Cross-scale determinants of palm species distribution

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ABSTRACT

We investigate palm species distribution, richness and abundance along the Mokoti, a seasonally-dry river of southeastern Amazon and compare it to the patterns observed at a large scale, comprising the entire Brazilian territory. A total of 694 palms belonging to 10 species were sampled at the Mokoti River basin. Although the species showed diverse distribution patterns, we found that local palm abundance, richness and tree basal area were significantly higher from the hills to the bottomlands of the study region, revealing a positive association of these measures with moisture. The analyses at the larger spatial scale also showed a strong influence of vapor pressure (a measure of moisture content of the air, in turn modulated by temperature) and seasonality in temperature: the richest regions were those where temperature and humidity were simultaneously high, and which also presented a lower degree of seasonality in temperature. These results indicate that the distribution of palms seems to be strongly associated with climatic variables, supporting the idea that, by 'putting all the eggs in one basket' (a consequence of survival depending on the preservation of a single irreplaceable bud), palms have become vulnerable to extreme environmental conditions. Hence, their distribution is concentrated in those tropical and sub-tropical regions with constant conditions of (mild to high) temperature and moisture all year round.

KEY-WORDS

Amazon, diversity, moisture, palms, tropical forests.

Determinantes meta-espaciais da distribuição de palmeiras

RESUMO

Investigamos a distribuição, riqueza e abundância de espécies de palmeiras ao longo do Rio Mokoti, um rio sazonalmente seco do sudoeste da Amazônia, comparando posteriormente os resultados com os padrões observados em uma escala espacial mais ampla, englobando a totalidade do território brasileiro. Um total de 694 palmeiras pertencentes a 10 espécies foi amostrado na bacia do Rio Mokoti. Apesar das espécies terem mostrado padrões de distribuição diversos, a abundância e riqueza de palmeiras, além da área basal das árvores, foram significativamente superiores nas baixadas do que nas serras da região estudada, revelando uma forte influência de umidade sobre estes parâmetros. A análise englobando a escala espacial mais ampla também mostrou uma forte influência de pressão de vapor (uma medida de umidade do ar, modulada por temperatura) e sazonalidade sobre a temperatura: as regiões cuja riqueza de palmeiras foi mais alta foram aquelas onde a temperatura e a umidade foram simultaneamente altas, e que apresentaram menor sazonalidade na temperatura. Estes resultados indicam que a distribuição de palmeiras parece estar fortemente associada a fatores climáticos, apoiando a idéia de que ao adotar uma estratégia em que "todos os ovos são colocados em uma mesma cesta" (conseqüência da sobrevivência depender da preservação de um único broto insubstituível), as palmeiras tornaram-se vulneráveis a condições ambientais extremas. Desta forma, estas têm sua distribuição concentrada naquelas regiões tropicais e subtropicais com condições constantes tanto de temperatura (amenas a altas) como de umidade ao longo do ano.

PALAVRAS-CHAVE

Amazônia, diversidade, umidade, palmeiras, florestas tropicais.

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INTRODUCTION

Explaining the high diversity of plant species in wet lowland tropical forests is a major challenge for ecologists, who have explored the potential influence of factors ranging from climate (Gentry, 1982;1988) and chance (Hubbell, 1979) to niche specialization (Terborgh, 1985; Svenning, 2001) on the high number of species in these areas. In the Amazonian region there is a general increase in plant-species richness with increasing precipitation (Gentry, 1982; 1988), and palms seem to follow this trend (Svenning, 2001).

The family Arecaceae, with approximately 2800 species and high morphological diversity, constitutes one of the best-known tropical families of flowering plants (Tomlinson, 1979). Although possessing a wide range of ecological adaptations (Uhl & Dransfield, 1987), an extreme vulnerability to climatic hazards is found among palms, a consequence of their general constitution as "solitary perennating bud", with no "reserve buds" - if the apex is injured, the whole shoot dies (Richards, 1996). Globally, low temperatures seem to be the major climatic restriction for the distribution of the family, as most species are found throughout the tropical and subtropical region, with very few occurring in temperate areas (Uhl & Dransfield, 1987). Within the tropics, however, moisture appears to play a more important role. Palms are absent from deserts and semi deserts, with the exception of where groundwater is near the surface, showing a strong preference for wet habitats, where they may be dominants (Tomlinson, 1979). The paucity of palm species in Africa as compared to that in the Neotropical region and southeastern Asia exemplifies this, having been explained as a consequence of the history of drought of that continent - a possibility supported by the relatively high diversity of palms in the adjacent and moister Madagascar (Moore, 1973).

