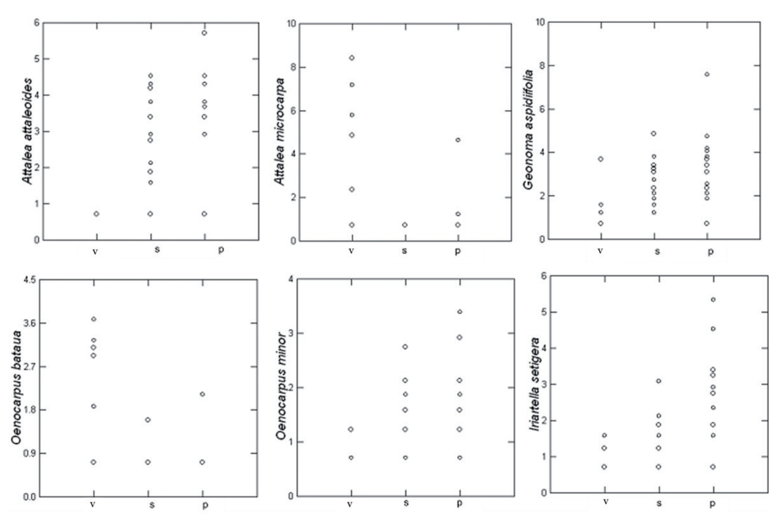

Figure 5. Relationship between adults of *Attalea microcarpa, A. attaleoides, Geonoma aspidiifolia*,Oe*nocarpus bataua O. minor* and *Iriartella setigera* and the relief. v=valley, s=slope, and p= plateau.

port 11 species in 4 ha, where only five palm species represented 98.9% of the community (Kahn and Mejia, 1990). These results indicate the importance of palm population ecology studies in the forest community dynamics.

A previous study performed 45 Km from Ducke Reserve showed that the composition of the palm community differed in relation to the hydrological conditions of the soil (Kahn and Castro, 1985). The authors found that the population density of palms was influenced by the hydromorphic condition and concluded that the higher density near small streams could be related to the high light intensity penetrating the understory in these flooded areas. Similar results were found by Peres (1994) in Terra Firme forest near Urucu River, showing that palm density, including all the species, was higher in less drained areas (81 ind. ha^{-1}) than in well drained areas (36 ind. ha^{-1}).

The changes in species composition, qualitative (seedlings and adults) and quantitative (seedlings), increased significantly in plateau (Figures 6 and 7).

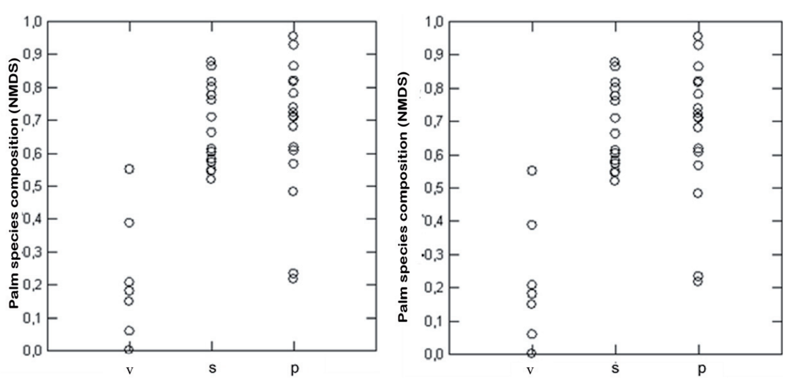

Figure 6. Relationship between qualitative and quantitative composition of seedling and the relief. v=valley, s=slope, and p= plateau.

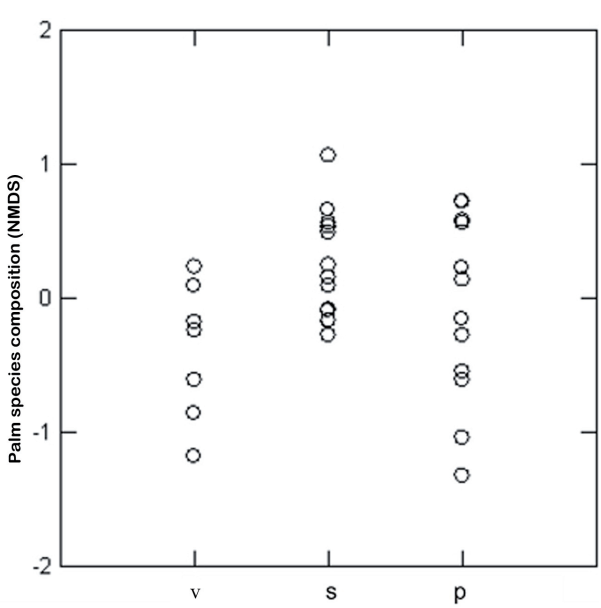

Figure 7. Relationship between qualitative composition of adults and the relief. v=valley, s= slope, and p= plateau.

These flat areas are more exposed to the wind action, which causes tree fall and consequent formation of small clearings and of a gradient of luminosity, probably creating new and different niches and favoring species coexistence (Kahn and Castro, 1985; Kahn, 1986; Gale, 2000; Brokaw and Busing, 2000). Another factor that can be considered favorable to the increase of changes in species composition is the soil type found in plateaus, that is more fertile than the soil of valley and slope areas (Vormisto *et al.,* 2004; Costa *et al*., 2009), where nutrients leaching in the surface horizons is more intense and constant. Since soil conditions are good in plateau areas, competition by space becomes important. However, experiments are still needed to investigate this possibility.

Conclusion

The distribution and abundance of this group of nine palm species, of relatively low ecological density, in the Terra Firme forest of Ducke Reserve, are related to topographic gradients, corroborating previous results of palm communities in the same area. The variation of species composition in different topographic levels probably occurs due to different responses of the species to the environmental heterogeneity of the forest, produced by spatial variation in the abundance of the structural components of the forest. In the context of a complex environment, the topographic gradient certainly contributes for and enables the existence of different ecological niches, favoring the coexistence among species, not only of palms, but also of other organisms, including other groups of plants, invertebrates and vertebrates (Oliveira *et al*., 2008).

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