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Tree species diversity in a seasonally-dry forest: the case of the Pinkaití site, in the Kayapó Indigenous Area, southeastern limits of the Amazon[1].

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ABSTRACT

This study investigates patterns of forest structure and tree species diversity in an anthropogenic palm grove and undisturbed areas at the seasonally-dry Pinkaití research station, in the Kayapó Indigenous Area. This site, managed by the Conservation International do Brasil, is the most southeastern site floristically surveyed in the Amazon until now. The secondary and a nearby undisturbed forest were sampled in a group of 52 floristic plots of 0.0625-ha (25x25-m) where all trees with DBH ⩾ 10 cm were measured and identified. The analyses were complemented with other two floristic plots of 1-ha (10x1000-m). The present study has shown that the Pinkaití, like other seasonally-dry forests, have great heterogeneity in forest structure and composition, associated with biotic characteristics of the most important tree species, natural disturbance and history of land-use. The palm grove, moderately dominated by the arborescent palm *Attalea maripa* (Aubl.) Mart., presented high tree species diversity and was floristically similar to undisturbed forests at the study site. It is discussed the importance of large arborescent palms for the seasonally-dry Amazon forests regeneration.

KEY WORDS
Amazon, anthropogenic forest, arborescent palms, floristics, tropical forests.

Diversidade de espécies arbóreas em uma floresta sazonalmente seca: o caso da base de pesquisas do Pinkaití (PA), na Terra Indígena Kayapó, limite sudoeste da Amazônia

RESUMO

Este estudo compara a florística e estrutura e a diversidade de espécies arbóreas de um palmeiral antropogênico e áreas não perturbadas na floresta sazonalmente seca da base de pesquisas ecológicas do Pinkaití, na Terra Indígena Kayapó. Esta base de estudos, administrada pela Conservation International do Brasil, é a área mais ao sudoeste até o momento floristicamente amostrada na Amazônia. Uma mancha de floresta secundária e uma floresta não perturbada adjacente foram amostradas com um grupo de 52 parcelas de 0,0625-ha (25x25-m) onde todas as árvores com DAP ⩾ 10 cm foram medidas e identificadas. As análises foram complementadas com outras duas parcelas de 1-ha (10x1000-m). Este estudo mostrou que o Pinkaití, como outras florestas sazonalmente secas, tem grande heterogeneidade na estrutura e composição da floresta, associada com características bióticas das espécies arbóreas mais importantes, perturbação natural e histórico de uso do solo. O palmeiral, moderadamente dominado pela palmeira arborescente Attalea maripa *(Aubl.) Mart., apresentou alta diversidade de espécies arbóreas e é floristicamente semelhante às florestas primárias da área de estudos. É discutida a importância de palmeiras arborescentes de grande porte no processo de regeneração das florestas amazônicas sazonalmente secas.*

PALAVRAS-CHAVE
Amazônia, florística, floresta antropogênica, floresta tropical, palmeiras arborescentes.

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INTRODUCTION

The variety of seasonal forests that occur in the Amazon are difficult to define and grade continuously from dense to open and from evergreen to seasonally-dry forests. Dense forests, characterised by a rather uniform 25 to 45 m high continuous and evergreen canopy, with sparse emergent trees, frequently taller than 50 m, dominate wetter areas (>2500 mm rainfall per year). This is the dominant physiognomy in the central Amazon where the dry periods are relatively weak, and is frequently found in isolated patches along the transitional region. Semi-deciduous and deciduous forests occur in patches through the gradient between evergreen forests and savannah. Open forests, distinguished by the greater discontinuity of the canopy, are more frequently found in transitional zones, where savannahs gradually replace the forest (RADAM, 1974; Pires, 1984; Prance & Brown, 1987; Daly & Prance, 1989).

Seasonally-dry transitional forests, spread along the northern and southern limits of the Amazon basin, are connected by a large NW-SE arch which receives less than 2000 mm of rain annually. Their distribution coincides with one third of the Amazon that repeatedly experiences strong seasonal droughts (Nimer, 1977; Nepstad *et al.*, 1999). The Amazon forest extends as far as climate and edaphic constraints allows, and portions of its periphery show different types of transitional vegetation to extra-Amazonian floras and physiognomies. In general, the transitional forests of the northern Amazon are characterised by rather abrupt transitions from dense forest to savannah whereas the southern perimeter usually shows mosaic-like transitions involving semi-deciduous and liana forests (RADAM, 1974; Daly & Prance, 1989).

The transitional forests at the latitudinal limits of the Amazon lay upon the Precambrian shield of Guiana in the north and the Brazilian or Guaporé shield in the south (Putzer, 1984). Along the edges of the Amazon basin there are still intact sedimentary Precambrian plateaus and the vast majority of the highly weathered soils have been developing for over 20 million years from sediments derived from the rocks of the shields (Irion, 1978; Jordan, 1987). These regions show a variety of topographies, with numerous small elevations and are geologically more diverse than the core of the Amazonian intracratonic depression (Daly & Prance, 1989). Rivers dissecting these areas have well-defined beds, stable banks, and often form rapids, which mark the interface of the lower basin with the crystalline shields (Sioli, 1984).

For a long time, transitional forests have been considered as a distinct formation within the Amazon, although this notion has been changing historically (Daly & Prance, 1989). The strong presence of *Attalea phalerata* Mart. ex Spreng. (Babassu palm) and *Bertholletia excelsa* Humb., Bonpl. & Kunth (Brazil-nut) along the southeastern periphery of the Amazon was recognised early on, and considered as a distinct forest physiognomy denominated “zona dos cocaes” (Sampaio, 1945). More recently, forests with canopies highly entangled by lianas, and having a generally low basal area (18-24m^2.ha^{-1}), were described as “liana forests” (Pires & Prance, 1985).