Remarkably diverse palms communities, with up to 34 species within 21 genera, are found in "terra-firme" (unflooded) forests in the Peruvian Amazon (Kahn & Mejia, 1991). Palm species diversity hits its highest point in "terra-firme" forests of wetter central and western Amazonian lowlands, decreasing eastwards towards the seasonally-dry Amazonian forests. Diversity also seems to be lower in those forests frequently subject to flooding, although some palm species are noticeably abundant in such regions as well as in the network of valleys weathered by small rivers draining the plateaus of the Amazon, where soils are permanently waterlogged and inundations occur irregularly during the rainy season (Kahn & Castro, 1985; Kahn & de Granville, 1992).

Within this framework, the aim of this work was two-fold: firstly, to contribute to the understanding of the climatic determinants of palm richness and distribution both at a local and regional spatial scale. Secondly, by using the climatic model obtained at the regional scale, to explain the regional richness of palms, we generate a predictive map in which palm richness is estimated at a global scale.

MATERIAL AND METHODS

LOCAL PATTERNS OF PALM DISTRIBUTION

The Pinkaití Research Station (7° 46'S; 51° 57'W), managed by the NGO Conservation International of Brazil (CI-Brasil), is located at the Kayapo Indigenous Land, municipality of Ourilância do Norte, PA, Brazil. The research station comprises an area of 10,000 ha within the territory of A'Ukre village, where the native indigenous population has committed to stopping any hunting or logging activities to enable the development of scientific research in an undisturbed area of seasonally-dry forest within one of the most degraded regions of the Amazon (Zimmerman et al., 2001).

The climate in the study region is tropical dry, with monthly temperatures ranging from 25 to 27 ºC (Holdridge, 1967; Salati & Marques, 1984). At the forest management farm Marajoara, 130 km far from the Pinkaití Station, annual precipitation between 1995 and 2001 ranged from 1636 to 2170 mm, with more than 90% falling between November and May (Grogan, 2001). Following a westward gradient of increasing pluviosity in the Eastern Amazon (Nimer, 1977), the climate in the Pinkaití is slightly wetter; with average annual rainfall indexes close to 2200 mm.

The forest at the study site (RADAM, 1974) 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 unfavorable 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) centered on the A'Ukre's village is savannah, distributed largely along a few upland plateaus (Malcolm et al., 1999). A corridor of grassy savannah running more or less across the Pinkaití site region divided the forests of the upper and lower Amazon during dry periods of the Pleistocene and during a dry post-Pleistocene episode (Haffer, 1969).

The structure of palm communities, species composition and abundance, and the forest structure (basal area and number of trees) in the hills, uplands and bottomlands of the Pinkaití Research Station were studied in respectively three regions: at the spring, at an intermediate position and at the mouth of the Mokoti, the main river that crosses the area (Figure 1a). The Mokoti river source is at 281 m above the sea level. The river

extends along a meandering course for 8347 m until reaching the left margin of the Pinkaití river at 254 m altitude. The soil distribution patterns along the river follow predictable sequences across the topographic relief, with sandy profiles predominating on bottomlands, dense dark red clays found in uplands, often mixed with lateritic gravel in the hills (Grogan, 2001). In the bottomlands the soil becomes soaked and this area is occasionally affected by flash floods at the height of the rainy season, while the uplands and hills remain unflooded throughout the year.

Due to the morphological and demographic diversity of the studied palms, different criteria had to be used to assign individuals of different groups of species to the adult class. First, among those species that develop a subterranean stem (which emerges to the surface with its approximated maximal diameter) the individual palms with an external and visible stem were considered as adults. Secondly, among the arborescent palms, whose stems grow externally in diameter, we considered those individuals with diameter at breast height (DBH) $\geq$ 5 cm. It is important to stress, however, that by using this criteria we may consider individuals that have not reached sexual maturity yet. Therefore, although the data is appropriate to the analysis of the distribution of palm species in the region, it may not be suitable for the analysis of the local structure of palm populations. Finally, among abundant clonal species, those genets that revealed signs of present or past reproductive activity were counted as adults.

