

# Forest spatial heterogeneity and palm richness, abundance and community composition in Terra Firme forest, Central Amazon

RENATO CINTRA<sup>1,3</sup>, ARIMATÉA DE CARVALHO XIMENES<sup>2</sup>, FÁBIO R. GONDIM<sup>2</sup> and MARCELA S. KROPF<sup>2</sup>

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**ABSTRACT** – (Forest spatial heterogeneity and palm richness, abundance and community composition in terra firme forest, Central Amazon). The mechanisms that maintain tree diversity in tropical rain forests are still in debate. Variations in forest structural components produce forest microenvironmental heterogeneity, which in turn may affect plant performance and have been scarcely analyzed in the Amazon. Palms are widespread in the Neotropical rainforests and have relatively well known taxonomy, apart from being ecologically and economically important. The understanding of how palms respond to variation in the forest structural components may help to explain their abundance and richness in a given area. In this study, we describe a palm community and analyze how it is affected by forest microenvironmental heterogeneity. In a pristine “Terra Firme” forest at Reserva Ducke, Manaus, we recorded all adult palm trees in twenty 100 × 10 m plots. In the same plots we recorded the variation in canopy openness, the leaf litter thickness and counted all non-palm forest trees. A total of 713 individuals in 29 palm species were found. The three most abundant species were *Astrocaryum sciophilum* (Miq.) Pulle, *A. gynacanthum* Mart. and *Attalea attaleoides* (Barb. Rodr.) Wess. Boer. The most locally abundant species were also very frequent or occurred in a larger number of plots. There were no significant effects of litter depth, forest canopy openness and forest tree abundance on palm richness. However, in areas where leaf litter was thicker a significant lower number of palm trees occurred. In microsites where proportionally more incident light was reaching the forest understory, due to higher canopy opening, significantly more palm trees were present.

Key words - Amazonia, canopy openness, leaf litter, palm community, Reserva Ducke

**RESUMO** – (A heterogeneidade espacial da floresta e a riqueza, abundância e composição da comunidade de palmeiras em floresta de terra firme na Amazônia Central). Os mecanismos que mantêm a diversidade de plantas em florestas tropicais estão ainda em debate. Variações nos componentes estruturais da floresta produzem heterogeneidade microambiental na floresta, que por sua vez devem afetar as plantas, e raramente têm sido analisados na Amazônia. As palmeiras são amplamente distribuídas em florestas neotropicais e tem a sua taxonomia bem conhecida, além de sua importância ecológica e econômica. O entendimento de como as palmeiras respondem às variações nos componentes estruturais da floresta pode ajudar a explicar a abundância e a riqueza delas em uma dada área. Neste estudo descrevemos uma comunidade de palmeiras e analisamos como ela é afetada pela microheterogeneidade ambiental da floresta. Em uma floresta de terra firme na Reserva Ducke, Manaus, registramos todas as palmeiras adultas em 20 parcelas de 100 × 10 m. Nas parcelas também registramos a variação na abertura do dossel, a profundidade de folhicho e o número de árvores da floresta. Setecentos e treze indivíduos de 29 espécies de palmeiras foram registrados. As três espécies mais abundantes foram *Astrocaryum sciophilum* (Miq.) Pulle, *A. gynacanthum* Mart. and *Attalea attaleoides* (Barb. Rodr.) Wess. Boer. As palmeiras mais abundantes localmente também foram muito frequentes e ocorreram na maioria das parcelas. Não houve efeito significativo da profundidade de folhicho, abertura do dossel da floresta e abundância de árvores, na riqueza de espécies de palmeiras. Em microsítios com maior profundidade de folhicho ocorreu significativamente menor abundância de palmeiras. Quanto maior a abertura do dossel da floresta, um número significativamente maior de palmeiras estava presente.

Palavras-chave - abertura do dossel, Amazonia, comunidade de palmeiras, folhicho, Reserva Ducke

## Introduction

The mechanisms that maintain tree diversity in tropical rain forests are still in debate by tropical biologists. Many interesting studies have been published on how

forest environmental heterogeneity affects plant richness and distribution in the tropical rain forest. Some studies defend the idea that the high tree richness of tropical rain forests could be a result of stochastic events such as the physical action of tree-fall gaps, which creates space and more illuminated environment for plants to colonize (Brandani *et al.* 1988, Swaine & Whitmore 1988, Condit *et al.* 1996). Because of the similar ability for competition among species to colonize frequent created gaps there will always be a high number of tree species in a given site (Hubbell & Foster 1986).

1. Instituto Nacional de Pesquisas da Amazônia, Departamento de Ecologia, Caixa Postal 478, 69011-970 Manaus, AM, Brasil.
2. Universidade Santa Ursula, Rua Fernando Ferrari 75, 22231-040 Rio de Janeiro, RJ, Brasil.
3. Corresponding author: cintra@inpa.gov.br

Some authors tried to explain plant richness in tropical rain forests based on meso-scale environmental heterogeneity, such as niche differentiation (Ricklefs 1977, Connell 1978, Ashton 1989, Clark *et al.* 1998, 1999) and negative density dependence (Janzen 1970, Clark & Clark 1984, Terborgh *et al.* 1996). However, in any environment most of plant population and community are submitted to a relatively high degree of small-scale environmental heterogeneity (Fowler 1988, Svenning 1999).

Apart from being ecologically and economically important, palms are one of the most abundant, and widespread plant families in Neotropical rainforests and their taxonomy is relatively well known (Gentry 1991, Henderson *et al.* 1995). Palm fruits, seeds and seedlings are consumed both by invertebrates and vertebrates and in some sites, in periods of scarcity of fruits in the forest, palms are among the few available food resources to support vertebrate biomass (Terborgh 1986). In the Amazon region palms have been traditionally used by humans for food and many other purposes including house construction.