The high a-diversity is one of the most distinctive ecological characteristics of tropical rain forests (Richards, 1996; Whitmore, 1990), especially the Amazon forests (Gentry, 1988). The Amazon forests have a large number of rare species and a few dominant (5-15) contributing up to 50% of the individuals (Pires & Prance, 1985). However, because plant a-diversity and annual rainfall across the Neotropics tend to be highly correlated, the local tree species richness in the transitional, seasonally-dry forest is expected to be generally lower than their equivalents in wetter areas of the Amazon (Gentry, 1988). But their composition often varies in a very complex way, even within areas of few hectares or less in extend, resulting in a high b-diversity (Oliveira & Mori, 1999; Richards, 1996). In the Amazon forest, large-scale variations both in the structure and the floristic composition seem to be chiefly determined by basin-wide variation in rainfall seasonality, but locally, geomorphology and hydrology play important roles (Gentry, 1988; Araújo *et al.*, 1999; Campbell *et al.*, 1986; Fearnside, 1999).

Nevertheless, physiognomic characteristics such as open canopy, low basal areas, large profusion of lianas and high abundance of pioneer tree species that typify a large part of the transitional Amazon forest have been interpreted as relics of anthropogenic activity and disturbance by pre-Columbian societies (Ballée & Campbell, 1990). Numerous monodominant forest enclaves of 2-3 ha of *Attalea* spp. in the Brazilian States of Pará and Maranhão are often associated with old human settlement sites and these species are usually considered good indicators of ‘anthropogenic forests’ (Balée, 1988, 1989). Indeed, large arborescent palms are among the most frequently noted disturbance indicators of Amazonian archaeological sites, and the vast palm forests, which cover almost 200,000 km^2 of the Brazilian Amazon, appear to be an artefact of intense human disturbance and use of the forest (May *et al.*, 1985).

The aim of this study is to investigate forest structure and composition variation, identifying patterns of tree species diversity within an anthropogenic palm grove, locally called *palmeiral*, and undisturbed areas at the Pinkaití research station, a seasonally-dry forest site on the Kayapó Indigenous Area, Southern Pará, Brazil. To identify spatial patterns of forest heterogeneity, detrended correspondence analysis (DCA) was conducted with 52 plots of 0.0625-ha (25x25m) spread along transects intercepting the *palmeiral* and a nearby, undisturbed, forest.

MATERIAL AND METHODS

Study site

The Pinkaití Research Station (7° 46’18"S; 51° 57’42"W), managed by the NGO Conservation International do Brasil (CI-Brasil) is located at the municipality of Ourilândia do

Norte, Southern Pará, Brazil (Fig 1a). It was build at the border of the Riozinho river (or Anfrísio's Little River in some maps), a second-order tributary of the upper Xingu River, within the Kayapó Indigenous Area (3,284,005 ha). This area, contiguous with other eight contiguous indigenous areas form a continuous block of indigenous lands, with a great variety of indigenous peoples, which spans over more than 14 million ha in Pará and Mato Grosso (ISA, 2000).

The Kayapó, originally distributed along the Tocantins and Araguaia Rivers, since the beginning of the XIX century started shifting towards the Xingu river basin due to growing conflicts with the Brazilian national society, until their pacification in the decade of 1950 (Turner, 1999). Kayapó Indigenous Area protects a unique and vulnerable Amazonian forest type poorly represented in existing nature reserves. Several endangered vertebrate species typical of the seasonally-dry, transitional Amazonian forests were recorded at relatively high densities within this area (Nascimento, 1999).

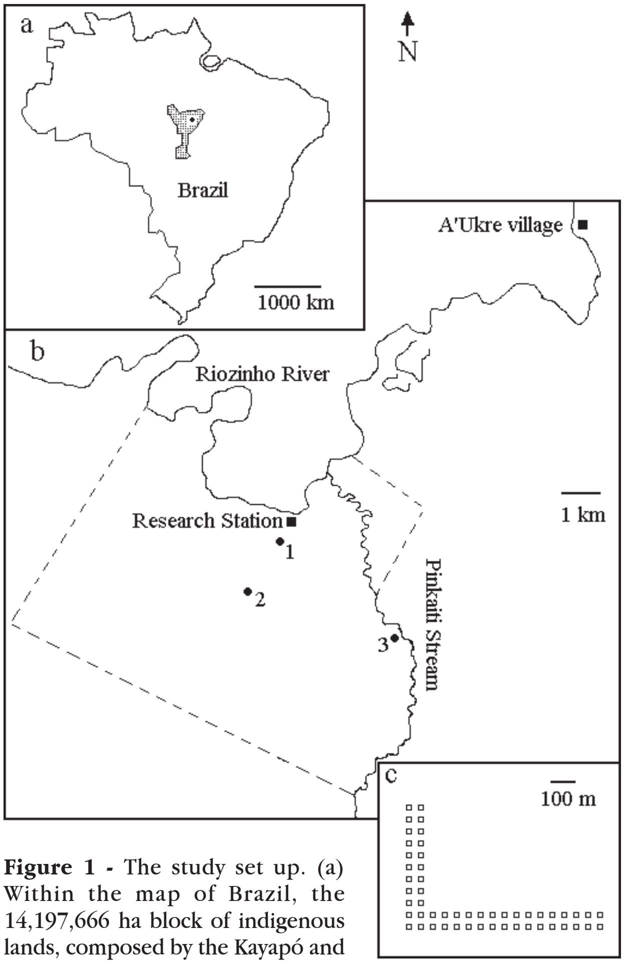

Figure 1 - The study set up. (a) Within the map of Brazil, the 14,197,666 ha block of indigenous lands, composed by the Kayapó and the contiguous Badjonkore, Baú, Capoto/Jarina, Menkragnoti, Paraná, Batovi, Wawi and Parque do Xingu; the black dot indicates the Pinkaití site position (ISA, 2000; adapted). (b) The biological research station area; the numbers indicate the position of "1" the 52 0.0625-ha (25x25-m) floristic plots, "2" the Brazil-nut grove and "3" the Pinkaití stream 1-ha (1000x10-m) plots from C. Baider's (2000). (c) Distribution of the 52 0.0625-ha (25x25-m) plots.