One group of ten plots of 600 m^2 (60 x 10 m) was established at the hills, another at the uplands and another at the bottomlands of the Pinkaití site. Within each plot all palms were identified and counted and all trees with DBH $\geq$10 cm measured. To capture a wide and standardized range of edaphic conditions within the areas, the plots were centered at bends of the river, being 10 m wide at both river margins and extending for 30 m inland - parallel to the main curve axis - in both sides of the river (total plot extension = 60 m; see Figure 1b). To reduce the effect of environmental variation associated to the transitions from the hills to the uplands and bottomlands, while still preserving the independence of the sampling units, within each area the plots were set in river bends that were as close as possible to one another, provided they did not overlap (Figure 1b).

The structure of the forest in the three plot types, measured through the number and basal area of trees with DBH $\geq$10cm, as well as the number of individuals of each palm species, was compared with the use of Mann-Whitney tests, as the data did not conform to a normal distribution (Zar, 1999). Detrended Correspondence Analysis (DCA) was carried out using CANOCO 4.0 for Windows. 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
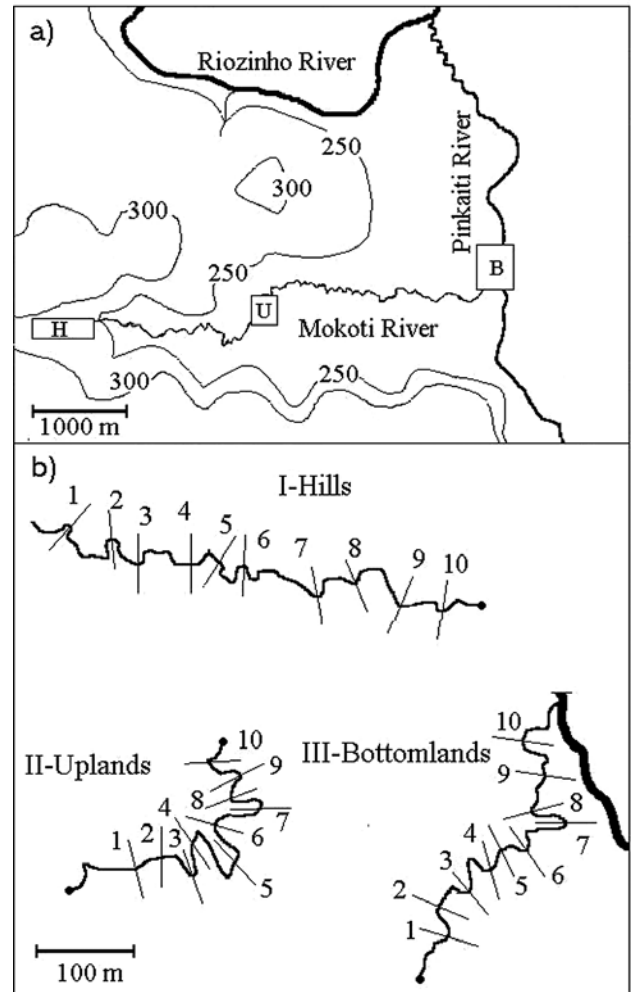
Figure 1 - Local palm study setup, illustrating (a) the location of the areas sampled at the hills (H), uplands (U) and bottomlands (B) of the Mokoti river basin and (b) the positioning of the 10 plots of 600 m^2 (60 x 10m) at each of the areas.

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 the species are plotted onto the same diagram of floristic quadrates, they tend to appear near the quadrates where they are most abundant. 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 those palm species with more than 10 individuals were included in the DCA.

LARGE-SCALE PATTERNS OF PALM DISTRIBUTION

Regional patterns of palm richness were estimated from maps showing occurrence points of the 283 species, sub-species and varieties of palms found within the Brazilian territory (Lorenzi *et al.*, 2004). The territory was divided into 47 units of approximately 150,000 km^2 and species richness was inferred for the point corresponding to the center of each square. To

