

Gradients within gradients: The mesoscale distribution patterns of palms in a central Amazonian forest

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Abstract

Questions: What are the relative contributions of environmental factors and geographic distance to palm community structure at the mesoscale, and how do they depend on the length of the environmental gradient covered? How do soil and topography affect variation of the canopy and understory palm community structure at the mesoscale? How does fine-scale variation within the broad edaphic/topographic classes affect palm community composition?

Location: Reserva Ducke, terra-firme forest, Manaus, Brazil.

Methods: Palms were sampled in 72 plots 250 m × 4 m, systematically distributed over an area of 100 km². Soil, topography and distance to watercourses were measured for all plots. The relationship between community structure axes, summarized by NMDS ordinations, and environmental predictors, was analysed with multivariate regressions. Matrix regressions were used to determine the proportions of variance explained by environmental and geographic predictors.

Results: Floristic variation at the mesoscale was mostly related to environmental variation, and the proportion of variance explained depended on the amplitude of the environmental gradient. Soil was the main predictor of floristic change, but its effects differed between life forms, with the understory palm community structured within one of the edaphic/topographic classes, in association with distance to watercourses.

Conclusions: Dispersal limitation does not explain palm composition at the mesoscale, and the amplitude of environmental gradients covered by the analysis can be as important as the scale of analysis, in determining the relative contributions of environmental and geographical components to community structure. Soil and topography can predict a large proportion of palm composition, but gradients differ in scale, with some environmental gradients being nested within others. Therefore, although all environmental gradients are nested within distance, they do not necessarily coincide.

Keywords: Beta-diversity; Canopy palm; Environmental gradient; Tropical forest; Understory.

Nomenclature: Ribeiro et al. (1999) with some modifications mentioned in the Methods section.

Introduction

Palms are important structural components of neotropical forests and have important economic and practical uses (Dahlgren 1944; Henderson 1995). Most studies on palm species distribution and community composition were undertaken at two extreme scales – local (Kahn 1987; Svenning 1999; Vormisto et al. 2000; Cintra et al. 2005) or regional (Vormisto et al. 2004a). The mesoscale (10 - 100 km), which is intermediate between these extremes, has received much less attention (Clark et al. 1995). However, this is the scale at which most land-management decisions are made.

The relative importance of environmental vs. distance effects in determining the floristic patterns of tropical plant communities has been evaluated in a series of studies (Duivenvoorden et al. 2002; Tuomisto et al. 2003 a, b; Vormisto et al. 2004a; Jones et al. 2006). Only in the large-scale studies climate was included. In the local to mesoscale studies climate does not vary sufficiently to be considered, therefore in most studies the main environmental factors are linked to soil and topography. Some studies detected higher contributions of the environment (e.g. Tuomisto et al. 2003b; Jones et al. 2006), but others, especially at large scales, observed higher contributions of geographic distance (e.g. Vormisto et al. 2004a; Normand et al. 2006). The contribution of environmental factors can also change with scale (Normand et al. 2006) or, alternatively, may be more affected by the length of the gradients in the study areas (Jones et al. 2006) than by the extent of the study areas. Therefore, it is still not clear how the relative contributions of the environmental and geographic components change with scale, and if there is a consistent pattern for all plant groups.

It is well known that palm richness, abundance and composition respond to soil and topography (review in Svenning 2001), but a lack of systematic sampling, and sometimes lack of independence between samples,

impairs quantification and separation of these effects. Moreover, the association of species with topographic conditions cannot be generalized, because environmental differences correlated with topography vary from site to site (Vormisto et al. 2004b). Therefore, information on associations in new areas, besides experimental manipulation, is necessary to elucidate the factors determining distributions.

Large topographic variation has been shown to be associated with floristic differentiation in several studies of palms (Kahn 1987; Svenning 1999; Vormisto et al. 2000, 2004b), however, classification of topographic conditions in broad habitat classes may have impaired detection of fine scale differentiation. Silvertown et al. (1999) observed niche differentiation along a continuum of hydrological conditions, even in the absence of strong topographic variation, which suggests that variation inside broad topographic classes usually examined may be relevant for predicting species composition. Researchers often model environmental factors as habitat categories, which assumes that only one environmental gradient exists, or all components of the environment vary in the same manner, and that gradients are so steep that they can be modeled as boundaries between habitats. However, gradients in one factor (e.g. depth to the water table) may be nested within other gradients (e.g. distance from the stream).

Although palms comprise a wide variety of life forms and can occupy understory, mid-story to canopy positions in the forest, most studies of palm ecology do not distinguish between the patterns of occurrence of these functional groups (but see Kahn 1986). In the present study, we analyse the association between variation in floristic and environmental distances for understory and canopy/sub-canopy palms separately.