Some studies on palm distribution and abundance have been conducted in the Amazon forest to describe plant community distribution in a type of habitat and to compare it among different habitats (Kahn & Castro 1985, Kahn & Mejia 1990). Although studies on distribution and abundance of palms are available, they are still scarce. However, in the Amazon forest the effects of plant community succession (Losos 1995), forest fragmentation and edge effects (Scariot 1999), soil conditions (Peres 1994), leaf litter thickness (Cintra 1997a), tree-fall gap size and distance to the nearest gap (Uhl *et al.* 1988, Cintra & Horna 1997, Svenning 2000), seedling density and distance to the nearest neighbor and adult (Cintra 1997b), vegetation cover and light (Cintra & Terborgh 2000) have been demonstrated to affect palm seedling growth and survival and adult community composition. In the Brazilian Atlantic forest palms density dependence seems to be important only during the seedling stage (Matos *et al.* 1999).

Apart from studies analyzing the effects of forest fragmentation, soil conditions and plant succession (Scariot *et al.* 1989, Peres 1994, Losos 1995) there is scarce information on how variation in the degree of forest environmental heterogeneity affects the palm community.

The forest environmental heterogeneity produced by variation in the amount of incident light (i.e. degree of variation in forest non-tree fall canopy openness), the type of substrate (i.e. spatial variation in the amount of

leaf-litter) and density of other forest tree species may be important in determining where and why a given individual palm tree has successfully established in the forest (Kiltie 1981, Denslow 1987, De Steven 1988, Losos 1995, Cintra 1998, Cintra & Terborgh 2000). The use of these variables to investigate their effects on adults, instead of seedlings, may sound strange because most of the adult palms have established themselves when the forest floor dynamics, in terms of the amount of accumulated leaf litter, could have been different. Even today, leaf litter accumulation is known to vary seasonally and annually (Luizão & Schubart 1987). However, we do not believe that forest conditions would change so fast, in its ecological and evolutionary dynamics, to drastically affect the overall leaf litter accumulation.

Few studies have considered the combined effects of these factors on palm richness and community composition. These factors and many others are components of the forest heterogeneity and the degree of small-scale variation in each may contribute to affect the richness and composition of plant community (Ricklefs 1977). For instance, palm abundance can affect the growth and survival of seedlings of other tree species (Denslow *et al.* 1991), but also can be affected by shading of other tree species. Shading may create good conditions for palm seeds to germinate but bad conditions for seedlings to grow. A recent and excellent review on the role of microenvironmental heterogeneity on palms concluded that, the ecology of neotropical palms is significantly influenced by small-scale environmental heterogeneity, which sometimes leads to more than 30 palm species coexisting in given area (Svenning 1999, 2001). Among the myriad of forest heterogeneities, and since the Cretaceous, the disturbance and edaphic conditions have been advocated to affect palm distribution at small spatial scale as well (Wing *et al.* 1993).

Palm growth and mortality in the “terra firme” forest is very dynamic. There might be a significant range of variation in many forest structural components that could produce forest microenvironmental heterogeneity affecting the palm performance, and their effects on forest plants have been scarcely analyzed in the Amazon (but see Svenning 1999, 2001). The understanding of how palms respond to variation in the forest structural components may help to explain their local abundance and richness. It could also subsidize forest management and conservation actions to use palms in a sustainable way.

In this study we describe a palm community in terms of its components (species richness, abundance and community composition), in a site where access

was just recently created in a “terra firme” forest in Central Amazon. This was a good opportunity to work in a pristine community. As far as we know, in the Brazilian Amazon forest only one study with palms under similar conditions has been done (Peres 1994).

Apart from describing the palm community composition, we wanted to verify whether the most abundant species in a given microsite was also among the most frequent in the area. We also investigated how variations in non-palm forest tree abundance, in the degree of forest canopy openness and in leaf litter depth, affected the palm abundance, richness and community composition.

### Material and methods

The study was conducted during the rainy season (January – February, 2001), at INPA's Reserva Ducke, located 25 km from Manaus (03°08'S and 60°04'W). The Reserve has an area of 10,000 ha. The annual rainfall in the area is about 2,500 mm. Vegetation is a Terra Firme primary tropical rain forest which is never seasonally inundated by river level fluctuations. The soil is a oxisol, and the area has many small streams resulting in a topography of lowlands intercalated with plateaus reaching an altitude up to 140 m (Ribeiro *et al.* 1999).

We recorded all fruiting adult palm trees showing fruits, including those with evidence that have had fruited before (presenting racemes with old and dried fruits still attached), in twenty 100 × 10 m plots separated 200 m from one another along the four sides of a 100 ha block located in the continuous forest on the eastern side of the Reserve. Plots were always located on the right side of the trails and at least 3 m from the trail.