understand the potential role of climate on palm richness and distribution we obtained the environmental variables corresponding to each of the 47 points specified above. To this end, we used worldwide climate maps generated by the interpolation of climatic information obtained from ground-based meteorological stations (New *et al.*, 1999). The mean climate surfaces were available for the period from 1961 to 1990, with a monthly temporal resolution and 0.5º (latitude) by 0.5º (longitude) spatial resolution (New *et al.*, 1999). The climatic variables used were: precipitation, maximum, minimum and mean temperature saturation vapor pressure and wet-day frequency. The minimum and maximum monthly temperature estimates were calculated from the original climate surfaces by subtracting or adding, respectively, half the diurnal temperature range from the mean monthly temperature (New *et al.*, 1999). In order to summarize the information contained in this time-series and capture the seasonal features of the data, each climatic variable was processed with temporal Fourier analysis (processed dataset provided by D. J. Rogers; see Rogers & Williams, 1994; Rogers *et al.*, 1996; Rogers, 2000), extracting in this process the inter-annual variability of the monthly time-series into uncorrelated components of cycles that are repeated up three times per year. We used the following parameters of each variable: mean (a_0) value; amplitude of annual (a_1), biannual (a_2), and triannual (a_3) cycles and maximum (mx) and minimum (mn) values and the phase variables (reflecting the timing of occurrence of cyclic events). To explore the potential role of climate on variation in palm richness within the country we then conducted a stepwise regression analysis to determine which factors would better explain the observed patterns of richness. We scrutinized the data to determine whether it satisfied the assumptions of the regression, and (log or square-root) transformed those variables with distribution significantly departing from normality, discarding those variables for which normality was not achieved after transformation. After determining the eco-climatic constraints currently defining the distribution and richness of the palm family within the Brazilian territory, the resulting climatic model was used to generate a predictive map of palm richness at a global scale (because the climatic variables are in continuous interpolated surfaces, it was possible to extrapolate the prediction from the model to all regions of the world).

RESULTS

LOCAL PATTERNS OF PALM DISTRIBUTION

A total of 694 individual palms belonging to 10 species were sampled at the Mokoti River basin: *Astrocaryum aculeatum* G. Mey., *Astrocaryum gynacanthum* Mart., *Attalea maripa* (Aubl.) Mart., *Bactris acanthocarpa* Mart., *Bactris tomentosa* Mart., *Desmoncus polyacanthos* Mart., *Euterpe precatoria* Mart., *Geonoma baculifera* (Poit.) Kunth, *Oenocarpus distichus* Mart. and *Socratea exorrhiza* (Mart.) H. Wendl. Table 1 shows the mean values of

abundance of each palm species observed at the hills, uplands and bottomlands of the Mokoti river basin, together with the overall values of abundance, number of species and tree basal area at each of these sites. There was a significant increase in the abundance and richness of palms from the hills towards the uplands, and in turn from the uplands towards the bottomlands of the Mokoti basin river. This increase in richness and abundance follows a significant increase in tree basal area and in the number of sampled trees (Table 1).

The palm species *A. aculeatum*, *D. polyacanthos* and *O. distichus* were represented by less than 10 individuals and therefore not included in the ordination analysis. In Axis 1 of the scatter-diagram resulting from the DCA the plots at the bottomlands of the Mokoti River are separated from those in the hills and uplands, which are in turn set apart in Axis 2 (Figure 2). *G. baculifera* and *E. precatoria* were strongly associated with

Table 1 - Forest structure observed at the hills, uplands and bottomlands of the Mokoti river basin, southeastern Pará, Brazil. Different letters ("a" and "b" or "a", "b" and "c"), within a line, represent significant differences between plot types. Conversely, there were no significant differences among plots marked with the same later "a" or "b" ($p<0.05$) (e.g., the number of trees per hectare is not different between the Hills and Uplands – same 'a' letter -, not different between the uplands and bottomlands – same 'b' letter -, but different between the Hills and Bottomlands, as there is no letter in common).

	Hills	Uplands	Bottomlands
Number of trees per hectare	452[a]	517[ab]	573[b]
Tree basal area (m2) per hectare	20[a]	23[ab]	27[b]
Number of palms per hectare	167[a]	190[a]	800[b]
Number of palm species	6[a]	8[b]	9[c]
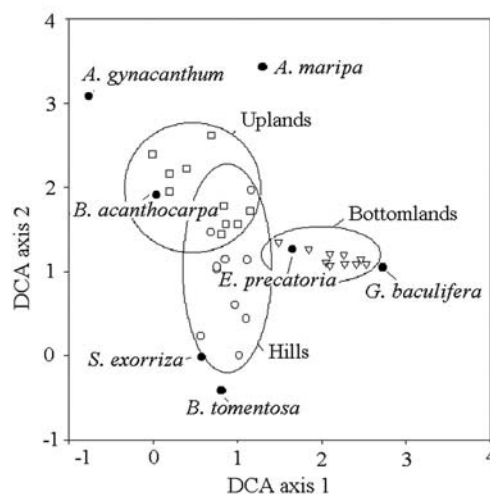
Figure 2 - Detrended Correspondence Analysis ordination of palm plots. Solid and open symbols represent species and plots, respectively, with squares corresponding to plots on uplands, circles to plots on hills and triangles to plots on bottomlands (Lengths of gradient 2.483 and 2.619 SD-units; Eigenvalue Axis 1=0.4897 and Axis 2=0.1847).