The objectives of this study were to determine (1) the relative contributions of environmental and geographical factors to variation in palm beta-diversity at the mesoscale (100 km²) and how these contributions depend on the amplitude of the environmental variation included; (2) how environmental factors (soil and topography) affect the variation of the canopy/sub-canopy and understory palm community composition at the mesoscale, and (3) how fine scale variation (distance to water courses) within the broad edaphic/topographic classes affects the variation in palm community composition.

Methods

Study site

The study was conducted in Reserva Florestal Adolpho Ducke (RFAD) of the Instituto Nacional de Pesquisas da Amazônia (INPA), located 26 km northwest of Manaus (02°55' S, 59°59' W at the reserve headquarters). The reserve covers 10 000 ha (10 km × 10 km) of terra-firme tropical rain forest, with a closed canopy 30-37 m high and emergents growing to 40-45 m. The understory is characterized by abundant palms with subterranean-stems, such as *Astrocaryum* spp. and *Attalea* spp. (Ribeiro et al. 1999).

Mean annual temperature is around 26 °C and mean annual rainfall is around 2400 mm (SD = 400, data from 1965-1980), with a dry season between July and October (Marques-Filho et al. 1981). Soils are derived from tertiary marine sediments from the Alter do Chão formation, and represent a continuum from clayey latosols on the ridges, becoming sandier as the inclination increases and altitude decreases (Chauvel et al. 1987) until the mineral fraction in the bottomlands is almost pure sand. RFAD is generally considered to contain relatively uniform terra-firme forest, with white sand vegetation, locally called '*campinarana*', being the only special type recognized.

Data collection

Plant assemblage data were collected in 72 plots systematically distributed over a 64-km² grid formed by 8 km long trails (see Costa et al. 2005). Each plot was at least 1 km away from any other. Plots were 250 m × 4 m (0.1 ha) and were positioned to follow the topographic isoclines and thus minimize altitude and soil variation within each plot. In central Amazonia, soil properties generally coincide largely with altitude, so long narrow plots oriented along topographic contour lines tend to be relatively homogeneous in soil chemical and physical conditions (Chauvel et al. 1987).

Fieldwork was carried out in January and February 2003. Every individual palm rooted inside the plot and greater than 1 m in height (measured by the height to highest leaf) was counted and identified. For vegetatively spreading multi-stemmed species, each clump was counted as one individual. Since the density of these species in our area is not high, we are confident of having counted separate genets in most cases. Species identification was done with the field guide 'Flora da Reserva Ducke' (Ribeiro et al. 1999), with some modifications. For *Astrocaryum*, we adopted the concepts of Kahn (2001), Kahn & Millan (1992) and Pintaud & Kahn (2002). The name *Maximiliana maripa* was adopted, instead of *Attalea maripa*, following Kahn & de Granville (1992).

We considered as canopy/sub-canopy palms those species with stems usually reaching more than 8 m in height, and the others as understory species. Species maximum sizes were obtained from Kahn & de Granville (1992), Ribeiro et al. (1999) and field observations.

Measures of the surface slope were taken with a clinometer perpendicularly to the main axis of the plot, every 50 m, and summarized as plot averages. One soil sample was taken at a depth of 5 cm at each 50 m, at the same points as for slope, and bulked to produce a composite sample for each plot. Before analysis, samples were cleaned of roots, air-dried and sieved through a 2-mm sieve. Texture analyses were done at the Soil Laboratory of the Agronomy Department at INPA, and chemical analyses (including Ca^{+2} , Mg^{+2} , K^+ , Na^+) at the Soil Laboratory of EMBRAPA-Manaus. Distance from stream margin was measured directly with a measuring tape and compass for plots less than 100 m from streams and derived from a cartographic map for the others.

Data analysis

The dimensionality of the plant assemblage composition was reduced by multivariate analysis. Ordinations were performed with Non-Metric Multidimensional Scaling (NMDS), in one and two dimensions, and the percentage of variation captured by each solution compared to decide the dimensionality to be used. Since one-dimensional solutions captured a high proportion of variance (76 to 89 %), we represented community composition by these one-dimensional solutions. Variation captured by the NMDS solutions were derived from the regression between the original floristic distances between samples, calculated with the same dissimilarity index used in the ordination over the site-standardized data table, and the output distances between samples obtained in the final NMDS solution (McCune & Grace 2002).