Our study area is part (1/64) of a grid of trails (8 × 8 km) located at 1 km intervals covering 6,400 ha of the whole Reserve. In the 100 × 10 m plots, the number of leaf litter layers was counted at the center and corners of ten 1 m<sup>2</sup> subplots in a transect of 10 × 1 m starting at the beginning of each of the twenty 100 × 10 m plots. The variation in the forest canopy openness was recorded in the same ten subplots using a Spherical Crown Densiometer (Concave - model C - Robert E. Lemonn, Forest Densiometers, 5733 SE Cornell Dr. Bartlesville, OK, USA), and four reading estimates were taken, each oriented towards the cardinal points, east, west, south and north. All forest trees above 5 cm DBH (diameter at breast height) were also counted within each 100 × 10 m plots. Finally, we counted all arborescent and non-arborescent adult palm trees, within the same twenty 100 × 10 m plots. Only individual adult palms were considered, that is, those palms with evidence of reproductive activities (showing recent and/or old fruits). Palms were identified in the field using a book, the field guide of identification for vascular plants of Reserva Ducke (Ribeiro *et al.* 1999) and

the help of one of the book's author, (Assunção, P.A.C.L). Statistical analysis – To verify the effects of the independent variables (i.e. leaf litter depth, forest canopy openness and non-palm forest tree abundance) on the dependent variables (i.e. palm richness and palm abundance) we constructed a multiple regression analysis model for each dependent variable using Systat (Wilkinson 1998). To analyze palm community composition, we used the number of adult palm tree to construct a quantitative data matrix: the rows (objects) are sites - the experimental plots - and the columns (attributes) are the abundance or number of each palm species recorded. Similarities in palm community composition, in the twenty 100 × 10 m plots, were verified by using a multidimensional scaling ordination analysis (MDS). This ordination analysis technique has a test for the significance of the independent variables and shows the relationship between objects in two dimensions. A dissimilarity matrix was constructed using the Bray-Curtis index on the raw data matrix. This index has been highly recommended for use in ecological studies (Minchin 1987, MacNally 1994). The MDS analysis was used to generate a single ordination of palm species within sites (plots) based on the Bray-Curtis distance matrix. The computer program PATN (Belbin 1982) was used to run the ordination multivariate analysis. The Bray-Curtis index is calculated according to the following formula:

$$D = \sum |^{i}d_{ik} - ^{j}d_{jk}| / \sum (^{i}d_{ik} + ^{j}d_{jk})$$

Where,  $^{i}d_{ik}$  = the data value for the  $i^{\text{th}}$  row and  $k^{\text{th}}$  column of the data matrix;  $^{j}d_{jk}$  = the data value for the  $j^{\text{th}}$  row and  $k^{\text{th}}$  column of the data matrix.

Because this index may put more weight on more abundant species, the palm species abundance values in the raw data matrix were standardized by dividing each one by the total of their sum. The resulting MDS1 and MDS2 scores from the ordination analysis were used as dependent variables in a multivariate multiple regression analysis in which model the independent variables were the following: (1) leaf litter depth, (2) forest canopy openness, and (3) abundance of forest trees. Finally, a multivariate and robust test (Pillai-Trace) was used to verify whether changes in palm community composition were significantly affected by the above three independent variables. This analysis was done using the program Systat (Wilkinson 1998).

### Results

A total of 713 individuals of 29 breeding palm species were found in the 20 plots. The three most abundant species were *Astrocaryum sciophilum* (Miq.) Pulle, *Astrocaryum gynacanthum* Mart. and *Attalea attaleoides* (Barb. Rodr.) Wess. Boer. (table 1). *Astrocaryum sciophilum* (Miq.) Pulle was as much as twice more abundant than the second and third more abundant species.

*Bactris elegans* Barb. Rodr. and *Oenocarpus bataua* Mart. were the 4<sup>th</sup> and 5<sup>th</sup> most abundant in the samples (table 1) but these two species had the highest abundance of individuals (25) in a given plot. *Oenocarpus minor* Mart. and *Oenocarpus bataua* Mart., were present in low numbers whenever they occurred, however they were present in about 40% of the sampled plots (table 2). Six palm species (about 20%) were very scarce and occurred only once in the plots surveyed.

In general, the most “locally” abundant species also had a higher “regional” frequency or occurred in a larger number of plots (table 1, figure 1). There was a significant relationship between palm density and the frequency of occurrence in the plots ( $r^2 = 0.51$ ;  $n = 29$ ;  $DF = 1$ ;  $F = 29.173$ ;  $P < 0.0001$ ).

There were no significant effects of litter depth, forest canopy openness and forest tree abundance on palm richness (table 3, figure 2). However, there were significant effects of leaf litter depth and forest

Table 1. Number of individuals, densities, and frequency of reproductive individuals (adult palms) recorded in Terra Firme Forest at Reserva Ducke in the Central Amazon.