the bottomlands. The former is found in this area at densities of hundreds of individuals per hectare, while it occurs at low densities in uplands and is totally absent from the hills. The latter is found in all sampled areas, but its density is significantly higher at the bottomlands of this river. *A. gynacanthum* was found exclusively at the uplands. The two species of the genera *Bactris* appear to have opposite behavior: *B. acanthocarpa* was associated with the uplands, where the species is found at higher densities (although this difference was not significant), whereas *B. tomentosa* was associated with the hills, where it is more abundant, followed by the bottomlands, being finally rarer at the uplands. It is possible to see in the scatter diagram that *A. maripa* lies at an intermediate position between the uplands and bottomlands plots. The density of palms of this species is also significantly higher at the river bottomlands. *S. exorrhiza*, in contrast, was associated with the hills, where it reached its highest density, followed by the bottomlands and uplands, showing no significant difference in abundance between the three sites (Table 2).

LARGE-SCALE PATTERNS OF PALM DISTRIBUTION

Within the Brazilian territory, palm richness reaches its highest values, with more than fifty species found per 150,000 km², in two areas of the Amazon, one at the center of the basin, around the city of Manaus, and the other at its westernmost parts, in the State of Acre. However, it is important to note that some of these patterns may be due to geographic differences in sampling effort (Nelson et al., 1990).

From these areas, palm richness decreases towards dryer areas to the north, south and west. The major South American disjunction (Brieger, 1969), a wide transversal corridor roughly superposed to the distribution of the Central Brazilian savannahs,

with lower annual rainfall, where the richness of palms falls to levels between ten and twenty species, separates the Amazon and the Atlantic forests. The wetter Atlantic forest constitutes another center of high species diversity, with more than thirty species found in the State of Espírito Santo and adjacent Southern Bahia. From this area, species richness decreases towards the interior of the country and along the coast, to the north and to the south. Less than ten species are found in the dry region in the northeast of the country. Within Brazil the effects of minimum temperature on palm species distribution are more evident in the southernmost part of the country, with less than 10 palm species per sampled region. These values are found up to the Pantanal in Mato-Grosso do Sul, where low minimum temperatures are common during the austral winter due to invasions of polar winds, which cross the Andes on a continental route (Nimer, 1977).

The environmental model resulting from the stepwise regression analysis shows the limiting role of eco-climatic factors on palm distribution and richness, and provides us with additional insights (Table 3). The first predictor selected, which alone accounted for approximately 53% of the variance in palm richness, was vapor pressure, namely the annual mean of the values of vapor pressure registered monthly. We tested the association between richness and vapour pressure, and alone it explains 52.8% of the variability. Vapor pressure results from the number of water vapor molecules in the air (the greater the moisture vapor content of air, the greater the vapor pressure), and is thus linearly related to absolute humidity. It is also modulated by temperature, with higher values of vapor pressure corresponding to warmer places. The selection of this variable therefore indicates that richness hits its highest levels in simultaneously warmer and more humid places, specifically in those places where the interaction of temperature and humidity (which is in turn strongly influenced by precipitation) does not allow vapor pressure to fall below certain levels.

Table 2 also shows that the second best predictor of richness (negatively related to it) was the amplitude of the annual cycle of temperature (maximum temperature), meaning the degree of seasonal variation in the maximum observed values of temperature during any one year. This is an interesting result, as

Table 2 - Abundance of each palm species, in individuals per hectare, observed at the hills, uplands and bottomlands of the Mokoti river basin, southeastern Pará, Brazil. Different letters, within a line, represent significant differences between plot types (Mann-Whitney U, p<0.05). Conversely, there were no significant differences among plots marked with the same later.

Species	Hills	Uplands	Bottomlands
Desmoncus polyacanthos *	_	_	1
Oenocarpus distichus *	_	_	**1**
Astrocaryum aculeatum *	1	6	1
Astrocaryum gynacanthum *	_	35	_
Attalea maripa *	6ᵃ	10ᵃ	23ᵇ
Socratea exorrhiza **	28ᵃ	6ᵃ	15ᵃ
Bactris tomentosa *	31ᵃ	1ᵇ	20ᵃ
Bactris acanthocarpa *	40ᵃ	61ᵃ	30ᵃ
Euterpe precatoria **	58ᵃ	58ᵃ	223ᵇ
Geonoma baculifera ***	_	10ᵃ	483ᵇ

* Individual with visible stem, **Individuals with DBH e" 5cm, *** Reproductive genets.