In 1992, the Pinkaití project was initiated at the request of the leadership of the Kayapó Indian village of A'Ukre, which controls approximately 310,000 ha of forests and savannah, with the objective of providing economic alternatives to logging and protecting a population of mahogany trees. The Kayapó committed themselves to do not hunt or log in an area close to 10,000 ha, where the biological research station was set (Zimmerman *et al.*, 2001).

The climate is tropical dry, with monthly temperatures ranging between 25 and 27°C (Holdridge, 1967; Salati & Marques, 1984). At the forest management farm Marajoara, 130 km on a straight line of the Pinkaití, annual precipitation between 1995 and 2001 ranged from 1636 to 2170 mm, with >90% falling between November and May; in some years no rain fell for 3-4 moths during the dry season (Grogan, 2001). Following a westward gradient of increasing pluviosity in Eastern Amazonia (Nimer, 1977), the climate in the Pinkaití is slightly wetter with average rainfall close to 2200 mm yearly.

Geologically, the study site lies within the pre-Cambrian crystalline shield of Brazil. Elevation ranges from 200 to 450 m above sea level and the relief is irregular, characterised by rolling slopes that are interrupted by granitic outcrops. Rocky ridges throughout the area are 100-250 m in altitude (RADAM, 1974). The soils distribution patterns follow predictable sequences across topographic relief with gray or bleached-white sandy profiles predominating on low ground adjacent to the lowest order seasonal streams and dense dark red clays found at higher elevations, often mixed with lateritic gravel (Grogan, 2001).

In the rainy season, the water level rises up to 7 m in Riozinho river (Baider, 2000); for long periods, thereafter, large floodplain areas are found and remain under more than a meter of water, usually for few days.

The RADAM Project (1974), with vegetation maps produced with the use of radar imagery and field inventories still provides the most comprehensive description of the studied area. The Pinkaití station area is approached in the volume 4 (FOLHA SB.22 ARAGUAIA E PARTE DA FOLHA SC.22 TOCANTINS), within the map Gorotire (SB.22-Y-D). The Gorotire region is highly representative of the vegetation mosaics of the southern Amazon known as dry belt archway. The forest at the study site is structurally heterogeneous, consisting of easily distinguishable types that form mosaics of dense forest (mostly insular in residual plateaus) and open forest (in isolated patches or bottomlands), including extensive areas of liana forest (*sensu* Pires & Prance, 1985). Woodland and grassland savannahs are more concentrated to the east, following the rainfall gradient. Patches of grassland savannah at this site also seem to coincide with edaphic conditions that are unfavourable to forest cover (RADAM,

1974) and their distribution seems to be affected by fires occasionally started by the Kayapó Indians. Approximately 15 % of an 80 x 80 km area (640,000 ha) centred around the A'Ukre's village is savannah, distributed largely on a few upland plateaus (Malcolm *et al.*, 1999). During dry periods of the Pleistocene and during a dry post-Pleistocene episode when the forests of the upper and lower Amazon had been divided by a corridor of grassy savannah running more or less across the Pinkaití site region (Haffer, 1969).

C. Baider (2000) estimated the Pinkaití tree species a-diversity with two 1-ha (10x1000m) quadrats set up in tall open forest type, and found that it is low, if compared to more aseasonal sites elsewhere in the Amazon (Gentry, 1988). One of them was located within a Brazil-nut (*Bertholletia excelsa* Humb., Bonpl. & Kunth) grove (hereafter, Brazil-nut grove plot), approximately 3 km inland from Riozinho River and had 594 trees of 102 species. The other crossed a forest along a permanent river valley (from now on, Pinkaití Stream plot) and had 540 individuals of 98 species (Fig 1b).

Floristic plots

To compare patterns of tree species diversity within an anthropogenic forest and undisturbed areas at the Pinkaití, was selected a palm grove that, according to the Kayapó, was cleared for subsistence crops (*roças*), in the first half of last century. A member of A'Ukre community, Beptoti Pompe, related that when his father, the old chief Tiquiri was young, the Kayapos displaced a group of *caboclos* (probably rubber-tapers) who lived on the area now occupied by the research station.

As the old Kayapó are illiterate and did not know to count the years, it is difficult to precise exactly when these Indians occupied the Riozinho River valley, displacing the *caboclos* that lived where today is the Pinkaití Research station. However, iron tools found in the palm grove testify its former occupation and the conflict with the *caboclos* is recalled by the oldest members of A'Ukre village. Their fields were, probably, similar to those found around A'Ukre village, where *terra firme* (= unflooded) forest patches of a few hectares, are periodically cleared, mainly for the cultivation of manioc, corn, beans, yam and sweet potatoes (Morsello, 2002). Some of these cops are still occasionally found in the immediacy of the Pinkaití station's houses. The proximity of the research station with the probable site occupied by the Brazilians that lived in this area is not incidental, since this is one of the rare land patches along the Riozinho river that do not flood at the top of the rainy season.