| Palm species   | Total number of individuals<br>(a) | Average abundance<br>(adults / 200.1 ha)<br>(a / 20) | Maximum abundance per plot | Frequency* |
|--|------------------------------------|--|----------------------------|------------|
| <i>Astrocaryum sciophilum</i> (Miq.) Pulle   | 193                                | 9.65   | 19                         | 19         |
| <i>Astrocaryum gynacanthum</i> Mart.   | 90                                 | 4.50   | 13                         | 18         |
| <i>Attalea attaleoides</i> Wess. Boer  | 87                                 | 4.35   | 18                         | 17         |
| <i>Bactris elegans</i> Barb. Rodr.   | 76                                 | 3.80   | 25                         | 12         |
| <i>Oenocarpus bataua</i> Mart.   | 44                                 | 2.05   | 25                         | 4          |
| <i>Bactris acanthocarpa</i> Mart. var. <i>humilis</i> Bar. Rodr.                       | 30                                 | 1.40   | 8                          | 10         |
| <i>Geonoma deversa</i> (Poit.) Kunth   | 29                                 | 1.30   | 5                          | 11         |
| <i>Euterpe precatória</i> Mart.  | 20                                 | 1.0  | 9                          | 8          |
| <i>Oenocarpus bacaba</i> Mart.   | 18                                 | 0.95   | 2                          | 11         |
| <i>Oenocarpus minor</i> Mart.  | 18                                 | 0.90   | 3                          | 10         |
| <i>Bactris maraja</i> Mart. var. <i>maraja</i>   | 17                                 | 0.85   | 16                         | 2          |
| <i>Attalea microcarpa</i> Mart.  | 12                                 | 0.60   | 6                          | 2          |
| <i>Bactris gastoniana</i> Barb. Rodr.  | 11                                 | 0.55   | 4                          | 4          |
| <i>Geonoma aspidifolia</i> Spruce  | 10                                 | 0.50   | 5                          | 4          |
| <i>Bactris tomentosa</i> Mart. var. <i>sphaerocarpa</i><br>(Mart.) Henderson           | 11                                 | 0.50   | 4                          | 3          |
| <i>Syagrus inajai</i> (Spruce) Becc.   | 9                                  | 0.45   | 2                          | 6          |
| <i>Socratea exorrhiza</i> (Mart.) H. Wendl.  | 9                                  | 0.45   | 3                          | 5          |
| <i>Iriartella setigera</i> (Mart.) H. Wendl.   | 6                                  | 0.30   | 1                          | 5          |
| <i>Geonoma maxima</i> (Poit.) var. <i>maxima</i>                                       | 6                                  | 0.30   | 3                          | 3          |
| <i>Astrocaryum murumuru</i> Mart. var. <i>ferrugineum</i><br>(Kahn & Millan) Henderson | 5                                  | 0.25   | 2                          | 4          |
| <i>Bactris killipii</i> Burret   | 2                                  | 0.10   | 1                          | 2          |
| <i>Desmoncus polyacanthus</i> Mart.  | 2                                  | 0.10   | 1                          | 2          |
| <i>Bactris acanthocarpa</i> Mart. var. <i>trailiana</i><br>(Barb. Rodr.) Henderson     | 2                                  | 0.10   | 1                          | 2          |
| <i>Bactris hirta</i> Mart.   | 1                                  | 0.05   | 1                          | 1          |
| <i>Bactris simplicifrons</i> Mart.   | 1                                  | 0.05   | 1                          | 1          |
| <i>Geonoma stricta</i> (Poit.) Kunth var. <i>stricta</i>                               | 1                                  | 0.05   | 1                          | 1          |
| <i>Geonoma maxima</i> (Poit.) Kunth var. <i>spixiana</i><br>(Mart.) Henderson          | 1                                  | 0.05   | 1                          | 1          |
| <i>Geonoma maxima</i> (Poit.) Kunth var. <i>chelidonura</i> (Spruce)<br>Henderson      | 1                                  | 0.05   | 1                          | 1          |
| <i>Mauritia flexuosa</i> L.f.  | 1                                  | 0.05   | 1                          | 1          |

\* Number of plots in which the palm species occurred.

Table 2. Abundance of adult palms in terra firm forest at Reserva Ducke, Central Amazon.