Two NMDS ordinations were carried out with the plant data; one based on quantitative and another using presence-absence data. Quantitative ordinations used the Bray-Curtis distance measure (as in Legendre & Legendre 1998), calculated over a site-standardized data matrix. Standardization involved division of each species abundance by the total abundance in each site, in order to transform them to proportions of each site's abundance. The ordinations of quantitative data (density) were used to capture the patterns displayed by the most abundant species, as these will have the greatest quantitative contribution to the differences between sites. The presence-absence ordination used the Sørensen index, which is equivalent to the Bray-Curtis measure in binary form (Legendre & Legendre 1998). This ordination tends to capture mainly the patterns of the rarer species, because the more abundant species tend to occur in most sites,

and therefore may contribute little to the differences between sites. Separate ordinations were done for canopy and understory species.

The resulting ordination axes, describing the community composition, were used as dependent variables in multiple regressions to test the effects of topography and soil. Soil was represented by clay content and exchangeable base content. Values of clay content were double-log transformed to obtain linear relationships with the ordination scores. The only topographic variable used in the analysis was slope, since altitude is highly correlated with clay content ($r = 0.94$, Costa et al. 2005).

The partial contributions of geographical distance and environmental factors on palm species composition were assessed with linear multiple regression between distance matrices, with significance testing by permutation (Manly 1997a). Two floristic distance matrices were constructed for each palm group, one based on relative abundances, with the Bray-Curtis measure, and one based on presence-absence data with the Sørensen measure. One distance matrix was separately constructed for each of the environmental variables (slope, clay and exchangeable base contents), with the Manhattan index. Three regressions were run for each floristic data set: (1) the complete model, including geographic distances and the three matrices of environmental distances, (2) the environmental model, including only the three environmental distance matrices and (3) the geographic model, including only geographic distances. Coefficients of determination (R^2) for each model were used to calculate the components of variation in floristic composition, following Legendre et al. (2005). The relative contributions of environmental and geographic factors were assessed for the whole data set, and separately for clayey plots (clay content above 10%), in order to examine the effect of a restriction in the length of the edaphic/topographic gradient.

Analysis of fine-scale distribution patterns was done only for understory palms in bottomland plots, because they were the most heterogeneous in composition. Bottomland plots ($n = 19$) were considered as those with less than 65 m of altitude and less than 12° of slope, and upland plots as those with more than 65 m of altitude. Altitude in Reserva Ducke varies from about 40 to 110 m a.s.l., and areas below 65 m encompass headwaters and watercourse margins. An NMDS ordination of the 19 bottomland plots was performed, and this captured 68% of variance in a one dimensional solution. Distance to watercourses was then used to predict composition in the bottomland plots, composition being represented by the one-dimensional NMDS solution.

Ordinations were done with the PATN package (Belbin 1992), Mantel tests with the RT package (Manly 1997b) and the inferential tests with SYSTAT 8.0 (Wilkinson 1990).

Results

Community composition

We found 38 species and 43 botanical entities (Table 1) in a total of 16 980 individuals. The varieties of *Bactris acanthocarpa*, *Bactris hirta* and *Geonoma maxima* and the two morphological forms of *Bactris hirta* (pinnated and bifid forms) were counted separately and considered as separate botanical entities in the analysis. The mean density of understory palms was 0.16 (\pm 0.05) individuals/m² and canopy palms had 0.08 (\pm 0.06) individuals/m². Of the botanical entities, 32 were classified as understory species and 11 as canopy species (Table 1).

Relative contributions of environmental and geographical factors to palm beta-diversity

Floristic dissimilarities were not related to the geographic distance between plots when the effect of the environmental distance was partialled out, for canopy palms quantitative and qualitative data, or the quantitative data for understory palms. Therefore, the total variance explained for each of these data sets was entirely accounted for by environmental distances (Table 2). Only models for understory qualitative data included geographic distances as a significant predictor of floristic distances. Environmental distances explained 46 % of the understory qualitative floristic distances, 3 % was accounted for by geographic distances and 2 % was mixed environmental and geographic contribution.

The predictive capacity of geographic distance did not become greater when the amplitude of the soil gradient was shortened by restriction of analysis to plots with clay content above 10 % (Table 2). For most analyses, the effect of geographic distances was not significant, and when it was, the total percentage of variance explained was never greater than 2%.

Table 1. Palm taxa found at Reserva Ducke, Manaus, Brazil, classified by habit.