Departing from a point more or less in the centre of the palm grove dominated by the large arborescent palm *Attalea maripa* (Aubl.) Mart., 52 plots of 0.0625-ha (25x25-m) were set, distant at least 25 m from each other, established along two orthogonal transects. The first transect was 600 m in length and progressed northwards towards the Riozinho River. The other was 800 m in length, extended to the east, crossing an undisturbed area with low palm density, visibly dominated by the legume tree *Cenostigma tocantinum* Ducke, locally known as *pau-preto* (Figure 1c).

In all quadrats, all trees reaching diameter ≥ 10 cm at 1.3 m height were measured to the nearest millimetre, and the height of all trees (upper crown) was visually estimated. Samples were taken for almost all individuals except the very easily identifiable ones, like *Bertholletia* or palms. Field identification was performed in the field by Mr. M. R. Cordeiro, and confirmation at IAN Herbarium (from Embrapa Amazonia Oriental, Belém), where all material has been deposited.

Data analysis

Correspondence analysis was carried out using CANOCO for Windows 4.0. The ordination arranges the floristic plots as points in a scatter diagram in an ecologically structured way. Data points that are close together correspond to plots that are compositionally similar, whereas those that are farther apart are more dissimilar. Species are also represented as points, and those that tend to occur in the same plots, converge in the scatter plot, whereas those that occur in different plots appear farther apart. If species are plotted on the same diagram of floristic quadrats, they tend to appear near the quadrats where they are most abundant (Jongman *et al.*, 1995).

To reduce the importance of rare species, whose distributions are difficult to explain ecologically and could weaken the overall ordination results (Jongman *et al.*, 1995), only tree species with more than 10 individuals were included in the analysis. This procedure resulted in the selection of only 29 out of a total of 175 tree species. To strengthen the interpretation of the Detrended Correspondence Analysis, 52 randomly assorted samples of 6,25% of the Brazil-nut grove and Pinkaití were selected and incorporated in the analyses.

For the fitossociological analysis of the Pinkaití site, four different areas were considered: (1) the palm grove, with 24 0.0625-ha plots and (2) the *pau-preto* forest, with 28 0.0625-ha plots, whose distinction was observed in the field and confirmed by the ordination analysis of tree species abundance and composition (see below), the (3) The Brazil-nut grove and the (4) Pinkaití Stream 1-ha plots, from C. Baider (2000). To describe the structure of the main populations of the four areas, were calculated importance value index (IVI), Shannon diversity and similarity indices (Whittaker, 1972; Pielou, 1975).

RESULTS

The scatter-diagram from the DCA confirmed the separation of the 24 0.0625-ha plots from the palm grove plots from the 28 0.0625-ha plots in the adjacent *pau-preto* forest. The plots of the anthropogenic palm grove were clustered with the 52 randomly assorted samples of the Brazil-nut grove and Pinkaití the stream forest (Fig 2). In contrast, Sorensen Similarity Index indicated that the

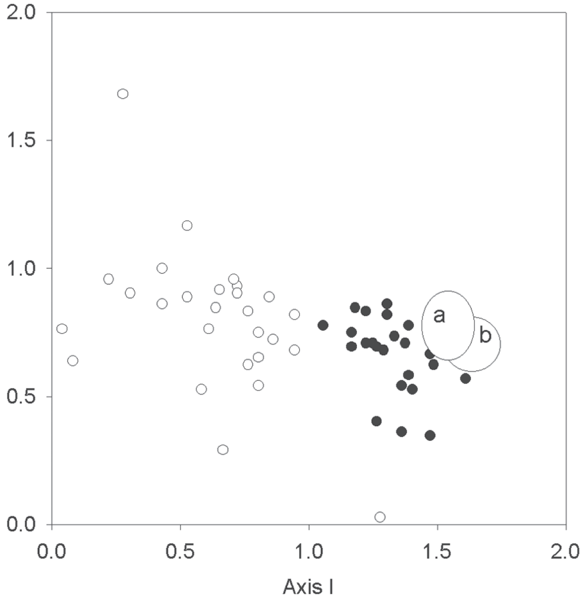

Figure 2 - Detrended Correspondence Analysis ordination of floristic plots. Solid and open circles represent the palm grove and the *pau-preto* forest plots (0.0625-ha), respectively. The areas delimited by "a" and "b" mark the distribution of 52 randomly assorted samples of 6,25% of the Brazil-nut grove and Pinkaití stream plots, respectively. DCA axis 1 and 2 explained 25.6 % and 5.4 % of variation in species data, respectively (length of gradient 2.271 and 1.675 SD-units).

composition of the palm grove is more similar to the adjacent *pau-preto* forest than to the Brazil-nut grove and the Pinkaití stream forest (Table 1).

The palm *Attalea maripa* (Aubl.) Mart. was the most important species in the palm grove, followed by *Metrodorea flavida* Krause (Rutaceae), *Tetragastris altissima* (Aubl.) Swart (Burseraceae), *Theobroma speciosum* Willd. Ex Spreng. (Sterculiaceae) and *Protium subserratum* (Engl.) Engl. (Burseraceae). The *pau-preto* forest is strongly dominated by *pau-preto* trees (*Cenostigma tocantinum* Ducke, Leguminosae), followed in importance by *T. altissima*, *M. flavida*, *A. maripa* and *Cheiloclinium cognatum* (Mierc.) A.C. Smith (Hippocrateaceae). In both the Brazil-nut grove and Pinkaití the stream forest, *T. altissima* was the most important species. It is followed by *Astronium gracile* Engler (Anacardiaceae), *M. flavida*, *T. speciosum* and *Brosimum lactescens* (S. Moore) C. C. Berg (Moraceae) in the Brazil-nut grove and *M. flavida*, *Pouteria trilocularis* Cronq. (Sapotaceae), *Trichilia quadrijuga* Kunth (Meliaceae) and *B. lactescens* in the Pinkaití stream forest. The Shannon diversity index indicated that the Palm grove was, floristically, the most diverse area, followed by the Pinkaití Plot, the Brazil-nut grove and the *pau-preto* forest (Table 2).