| Plot number<br>Palm species*  | 1  | 2  | 3  | 4 | 5  | 6 | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | Total |
|---|----|----|----|---|----|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-------|
| <i>Astrocaryum sciophilum</i> (Miq.) Pulle <sup>1</sup>   | 16 | 18 | 10 | 8 | 11 | 8 | 11 | 2  | 11 | 6  | 19 | 10 | 6  | 16 | 13 |    | 10 | 3  | 11 | 4  | 193   |
| <i>Astrocaryum gynacanthum</i> Mart. <sup>4</sup>   |    | 1  | 4  | 3 | 4  | 3 | 4  | 1  | 2  | 2  | 9  | 13 | 9  | 6  | 2  |    | 9  | 8  | 8  | 2  | 90    |
| <i>Attalea attaleoides</i> Wess.Boer <sup>1</sup>   | 2  |    | 11 | 2 | 3  | 6 | 6  |    | 7  | 5  | 3  | 5  | 4  | 18 | 4  |    | 1  | 3  | 5  | 2  | 87    |
| <i>Bactris elegans</i> Barb. Rodr. <sup>3</sup>   |    | 1  |    | 3 |    | 3 | 25 | 1  | 9  | 7  | 2  | 7  | 11 |    | 3  |    | 4  |    |    |    | 76    |
| <i>Oenocarpus bataua</i> Mart. <sup>5</sup>   | 1  | 2  |    |   |    |   |    | 13 |    |    |    |    |    |    |    | 25 |    |    |    | 3  | 44    |
| <i>Geonoma deversa</i> (Poit.) Kunth <sup>3</sup>   |    |    | 1  | 1 | 3  | 2 | 4  | 4  | 1  | 4  | 1  | 3  | 1  |    |    |    | 5  |    |    |    | 30    |
| <i>Bactris acanthocarpa</i> Mart. var. <i>humilis</i><br>Bar. Rodr. <sup>1</sup>                    | 1  |    |    |   |    | 1 |    |    |    | 3  |    | 3  | 2  | 8  | 2  |    | 2  | 4  | 3  |    | 29    |
| <i>Euterpe precatória</i> Mart. <sup>5</sup>  |    |    | 2  | 2 |    | 1 | 1  | 2  |    |    |    |    | 2  |    |    | 9  | 1  |    |    |    | 20    |
| <i>Oenocarpus minor</i> Mart. <sup>5</sup>  |    | 3  | 2  |   |    |   | 1  |    | 2  | 1  | 2  |    |    | 2  |    |    | 3  |    | 1  | 1  | 18    |
| <i>Bactris maraja</i> Mart. var. <i>maraja</i> <sup>3</sup>   |    |    |    |   |    |   |    |    |    |    |    |    |    |    | 1  | 16 |    |    |    |    | 17    |
| <i>Oenocarpus bacaba</i> Mart. <sup>5</sup>   |    | 1  |    |   | 2  | 1 |    |    | 1  | 1  |    | 1  | 2  | 1  | 1  |    |    |    |    | 1  | 12    |
| <i>Attalea microcarpa</i> Mart. <sup>1</sup>  |    | 6  |    |   |    |   |    |    |    |    |    |    |    |    |    |    |    |    |    | 6  | 12    |
| <i>Bactris gastoniana</i> Barb. Rodr. <sup>2</sup>  |    |    |    |   |    | 4 | 2  |    | 2  |    | 1  |    |    |    | 2  |    |    |    |    |    | 11    |
| <i>Bactris tomentosa</i> Mart. var. <i>sphaerocarpa</i><br>(Mart.) Henderson <sup>2</sup>           | 1  | 1  | 4  | 4 |    |   |    |    | 1  |    |    |    |    |    |    |    |    |    |    |    | 11    |
| <i>Geonoma aspidifolia</i> Spruce <sup>2</sup>  |    | 1  | 2  | 5 |    |   |    |    |    |    |    |    |    |    |    |    |    |    | 2  |    | 10    |
| <i>Syagrus inajai</i> (Spruce) Becc. <sup>5</sup>   |    |    |    |   |    | 2 |    |    |    |    |    | 1  | 2  |    | 2  |    |    | 1  | 1  |    | 09    |
| <i>Socratea exorrhiza</i> (Mart.) H. Wendl. <sup>5</sup>  |    |    |    |   |    |   | 2  | 1  |    |    |    |    |    |    |    | 3  | 2  |    | 1  |    | 09    |
| <i>Iriartella setigera</i> (Mart.) H. Wendl. <sup>4</sup>   | 1  | 1  |    |   | 1  |   |    |    | 1  |    |    | 1  | 1  |    |    |    |    |    |    |    | 06    |
| <i>Geonoma maxima</i> (Poit.) var. <i>maxima</i> <sup>3</sup>                                       |    |    | 2  |   |    | 3 |    |    |    |    | 1  |    |    |    |    |    |    |    |    |    | 06    |
| <i>Astrocaryum murumuru</i> Mart. var.<br><i>ferrugineum</i> (Kahn & Millan) Henderson <sup>4</sup> |    |    | 1  | 2 |    |   |    |    |    |    |    |    |    | 1  |    |    |    |    |    | 1  | 05    |
| <i>Bactris killipii</i> Burret <sup>2</sup>   |    |    |    |   |    |   |    |    |    |    |    | 1  |    |    | 1  |    |    |    |    |    | 02    |
| <i>Desmoncus polyacanthus</i> Mart. <sup>6</sup>  |    |    | 1  |   |    |   |    |    |    |    |    |    |    |    |    |    |    |    |    | 1  | 02    |
| <i>Bactris acanthocarpa</i> Mart.<br>var. <i>trailiana</i> (Barb. Rodr.) Henderson <sup>2</sup>     |    |    |    |   |    |   |    |    |    | 1  | 1  |    |    |    |    |    |    |    |    |    | 02    |
| <i>Bactris hirta</i> Mart. <sup>2</sup>   |    | 1  |    |   |    |   |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 01    |
| <i>Bactris simplicifrons</i> Mart. <sup>2</sup>   |    |    |    |   |    |   |    |    |    |    |    |    |    |    |    |    |    | 1  |    |    | 01    |
| <i>Geonoma stricta</i> (Poit.) Kunth var. <i>stricta</i> <sup>2</sup>                               |    |    |    |   |    |   |    |    |    | 1  |    |    |    |    |    |    |    |    |    |    | 01    |
| <i>Geonoma maxima</i> (Poit.) Kunth<br>var. <i>spixiana</i> (Mart.) Henderson <sup>3</sup>          |    | 1  |    |   |    |   |    |    |    |    |    |    |    |    |    |    |    |    |    | 01 | 01    |
| <i>Geonoma maxima</i> (Poit.) Kunth<br>var. <i>chelidonura</i> (Spruce) Henderson <sup>3</sup>      |    |    |    |   |    |   | 1  |    |    |    |    |    |    |    |    |    |    |    |    |    | 01    |
| <i>Mauritia flexuosa</i> L.f. <sup>5</sup>  |    |    |    |   |    |   |    |    |    |    |    |    |    |    |    | 1  |    |    |    |    | 01    |
| Total   |    |    |    |   |    |   |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 713   |

\* Numbers after scientific names corresponds to palm life forms (1 = subterraneous stems, leaves can reach up to 7m height 2 = understory treelets up to 3 m height 1 cm DAP 3 = understory trees 3-7 m height and 2-5 cm DAP 4 = trees up to 12 m height 4-10 cm DAP 5 = trees up to 25 m height 15-60 cm DAP 6 = Liana; information on palms size were taken from Ribeiro *et al.* 1999).

canopy openness on palm abundance (table 4, figure 3). The abundance of adult palms was inversely related to leaf litter depth. However, palm abundance was directly related to canopy openness.

Finally, the results of multivariate multiple regression analyses indicated that there were no significant effects of leaf litter depth (Pillai Trace Test = 0.147; P = 0.304), canopy openness (Pillai Trace = 0.256; P = 0.109) or

forest tree abundance (Pillai Trace = 0.065; P = 0.606) on palm community composition.

