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
**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 km², of which, 12 km² 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.](image)
Data collection

Abundance data of seedlings and adults were used as dependent variables in Analyses 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.

Statistical Analyses

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 exorrhiza and some others, are relatively well distributed in the Amazon region (Henderson et al., 1999). 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 bataua and adults of Oenocarpus minor and Geonoma aspidifolia 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 aspidifolia, Om=Oenocarpus minor, Ot=Oenocarpus bataua.
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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.

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

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