All plots showed that Leguminosae, including the families Fabaceae, Mimosaceae and Cesalpiniaceae, was the most species-rich family. The Rutaceae, mostly represented by the understorey tree *M. flavida* is almost ubiquitous across all *terra firme* forest plots. At the palm grove, the Rutaceae was the family with the highest number of stems, followed by the Leguminosae and Palmae. At the *pau-preto* forest, Leguminosae was the most abundant family, chiefly represented by *C. tocantinum*. The Burseraceae and Rutaceae were the second-ranking families in number of individuals, mainly represented by *T. altissima* and *M. flavida*, respectively. In both the Brazil-nut and Pinkaití Stream plots, the Burseraceae was the most abundant family, chiefly represented by *T. altisissima* (Fig 2).

The palm grove had, by far, the lowest basal area, followed by the Brazil-nut grove, the *pau-preto* forest and the Pinkaití Stream Plot. The palm grove had the same median tree height as the *pau-preto* forest, substantially lower than the Brazil-nut grove and the Pinkaití Stream Plot (Table 3). The 24 0.0625-ha plots of the palm grove, compared to the adjacent 28 plots at the *pau-preto* forest had significantly lower basal area (Mann-Whitney U, $p<0.001$). However, no significant difference was found between the median height of these forest plots (Mann-Whitney U, $p=0.646$).

Table 1 - Floristic similarities estimated with the Sorensen Similarity Index, among the four considered areas at the Pinkaití, Southern Pará, Brazil.

	***pau-preto* forest**	**Brazil-nut grove***	**Pinkaití Plot***
Palm grove	0.590	0.449	0.449
pau-preto forest	-	0.505	0.505
Brazil-nut grove		-	0.495

* C. Baider (2000).

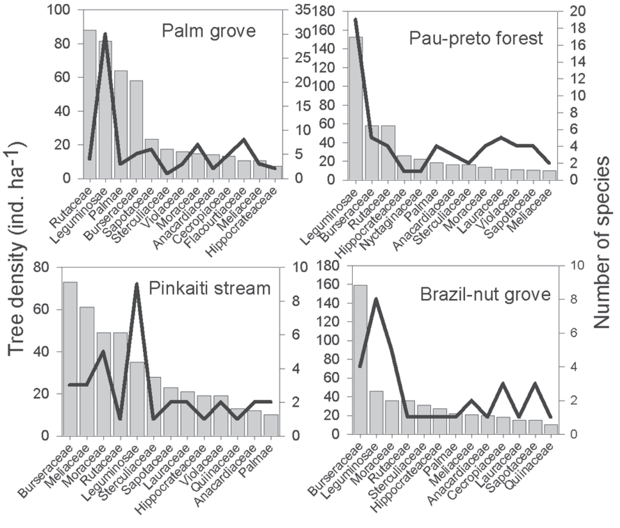

Figure 3 - Rank of family abundance in relation to density and species richness at the four study areas. Solid lines indicate number of species and bars indicate stem densities.

DISCUSSION

The findings of this study show that at the Pinkaití forest, like in other seasonally-dry Amazonian forests (RADAM, 1974; Gentry, 1988), a relatively small group of species, can occasionally become dominant in the tree community. The comparison of the palm grove with the adjacent *pau-preto* forest, the Brazil-nut grove, and the Pinkaití stream plots revealed that this palm dominated forest in an advanced stage of regeneration, floristically resembles the undisturbed areas of the Pinkaití Research Station. The successional nature of the palm grove is evident on the relative importance of the most abundant species and on the structure of this forest patch.

Large arborescent palms are generally rare in Amazonian dense, *terra firme* forests, where large palm trees are chiefly restricted to areas with high levels of natural or anthropogenic disturbance (Spruce, 1871; Kahn and Castro, 1985; Kahn *et al.*, 1988; Kahn and Granville, 1992; Ballée, 1988, 1989). The evidence from this study agree with others that found *Attalea maripa* to appear on sites of previous human disturbance (Pesce, 1985). The large arborescent palm *A. maripa* is the most important tree species in the palm grove, with 53 individuals per hectare. The palm was the second species in number of trees, after the Rutaceae *Metrodorea flavida*. Its higher percentage of IVI resulted mainly from the larger diameter of the palm's stem. The Sorensen Similarity Index indicated that the palm grove is floristically similar to the adjacent undisturbed *pau-preto* forest. The main compositional difference between these areas was mainly related to the strong dominance of *Cenostigma tocantinum* in the latter. Both the Brazil-nut grove and the Pinkaití Plots are moderately dominated by the Burseraceae *Tetragastris altissima.* Indeed, closed-canopy forests throughout the whole Gorotire region (7º 00 S-8º 00 S; 51º 00W-52º 30'W), where the study site is inserted, are largely dominated by *T. altissima* (RADAM, 1974).

The Shanon Diversity Index indicated that the tree species community of the palm grove is even more diverse than that of the Pinkaití river valley, among the undisturbed sites, the most diverse compared area. The Brazil-nut grove was intermediate in tree species diversity and the lowest values were found in the *pau-preto* forest.