Table 3 - Results of the stepwise regression analysis. Parameters are shown in order of entrance in the stepwise regression model. The last row shows the parameters and total variance (R²) explained by the full model. In all cases P < 0.001.

| Parameter	B*	No Parameters in the Model	F	R²
(P1) Vapor Pressure	0.17	1 (P1)	52.7	0.53
(P2) Amplitude of the Annual Cycle of Temperature (Maximum Temp.)	-12.86	2 (P1, P2)	34.6	0.60
(P2) Amplitude of the Annual Cycle of Temperature (Maximum Temp.)	-12.86	2 (P1, P2)	34.6	0.60

Intercept for the full Model = 96.7, *unstandardized coefficients.

it suggests that richness is higher in places with more stable maximum temperatures than in those regions characterized by a strong seasonality in this parameter. Finally, the last predictor selected was the mean of maximum temperature (i.e. the average of the maximum temperatures registered per month), which was negatively associated to richness, thus suggesting that in those places where maximum temperatures were highest palm richness was lower. It seems to us, however, that the latter association has resulted from the fact that, within the Brazilian territory, those regions with highest maximum temperatures correspond to regions where there is a very large variation in precipitation during the year (as indicated by the significant correlation between "maximum temperature" and "amplitude of the annual cycle of precipitation": r = 0.53, p<0.001, where p is Bonferroni-corrected). Areas with stronger seasonality in precipitation levels might have less palm species due to the palms' general vulnerability to climatic hazards resulting from the lack of reserve buds previously mentioned (Tomlinson, 1990; Richards, 1996).

The climatic model resulting from the regression analysis performed for the Brazilian territory was subsequently used to generate a predictive map of palm richness at a global scale. Given the discussed specificity of the last predictor selected (mean of maximum temperature) with the ecosystems of the Brazilian territory we decided to exclude this factor from the model to generate the predictive map for the globe, retaining the first two best predictors of richness. Figure 3 shows the resulting map. The color-coded levels of richness effectively indicate the predicted number of palm species in each region as based on their environmental suitability (in terms of vapour pressure and seasonality in temperature).

DISCUSSION

The finding that palm richness in Brazil is best predicted by vapor pressure and the amplitude of the annual cycle of temperature, with a marked presence of palms in stable areas of simultaneously high humidity and low annual oscillation of
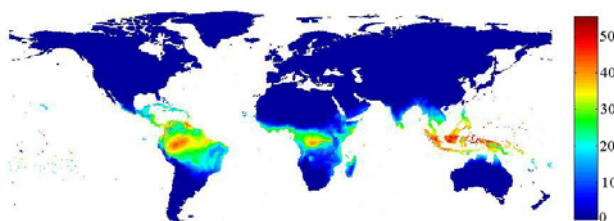
temperatures (Figure 4), reflects the basic physiological constraints characteristic of the palm family and its vulnerability to climatic hazards (Richards, 1996), particularly caused by the presence of a single, irreplaceable terminal bud (Tomlinson, 1990). From an ecological perspective, these findings are also compatible with the idea that water availability is a key constraint of plant richness, especially in those (tropical and subtropical) areas where energy is abundant (Hawkins *et al.*, 2003). Alternatively, insect and fungal pressure might increase with higher and more constant levels of moisture, thus mediating palm tree diversity through mechanisms of density-dependent mortality as observed elsewhere (Givnish, 1999). In any of these cases, by accounting for approximately 60% of the variation in palm richness, the climatic model strongly emphasizes the major influence of the selected environmental predictors - and of climate in general - on diversity gradients, and provides us with clues on palm tree communities' potential response to climate change.