## Discussion

The pattern of species richness and abundance found in this study confirmed what was found in general for tree communities in the Amazon forest. Some species

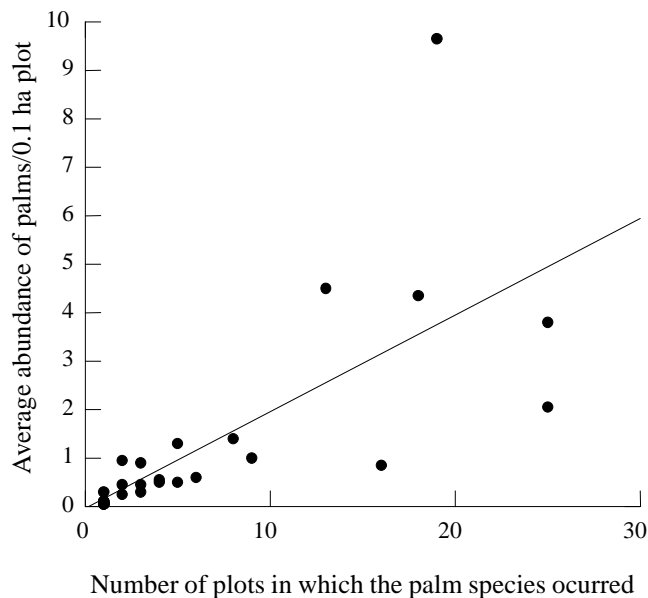


Figure 1. Relationship between palm density and frequency of occurrence in twenty 0,1 ha plots (the equation is  $y = -0.633x + 0.315$ , see also result section) in a Terra firme forest, Reserva Ducke, Manaus.

were “rare” or occurred in low abundance “locally” but they were relatively frequent “regionally” or occurred in many of the sampled plots, and few species are very abundant.

In the Peruvian Amazon, Pitman *et al.* (1999) recorded trees species in 21 plots totaling 36 hectares within an area of 400 km<sup>2</sup>. They found 825 tree species, with about 88% of them at densities of < 1 individuals/ha. They concluded that most trees species in the region were habitat generalist and widely distributed over Amazon Region.

Kahn *et al.* (1988) comparing palm community composition in eastern, central and western Amazon forest found palm species richness to be high in western site and in “terra firme” forests which was dominated by understory palm species under 10 m in height. In their own words, “the largest and one of the most diversified palm communities of the world is mainly represented by small understory species”. They found that adult arborescent palm are very uncommon in “terra firme” forest but the opposite was true for seasonal swamp forests (Kahn *et al.* 1988). The same author studying palms in wetland forest in the lower Ucayali valley in Peru found 11 species in a 4 ha plot, with five of them representing 98.9% of the community (Kahn & Mejia 1990).

We found that the five most abundant species represented 68.7% of the community sampled (tables 1, 2). These differences in palm abundance between our study and Kahn’s study could be because our area is a non-flooded “terra firme” forest and had more than twice the number of palm species. Even some species adapted to survive well in occasionally flooded forest or along forest streams such as *Socratea exorrhiza* (Mart.) H. Wendl., *Mauritia flexuosa* L.f. occurred in very small number in our plots.

Scariot *et al.* (1989) studying palms in a seasonal swamp in eastern Amazon found eight palm species with 3,975 individuals in an area of one hectare. They found that just one species *Orbignya phalerata* Mart. (= *Attalea speciosa* Mart. = *Attalea glassmanii* Zoua) represented 60% of this individuals and it occurred in great density in less humid areas. The authors suggested that the dominance of this species in the area could be due to high light intensity as a limiting factor and not

Table 3. Results of the multiple regression analysis of the effects of litter depth, forest canopy openness and forest tree abundance on Palm richness in Terra Firme forest, Reserva Ducke, Manaus ( $R^2 = 0.112$ ).

| Effect          | Coef   | Std. Error | Std. Coef. | Tolerance | t      | P     |
|-----------------|--------|------------|------------|-----------|--------|-------|
| Constant        | 9.421  | 3.246      | 0.000      | –         | 2.903  | 0.010 |
| Litter depth    | -0.248 | 0.227      | -0.291     | 0.782     | -1.093 | 0.290 |
| Canopy openness | -0.057 | 0.297      | -0.051     | 0.766     | -0.191 | 0.851 |
| Tree abundance  | 0.014  | 0.053      | 0.063      | 0.953     | 0.262  | 0.797 |

| Analysis of Variance |                |    |             |         |       |
|----------------------|----------------|----|-------------|---------|-------|
| Source               | Sum-of-Squares | DF | Mean-Square | F-ratio | P     |
| Regression           | 6.572          | 3  | 2.191       | 0.674   | 0.580 |
| Residual             | 51.978         | 16 | 3.249       |         |       |