The high tree species diversity of the palm grove forest might result from the advanced stage of forest succession and the environmental heterogeneity created by the *caboclos* that lived in this area. The area abandonment allowed the forest succession to proceed, with the

Table 2 - Forest composition at the four study areas considered at the Pinkaití site, Southern Pará, Brazil. For each area, are presented the 5 tree species with the highest importance value index (In parenthesis is the species percentage of IVI) and the Shannon diversity index.

	Palm grove	*pau-preto* forest	Brazil-nut grove*	Pinkaití Plot*
1st Species in IVI	*Attalea maripa* (14%)	*Cenostigma tocantinum* (29%)	*Tetragastris altissima* (15%)	*Tetragastris altissima* (8%)
2nd Species in IVI	*Metrodorea flavida* (10%)	*Tetragostris altissima* (8%)	*Astronium gracile* (4%)	*Metrodorea flavida* (5%)
3rd Species in IVI	*Tetragastris altissima* (4%)	*Metrodorea flavida* (7%)	*Metrodorea flavida* (10%)	*Pouteria trilocularis* (4%)
4th Species in IVI	*Theobroma speciosum* (3%)	*Attalea maripa* (5%)	*Theobroma speciosum* (3%)	*Trichilia quadrijuga* (4%)
5th Species in IVI	*Protium subserratum* (3%)	*Cheiloclinium cognatum* (4%)	*Brosimum lactescens* (3%)	*Brosimum lactescens* (3%)
Shannon Index	3.95	3.17	3.75	3.84

* C. Baider (2000).

Table 3 - Forest structure at the four study areas considered at the Pinkaití site, Southern Pará, Brazil. For each area, are presented the median tree DBH, median three Height and basal area per hectare.

	Palm grove	*pau-preto* forest	Brazil-nut grove*	Pinkaití Plot*
Median DBH	*14.8 cm*	*16.7 cm*	*16.2 cm*	*17.7 cm*
Median Height	*11 m*	*11 m*	*17 m*	*18 m*
Basal area	*15 m^2 .ha^{-1}*	*27 m^2 .ha^{-1}*	*24 m^2.ha^{-1}*	*40 m^2.ha^{-1}*

* C. Baider (2000).

development of pioneers, and their gradual replacement for late successional species dispersed from the undisturbed surrounding forest. High diversity have been related to intermediate levels of disturbance in widely different ecosystems like rainforests and coral reefs (Connell, 1978).

Among the forest plots, the DCA ordination indicated that the most floristically distinctive plots are those in the *pau-preto* forest, that also had the lowest diversity of tree species among the compared areas. The results are explained by the high dominance, both numeric and in terms of the total basal area, of the legume tree *C. tocantinum*. This species is typically restricted to large river edges in the study area, which is consistent with the local distribution of *Cenostigma* spp. elsewhere in the Xingu River basin (Campbell *et. al*, 1986). These species have great sprouting capacity and large hollow trunks that frequently dismount, giving "birth" to new trees, which, utilising resources from the original tree, can develop well in shaded areas. The palm grove, despite being a few hundred meters from the main perennial river of this area, never floods due to the proximity to an isolated mount by the river. In contrast, the *pau-preto* forest, further away from the mount is affected by flash floods that create the competitive conditions for *C. tocantinum* dominance.

In the southeastern limits of the Amazon, the Pinkaití research station is just a few kilometers from a large savannah patch on an upland plateau (Malcolm *et al.*, 1999), similar to the *cerrado* of Central Brazil (RADAM, 1974). The relatively high tree species diversity of the Pinkaití Stream Plot was expected and is consistent with the observation that in the Amazon there is a strong positive correlation between precipitation and community level plant species richness (Pires & Prance, 1985; Gentry, 1988; Campbell *et al.*, 1986; Daly & Prance, 1989). The benevolent environmental conditions created by the humidity of the Pinkaití River valley probably allowed the maintenance of the tropical rainforest while most of surrounding areas was replaced for open formations. Today, such humidity allows the maintenance of an evergreen forest at the valley while the forest in most of the research station area suffers from different levels o water stress and leaves shading (Baider, 2000).

Seasonally-dry Amazonian forests are typically characterised by high structural heterogeneity compared to more aseasonal forests of the central-western Amazon (Pires & Prance, 1985; Daly & Prance, 1989). The results presented here show that the Pinkaití forest is, structurally, highly variable, and these are conservative given that more open vegetation types occurring in the wider study area, such as vegetation associated with rock outcrops, were not sampled. The basal area of the Stream Plot (39.9 $m^2.ha^{-1}$) was the highest recorded in a sample of 14 one-hectare floristic plots spread across the Eastern Amazon (Baider, 2000).

The successional nature of the palm grove is evident on the structure of this forest patch. Its basal area is extremely low (15 $m^2.ha^{-1}$), significantly lower than that of the adjacent *pau-preto* forest. Such basal area is even lower than the limits (18-24 $m^2.ha^{-1}$) considered for liana forests (Pires & Prance, 1985). The average height of the palm grove forest, on the other side, is not significantly different from the adjacent forest.

With the *caboclo's* displacement and the abandonment of their crop fields, succession probably proceeded in this large forest gap as it does in large gaps in the region. In a first phase, grasses and bamboos rapidly form thick mats that hinder the growth and survival of mature forest species. Furthermore, lianas, using the structure of trees as support, severely suppress tree growth and survival (RADAM, 1974). Forest succession progresses to a second phase with the establishment and growth of large arborescent palms, chiefly *A. maripa* but also *Astrocaryum aculeatum* G. Mey , *Socratea exorrhiza* (Mart.) H.Wendl. and *Oenocarpus distichus* Mart. Palm trees are often spared in the process of trees felling for forest clearance, not only due to their utility for humans but also because of the hardness of their stem that makes their felling extremely laborious (Kahn & Granville, 1992).