Within the tropics, the predictive map of global palm diversity generated from the climatic model built for the Brazilian territory is consistent with the general knowledge of global palm distribution - with the major centers of diversity aligned along the Equator in the Amazon, the Congo basin and Southeastern Asia, with the largest number of species found in the latter area (Corner, 1966). The island of New Guinea, for example, which hosts 145 palms species belonging to 32 genera within its 808,510 km² of territory (Bachman *et al.*, 2003), is shown as a hotspot of palm diversity in the model.
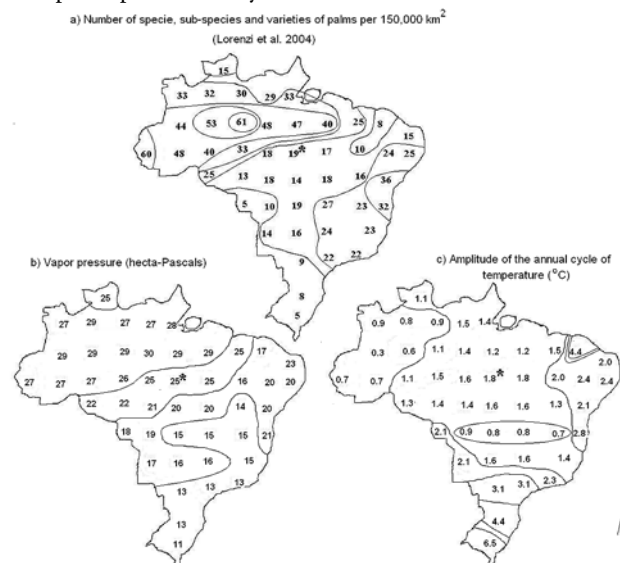
Figure 4 - Variation in (a) the number of specie, sub-species and varieties of palms per 150,000 km² (Lorenzi *et al.* 2004) and the main climatic parameters, as following from our model, underlying the richness of palms across the Brazilian territory: (b) vapor pressure (hecta-Pascals) and (c) amplitude of the annual cycle of temperature (ºC). Observe that while vapor pressure is positively related to palm richness, the amplitude in temperature is negatively related to it. The asterisk label the position of the Pinkaití research station and the Mokoti river basin.

Figure 3 - Predictive map of palm richness at a global scale. Color-coded levels of richness indicate the predicted number of species, sub-species and varieties of palms per 150,000 km² units in each region as based on their environmental suitability in terms of vapor pressure and seasonality in temperature.

The model is aimed at exploring the limits placed by eco-climatic variables on the distribution and richness of the family. Despite the potential limitations that heterogeneous efforts in the collection of data on palm richness along the Brazilian territory could impose on the final climatic model generated, the overall consistency between its predictions and general reports of palm diversity around the globe highlights the major role played by climate – and particularly the variables selected in our analyses – on palm diversity. Future studies reporting observed palm richness levels in different localities of the globe could enable a further test of the model with independent data sets. Moreover, the model can be used to identify those poorly studied areas potentially marked by a high diversity of palm species, providing additional criteria to direct sampling efforts. For example, Figure 4 suggests that the northwestern region of the Amazon is currently under-sampled, as there would not be any climatic factor – as given by our model – justifying the drop in richness in this region following the peak in diversity observed in the surroundings of Manaus, the capital of the Amazon state.

The model is additionally aimed at serving as a heuristic tool for the investigation of those cases in which factors other than climate might underlie the discrepancy between the model's prediction and reality. For example, although palms can survive in very dry regions (such as some regions of the Middle East and Central Australia), they do so only in those areas where the ground water is near to the soil surface. Since this latter variable was not made available to our analyses, it would be thereby possible to find a higher diversity of palms than that predicted by the model in dry regions with these conditions. The dynamics of island biogeography (MacArthur & Wilson, 1967) also seem to be the cause of some of the differences between the predicted and observed diversity of palms in some tiny islands of Micronesia: although the model predicts areas with richness values as high as 40 species per 150,000 km², well-known effects of insularity such as island size and distance from continental lands seem to underlie the less pronounced diversity observed in these islands. Within Brazil, the effects of insularity and the presence of subterranean water may respectively explain the structure and diversity of palm communities in ecosystems subjected to human induced or natural fragmentation (Scariot, 1999) and the formation of palm-dominated forests in areas that are climatically unsuitable for their occurrence (Lorenzi *et al.*, 2004).

At a local scale, the distribution maps of Lorenzi *et al.* (2004) indicate that the 150.000 km² area including the Pinkaití research station, located at the limits of the Amazon forest with the Cerrado of Central Brazil, has a number of species typical of the dryer regions of Central Brazil (with richness ranging from 10 to 20 species in areas of similar size). Five palms species were however found at the Mokoti basin beyond the distribution limits proposed by these authors: *Attalea maripa*, *Astrocaryum aculeatum*, *Bactris tomentosa*, *Euterpe precatoria* and *Geonoma*

baculifera. With these species, the richness of the region climbs to those ranges typical of the seasonally dry forest at the limits of the Amazon (20 to 40 species in areas of similar size).