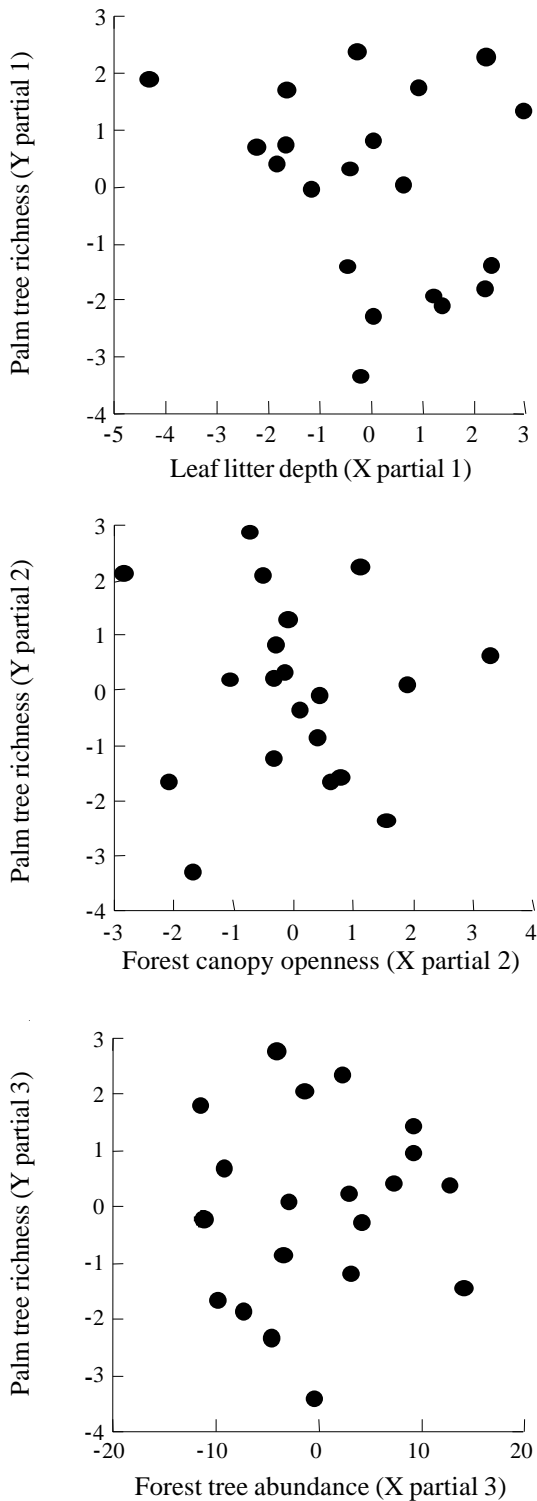


Figure 2. Partials of the multiple regression analysis on the effects of leaf litter depth (A), forest canopy openness (B), and forest tree abundance (C) on the dependent variable Palm richness. The partials resulted from the analysis presented in the table 2. Some numbers in the axis have negative values because the partial regression represents the deviation of the expected results if all other independent variables are hold constant in their observed means.

A water, because the seedlings were less abundant near the water.

The number of palm species recorded in our study is relatively high considering the area sampled (20,000 m<sup>2</sup>). We registered 29 palm species corresponding to 52% of the species occurring in the 10,000 ha area of the Reserva Ducke (Ribeiro *et al.* 1999). Our results were similar to those in a study conducted earlier at another INPA reserve, located 45 km from Reserva Ducke, in which 32 palm species were found in 1.2 ha (Kahn & Castro 1985).

We found *Astrocaryum sciophilum* (Miq.) Pulle, *A. gynacanthum* Mart. and *Attalea attaleoides* (Barb. Rodr.) Wess. Boer, to be the three most abundant palms in our area (table 1). *Astrocaryum sciophilum* (Miq.) Pulle was by far the most abundant and it occurred as much as twice as the second and third most abundant species. Two palm species, *Oenocarpus minor* Mart. and *O. bataua* Mart., were in low number wherever they occurred, however they were present in about 40% of the sampled plots (table 2). This suggests that *Oenocarpus* palms are relatively rare in a given microsite but they can occur in extensive areas in the forest and therefore tolerant to some degree of variation in the meso-scale forest heterogeneity conditions. It may also indicate that the microsites for these two species to establish are patchy in our area. This environmental heterogeneity may favor the local coexistence of such a high number of palm species (Svenning 2001).

Some of the palm species recorded in our survey *Astrocaryum sciophilum* (Miq.) Pulle, *A. gynacanthum* Mart., *Attalea attaleoides* (Barb. Rodr.) Wess. Boer, *Oenocarpus bataua* Mart., *Euterpe precatória* Mart., *Socratea exorrhiza* (Mart.) H. Wendl., *Mauritia flexuosa* L.f., and some others, are relatively widely distributed in the Amazon region in areas distant and can be found more than 1,000 km from our study site (Henderson 1995). Their relatively large range of occurrence suggests that these species may be very tolerant to a large variation in a gradient of environmental conditions of light incidence, soil, nutrient, humidity, and topographic levels. More studies surveying plots scattered throughout the region are needed to verify how the isolated and combined effects of these factors at large spatial scale affect palm distribution and variation in their community composition. Studies considering large spatial scale samples would also help to verify how strong the relationship is between local and regional plant diversity in the Amazon.

In tropical rain forest both leaf litter cover and leaf litter depth contribute to microenvironmental

Table 4. Results of the multiple regression analysis of the effects of litter depth, forest canopy openness, and forest tree abundance on Palm abundance in Terra Firme forest, Reserva Ducke, Manaus. ( $R^2 = 0.427$ )

| Effect            | Coef   | Std. Error | Std. Coef. | Tolerance | t      | P     |
|-------------------|--------|------------|------------|-----------|--------|-------|
| Constant          | 52.150 | 16.141     | 0.000      | –         | 3.231  | 0.005 |
| Leaf litter depth | -2.491 | 1.127      | -0.473     | 0.782     | -2.211 | 0.042 |
| Canopy openness   | 4.174  | 1.476      | 0.611      | 0.766     | 2.827  | 0.012 |
| Tree abundance    | -0.353 | 0.261      | -0.262     | 0.953     | -1.350 | 0.196 |

| Analysis of Variance |                |    |             |         |       |
|----------------------|----------------|----|-------------|---------|-------|
| Source               | Sum-of-Squares | DF | Mean-Square | F-ratio | P     |
| Regression           | 957.536        | 3  | 319.179     | 3.973   | 0.027 |
| Residual             | 1285.414       | 16 | 80.338      |         |       |

heterogeneity and are spatially unpredictable even at scales of few meters (Molovsky & Augspurger 1992, Cintra 1997a). In the Reserva Ducke, the microsite variation in leaf litter depth did not affect palm species richness, however it was inversely related to palm abundance, suggesting that palms are in higher numbers in areas of shallow leaf litter. The spatial variation in the amount of leaf litter and other forms of litter affect palm survival during the early stages of plant establishment probably by protecting from predation for both, seeds from large-seeded palms in microsites with thick litter (Cintra 1997a) and small-seeded palms in areas of thin litter layer (Svenning 2001).