At the Pinkaití, *A. maripa* seeds are avidly consumed, and dispersed, by agoutis (*Dasyprocta agouti*) particularly during the dry season, when alternative food resources are scarce (Jorge, 2000). Furthermore, large quantities of *A. maripa* seeds are often found in tapir (*Tapirus terrestris*) dung piles (Salm, 2002). Both the seed dispersors are relatively abundant at the Pinkaití where agoutis and tapirs are found at densities of 43.34 and 0.62 individuals per km^2 (Peres, 2000). As a result, *A. maripa* seedlings are virtually ubiquitous across this site, being found in the *pau-preto* forest at densities of approximately 10,000 per hectare (Salm, 2002).

Furthermore, a particularity of the *Attalea* stem development is the remote-tubular seedling development. After germination, the seedling stem has a positive geotropism characterised by the growth of a descending subterranean stem before ascending to develop the above-ground trunk (Bondar, 1964). Therefore, the underground palm stems are not easily destroyed by fire, which gives them an enormous advantage as a pioneer in burnt areas and to persist under severe disturbance regimes (Henderson *et al*., 1995).

In full-light conditions, the growth in height of *A. maripa* is relatively rapid and the stem of these palms can reach 8-m height aboveground in 16.5 ± 2.8 (S.D.) years after its emergence (Salm, 2004). During this phase, the canopy height is gradually raised and the canopy closes, reducing the light that reaches the juveniles. Palms are self-limiting because their regeneration is hampered by the shadow produced by adult palms. With the reduction of light in the understorey, liana recruitment becomes less frequent and their negative impact on the trees diminishes, liberating the trees to develop further. With the tree growth and the palm senescence, and replacement, the forest tends to progress to the mature stage.

The forests at the Pinkaití research station have great heterogeneity in composition and structure, associated with topography, soils and drainage (RADAM, 1974; Malcolm *et* *al.*, 1999; Baider, 2000). Beside habitat condition, the present study has shown that such differences are associated with biotic characteristics of the sampled population and history of land-use. Further studies of large arborescent palms distribution are necessary to shed additional light into the ecological consequences of human disturbance and their potential role for restoration of degraded areas within the seasonally-dry Amazonian forests.

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LITERATURE CITED

Araújo, T. M.; Higuchi, N.; Júnior, J. A. D. 1999. Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Pará, Brazil. *Forest Ecology and Management*, 117(1-3): 43-52.

Baider, C. 2000. *Demografia e ecologia de dispersão de frutos de* Bertholletia excelsa *Humb. Bonpl. & Kunth (Lecythidaceae) em castanhais silvestres da Amazônia Oriental*. Tese de Doutorado, Departamento de Ecologia/ Universidade de São Paulo, São Paulo. 252p.

Ballée, W. 1988. Indigenous Adaptation to Amazonian Palm Forests. *Principes*, 32(2): 47-54.

Ballée, W. 1989. The Culture of Amazonian Forests. *Advances in Economic Botanic*, 7: 1-21.

Ballée, W.; Cambell, D. G. 1990. Evidence for the successional status of liana forest (Xingu river basin, Amazonian Brazil). *Biotropica*, 22: 36-47.

Bondar, G. 1964. *Palmeiras do Brasil*. Instituto de Botânico de São Paulo, São Paulo, 2: 1-159.

Campbell, D. G.; Daly, D. C.; Prance, G. T.; Maciel, U. N. 1986. Quantitative ecological inventory of *terra firme* and Várzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia*, 38(4): 369-393.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302-1310.

Daly, D. C.; Prance, G. T. 1989. Brazilian Amazon. *In:* Campbell, D. G.; Hammond, H. D. (Eds.). *Floristic inventory of tropical countries.* New York Botanical Garden, New York. p. 401-426.

Fearnside, P. M. 1999. Forests and global warming mitigation in Brazil: opportunities in the Brazilian forest sector for responses to global warming under the "clean development mechanism". *Biomass and Bioenergy*, 16(3): 171-189.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, 75: 1-34.

Grogan, J. 2001. *Bigleaf Mahogany in Southeast Pará, Brazil, a Life History Study with Management Guidelines for Sustained Production form Natural Forests*. Ph.D. Thesis, Yale University, Yale. 422p.

Haffer, J. 1969. Speciation in the Amazonian forest birds. *Science*, 165:131-137.

Henderson, A.; Galeano, G.; Bernal, R. 1995. *Field Guide to the Palms of the Americas*. Princeton University Press, Princeton. 376p.

Holdridge, L. R., 1967. *Life Zone Ecology*. Tropical Science Centre, San José, Costa Rica. 206p.

Irion, G. 1978. Soil infertility in the Amazon. *Naturwissenschaften*, 65: 515-519.

ISA. 2000. *Povos Indígenas no Brasil 1996/2000.* Ricardo C. A. (Ed.). Instituto Socioambiental, São Paulo. 832p.

Jongman, R. H. G.; ter Braak, C. J. F. 1995. *Data analysis in community and landscape ecology.* Cambridge University Press, Pudoc, Wageningen. 321p.

Jordan, C. F. 1987. Soils of the Amazon forest. *In:* Whitmore, T. C.; Prance, G. T. (Eds.). *Biogeography and Quaternary history in tropical Latin America*. Oxford University Press, Oxford. p. 83-94.

Kahn, F.; Castro, A. 1985. The Palm Community in a Forest of Central Amazonia, Brazil. *Biotropica*, 20: 266-269.