Within the field study site, the palm family became more abundant and richer from the open and drier forest of the Mokoti hills to the denser forests at the uplands and, subsequently, to the moister bottomlands of this river basin. Although on the one hand it is clear that factors influencing richness are likely to be scale-dependent, on the other this result is consistent with the association between moisture and richness as captured in the climatic model at a larger spatial scale. It is important to notice, however, that it is not currently possible to determine the role played by other factors differing among the plots, such as their edaphic and topographic features and patterns of variation (e.g. Vormisto *et al.*, 2004a, 2004b), as well as their potential interaction with moisture differences. Further research involving the use of a larger number of plots and study regions where these factors are measured and combined should help separating the individual effect of each of them upon palm richness and abundance.

Our field data also indicate that moisture is associated with forest structure at the Mokoti basin, as suggested by the increase in total tree basal area observed from the hills towards the bottomlands. Alternatively, the steepness of slopes in the hills could have increased the likelihood of large trees falling with a higher frequency in the latter plot type, contributing to the overall progressive increase in basal area in the other two plots regions (but see Clark *et al.*, 1995 for an example where the abundance of large trees is higher in steeper regions).

In terms of palm community composition, our results suggest a potential role for niche specialization as found elsewhere (e.g., Svenning, 1999; 2001; Clark *et al.*, 1995; Kahn, 1987). In Costa Rica, for example, the distribution of five common palm species in an old-growth lowland forest is related to soil type, topographic position and slope angle, with closely related palm species having strong opposite edaphic associations (Clark *et al.*, 1995). In the Peruvian Amazon, the distribution of closely related palm populations was also heterogeneous in relation to topography (Kahn, 1987). Additionally, in a seasonally flooded forest in Serra dos Carajás, Brazil, eight species belonging to eight different genera were found in one hectare (Scariot *et al.*, 1989). The hypothesis that niche specialization affects palm community structure at the Mokoti river basin is also suggested by our data, as those species with dissimilar morphology and behavior were more likely to be associated. For example, the association of the prostrate *G. baculifera* and the medium-sized palm with erect stem *E. precatoria* was clearly observed for the bottomlands region, probably as a consequence of their distinctive habits. *Geonoma* was restricted to areas subjected to seasonal flooding, while *Euterpe* was found throughout the basin, in progressively lower densities towards the hills. Associations

between the two genera, which might be stabilized due to their great morphological dissimilarity, are indeed widespread and found even at the disjunct Atlantic forest (Silva-Matos, personal communication). Also, among the five species of *Bactris* occurring at the Pinkaití region, the two small palms with erect stem found at the Mokoti basin show an inverse relationship of abundance, as *B. tomentosa* was found in higher densities at the hills and the bottomlands and lower densities in the uplands while *B. acanthocarpa* had the opposite distribution. The large arborescent palms *A. maripa* and *S. exorrhiza* also showed opposite distribution patterns, *Attalea* being found at higher densities towards the bottomlands and *Socratea* being associated to the sampled plots at the hills.

The absence of other species with distribution predicted for the Pinkaití region, but not observed at the Mokotí River basin may have been due to factors ranging from local extinction, chance, dispersal constraints and the ecological specificities of the region. For example, although the vegetation becomes evidently dryer from the bottomlands towards the uplands and the hills, savannahs do not penetrate the Mokoti River basin as isolated patches of open vegetation do in nearby valleys. This absence of an exclusively open formation is in fact sufficient to explain the absence of species such as *G. brevispatha*, *S. comosa* and *S. petraea* in the Mokotí River basin, as these are species which, according to Lorenzi *et al.* (2004), are restricted to the Cerrado biome. Similarly, it could also explain the absence of *M. flexuosa*, which is observed in the Cerrado formations in the regional area but not associated with forests, characteristic of the smaller area comprising the Mokoti River basin (R. Salm, personal observation).

In conclusion, the data collected in the Mokoti river basin is compatible with the findings reported at a larger spatial scale, additionally supporting the idea that niche specialization might have a direct effect on palm community composition. Further research in different valleys at the limits of the Amazon forest is however needed to help separate the ultimate influence of individual ecological factors on palm communities in seasonally dry forests. At a larger spatial scale, our results stress the importance of climate as a major determinant of gradients of palm richness. Particularly, it highlights the importance of the combined effect of moisture and temperature, as well as seasonality, on palm diversity. These findings give support to the idea that, by "putting all eggs in one basket" - a consequence of survival depending on the preservation of a single bud - palms have become vulnerable to extreme environmental conditions, hence having its distribution limited to those tropical and sub-tropical regions with constant conditions of (mild to high) temperature and moisture all year round (Richards, 1996). Additionally, our model forecast at a global scale can be used in the identification of those factors other than climate underlying regional patterns of diversity.

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