The variation in the degree of canopy openness was directly related to palm abundance (table 4). More palms were found in microsites bearing larger canopy openness than in those microsites with small canopy openness. This is a result we would expect because where there is more canopy discontinuity, there will be more light penetration down to the shaded understory and more palms will be favoured after establishing in microsites under this conditions. These conditions would be more important for canopy palm species such as *Oenocarpus bataua* Mart. In Ecuador it has been recently showed that some understory palm species of the genus *Prestoea* and *Geonoma* showed preference for microsites with relatively high gap exposure (Svenning 2000). In Peruvian Amazon forest *Astrocaryum* seedling survival was found to be positively related to the amount of incident light (Cintra & Terborgh 2000). Forest architecture or the number of forest tree layers is also important and has been demonstrated to affect palm abundance in the Amazon (Kahn 1987). In our results the lack of effect of forest

tree abundance on palm richness and abundance could be due to mass effects produced by the high tree species diversity (Shmida & Ellner 1984).

In another site, 45 km from our study area a previous study (Kahn & Castro 1985) on palm community found that the palm community differed in relation to soil hydromorphic conditions. There was a distinct palm community composition in upland forest (well drained soils), in what they called transition zone (poorly drained soils), and in seasonal swamp forest (water-logged soils). The authors found that palm population density was also affected by hydromorphic conditions and concluded that their highest density could be due to greater light intensity penetrating in the understory of the open swamp forest.

Similar results were found by Peres (1994) in terra firme forest near the Urucu River, who showed that the palm density including all species was greater in areas of poorly drained (81 individual/ha) than on well-drained, high forest soils (36 individuals/ha).

Microenvironmental topographic heterogeneity also can affect palm distribution and community composition at large spatial scale. Within an area of about 9,000 ha, a gradient of palm species was found to clearly follow a gradient in changes of relief at the Reserva Ducke (Lima, A.P. unpublished data).

Some results of our study confirmed, as early studies did, that palms are a very abundant group of plants in the Amazonian forest. They also suggest that variation in palm densities in the Amazon are not only related to changes in edaphic conditions, as most of the studies showed before, but can be also related to spatial changes in the variation of forest canopy openings and amount of leaf litter.



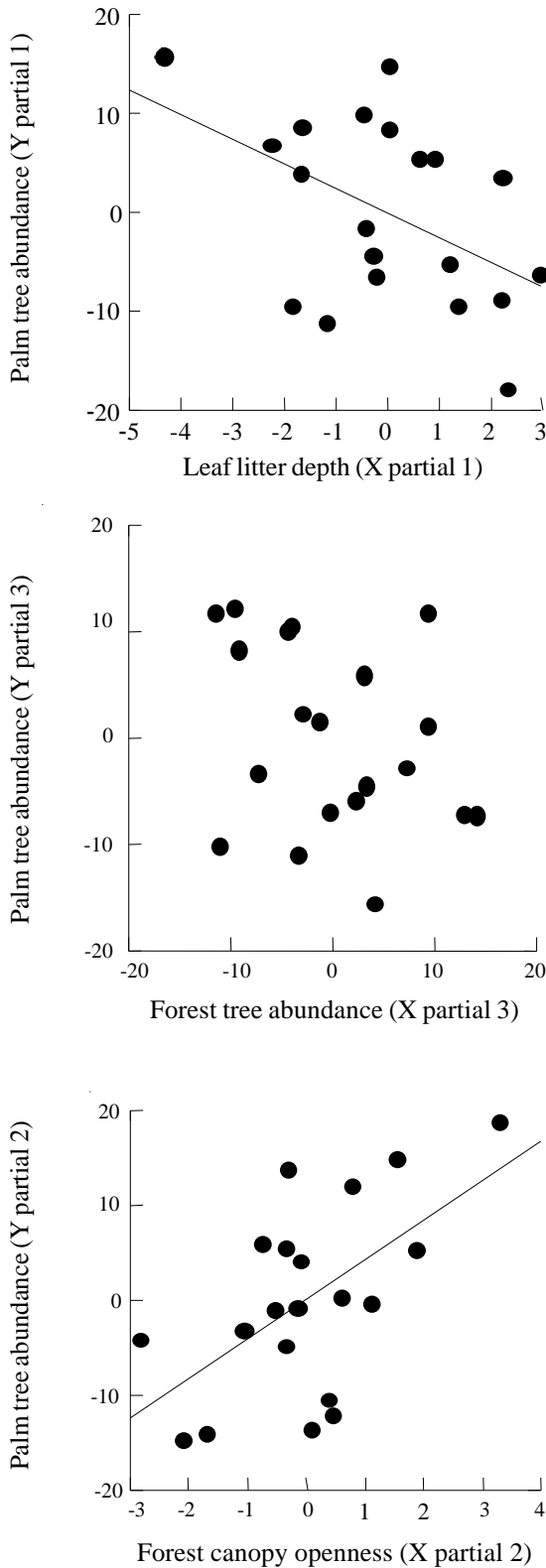


Figure 3. Partials of the multiple regression analysis of the effects of leaf litter depth (A), forest tree abundance (B), and forest canopy openness (C) on the dependent variable Palm abundance. The partials resulted from the analysis are presented in the table 3.

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