Kahn, F.; Mejia, K.; Castro, A. 1988. Species Richness and Density of Palms in Terra Firme Forests of Amazonia. *Biotropica*, 20: 266-269.

Kahn, F.; Granville, J. 1992. *Palms in forest Ecosystems of Amazonia*. Springer Verlag, New York. 226p.

Malcolm, J.; Zimmerman, B.; Calvacanti, R.; Ahern, F.; Pietsch R. W. 1999. Use of RADARSAT in the design and implementation of sustainable development in the Kayapó Indigenous Area, Pará, Brazil. *Canadian Journal of Remote Sensing*, 24: 360-366.

May, P. H.; Anderson, A. B.; Balick, M; Frazão, R. R. 1985. Subsistence Benefits from Babassu Palm (*Orbignya martiana*). *Economic Botany*, 39: 113-129.

Morsello, C. 2002. *Market Integration and Sustainability in Amazonian Indigenous Livelihoods: the Case of the Kayapó*. Ph.D. Thesis, School of Environmental Sciences/ University of East Anglia, Norwich, England. 301p.

Nascimento, H. S. 1999. *Hunting sustainability by the Kayapó Indians of A'Ukre, eastern Brazilian Amazonia*. M.Sc. thesis, University of East Anglia, Norwich. 122p.

Nepstad, D. C.; Veríssimo, A.; Alencar, A.; Nobre, C; Lima, E.; Lefebvre, P.; Schlesinger, P.; Potter, C.; Moutinho; P.; Mendoza, E.; Cochrane, M.; Brooks, V. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398(6727): 505-508.

Nimer, E. 1977. *Clima*. *In:* IBGE. *Geografia do Brasil Vol. I. Região Norte.* Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro. p. 39-58.

Oliveira, A. A.; Mori S. A. 1999. A central Amazonian *terra firme* Forest: high species richness on poor soils. *Biodiversity and Conservation*, 8: 1219-1244.

Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology*, 14: 240-53.

Pesce, C. 1985. *Oil palms and other Oil Seeds of the Amazon*. Michigan, Algonac. 200p.

Pires, J. M. 1984. *The Amazon forest*. *In:* Sioli, H. (Ed.). *The Amazon: limnology and landscape ecology of a mighty tropical river and its basin.* Dr. W. Junk Publishers, Dordrecht. p. 581-601.

Pielou, E. C. 1975. *Ecological diversity*. Wiley and Sons, New York. 165 p.

Pires, J. M.; Prance, G. T. 1985. Vegetation types of the Brazilian Amazonia. *In*: Prance, T.; Lovejoy, T.E. (Eds.). *Key Environments: Amazonia.* Pergamon, New York. p. 109-145.

Prance, G. T.; Brown, K. S. 1987. The principal vegetation types of the Brazilian Amazon. *In:* Whitmore, T.C.; Prance, G. T. (Eds.). *Biogeography and Quaternary history in tropical America*. Claredon Press, Oxford. p. 66-104.

Putzer, H. 1984. The geological evolution of the Amazon basin and its mineral resources. *In:* Sioli, H. (Ed.). *The Amazon. Limnology and landscape ecology of a mighty tropical river*. Dr. W. Junk Publishers, Dordrecht. p. 15-46.

RADAM 1974. *Projeto RadamBrasil*. Folha SB22 Araguaia e parte da folha SC 22 Tocantins. Rio de Janeiro, Instituto Brasileiro de Geografia e Estatística.

Richards, P. W. 1996. *The tropical rain forest*. Cambridge University Press, Cambridge. 575p.

Salati, E.; Marques, J. 1984. Climatology of the Amazon region. *In:* Sioli, H. (Ed.). *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River*. Dr. W. J. Junk Publishers, Boston, USA, pp. 85-126.

Salm, R. 2002. *The ecology of two large arborescent palms,* Attalea maripa *and* Astrocaryum aculeatum *in a seasonally-dry Amazonian Forest*. M.Sc. thesis, University of East Anglia, Norwich. 233p.

Salm, R. 2004. Densidade do caule e crescimento de *Attalea maripa* e *Astrocaryum aculeatum*: implicações para a distribuição de palmeiras arborescentes na floresta Amazônica. *Biota Neotropica*. 4 (1):

http://www.biotaneotropica.org.br/v4n1/pt/abstract?article+BN00104012004

Sampaio, A. 1945. *Fitogeografia do Brasil*. São Paulo, Companhia Editora Nacional. 372p.

Sioli, H. 1984. The Amazon and its main affluents: Hydrography, morphology of the river types. *In:* Sioli, H. (Ed.). *The Amazon: limnology and landscape ecology of a mighty tropical river and its basin.* Dr. W. Junk Publishers, Dordrecht. p.127-166.

Spruce, R. 1871. Palmae Amazonicae. *Botanical Journal of the Linnean Society* 11: 65-183.

Turner, T. 1999. Indigenous Rights, Environmental Protection and the struggle over forest resources in the Amazon: the case of the Brazilian Kayapo. *In:* Conway, J.; Keniston, K; Marx, L. (Eds.). *Earth, Air, Fire and Water: the Humanities and the Environment*. University of Massachusetts Press, Boston. p.226-261.

Whitmore, T.C. 1990. *An introduction to tropical forests*. Clarendon Press, Oxford. 226p.

Whittaker, R. H. 1972. Evaluation and Measurement of Species Diversity. *Taxon*, 21: 213-251.

Zimmerman, B.; Peres, C. A.; Malcolm, J. R.; Turner, T. 2001. Conservation and Development Alliances with the Kayapó of South-eastern Amazonia, a Tropical Forest Indigenous People. *Environmental Conservation,* 28(1): 10-22.

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