Community	Taxa
Canopy	<i>Astrocaryum ferrugineum</i>
	<i>Astrocaryum gynacanthum</i>
	<i>Euterpe precatoria</i>
	<i>Iriartella setigera</i>
	<i>Mauritia flexuosa</i>
	<i>Mauritiella aculeata</i>
	<i>Maximiliana maripa</i>
	<i>Oenocarpus bacaba</i>
	<i>Oenocarpus bataua</i>
	<i>Socratea exorrhiza</i>
	<i>Syagrus inajai</i>
Understory	<i>Astrocaryum acaule</i>
	<i>Astrocaryum sociale</i>
	<i>Attalea attaleoides</i>
	<i>Attalea microcarpa</i>
	<i>Attalea spec.1</i>
	<i>Bactris acanthocarpa</i> var. <i>acanthocarpa</i>
	<i>Bactris acanthocarpa</i> var. <i>intermedia</i>
	<i>Bactris acanthocarpa</i> var. <i>trailiana</i>
	<i>Bactris acanthocarpoides</i>
	<i>Bactris constanciae</i>
	<i>Bactris cuspidata</i>
	<i>Bactris elegans</i>
	<i>Bactris gastoniana</i>
	<i>Bactris hirta</i> (pinnated form)
	<i>Bactris hirta</i> (bifid form)
	<i>Bactris maraja</i>
	<i>Bactris schultesii</i>
	<i>Bactris simplicifrons</i>
	<i>Bactris syagroides</i>
	<i>Bactris tomentosa</i> var. <i>sphaerocarpa</i>
	<i>Desmoncus polyacanthos</i>
	<i>Geonoma aspidiifolia</i>
	<i>Geonoma macrostachys</i> var. <i>acaulis</i>
	<i>Geonoma maxima</i> var. <i>chelinodura</i>
	<i>Geonoma maxima</i> var. <i>maxima</i>
	<i>Geonoma maxima</i> var. <i>spixiana</i>
	<i>Geonoma stricta</i> var. <i>stricta</i>
	<i>Geonoma spec. 1</i>
	<i>Geonoma spec. 2</i>
	<i>Geonoma spec. 3</i>
	<i>Hyospathe elegans</i>
	<i>Oenocarpus minor</i>

Table 2. Probabilities associated with the null hypothesis for the effects of environmental and geographic distances on floristic distances, tested by regression between distance matrices, and the total variance explained for each data set.

		Slope	Clay content	Base content	Geographic distance	R ²
Canopy (all plots)	Quantitative	0.135	0.001	0.002	0.944	0.38
	Qualitative	0.322	0.001	0.001	0.911	0.22
Understory (all plots)	Quantitative	0.128	0.001	0.001	0.136	0.68
	Qualitative	0.330	0.001	0.008	0.001	0.49
Canopy (clayey plots)	Quantitative	0.003	0.422	0.825	0.004	0.02
	Qualitative	0.009	0.263	0.601	0.059	0.02
Understory (clayey plots)	Quantitative	0.940	0.006	0.130	0.143	0.02
	Qualitative	0.892	0.113	0.172	0.046	0.01

How environmental factors affect palm composition variation

Two plots were consistently identified as outliers in the regressions between community composition and environmental variables, for both understory and canopy palms, and were therefore removed from analyses. The outliers were represented by the only plot in a large swamp, in which *Mauritia flexuosa* was present, but most other canopy species were absent, and a plot in white sand vegetation, which was dominated by *Attalea microcarpa* in the understory and *Oenocarpus bataua* in the canopy. Removing these plots did not change the results about which predictors were significant in each model, but slightly decreased the percentage of variance explained.

Patterns of canopy/sub-canopy palms

The ordination of the canopy/sub-canopy palm community captured 76% of the variation in the original distances between plots in one dimension for quantitative data, and 77% for qualitative data. The first dimension of an ordination of the species composition with quantitative data was only significantly related to the soil clay content (Table 3), and this model explained 60 % of the variance in the NMDS axis used to represent composition. Using clay content as the single predictor of composition, the percentage of variance explained did not change. Analysis for qualitative data included base content as a significant predictor, in addition to the clay content (Table 3), but base content contributed only a third (10%) of the variance explained by the model (32%), after the other variables had been taken into account.

Patterns of understory palms

The ordination of the quantitative and qualitative data on the understory palm community captured respectively 89 and 84 % of the variation in the original distances between plots in one dimension. The species composition was significantly related to the soil clay and base contents, but not to the terrain slope, for both quantitative and qualitative data (Table 3). Both models (for quantitative and qualitative data) explained 73% of the variance in the NMDS axis used to represent composition. The effects of base content were small, and contributed only 11 (for quantitative data) or 7% (for qualitative data) to the total explained variance, after consideration of the contributions of the other variables.

There was great variation in the composition of understory palms in the plots with clay content below 10%, but plots with over 10% clay content had a similar composition (Fig. 1). The understory palm community was dominated by *Astrocaryum sociale* and *Attalea attaleoides* in the high-clay content plots. *Astrocaryum sociale* was the most abundant species in 48 of the 51 high-clay plots, accounting for 30 to 77 % of the number of individuals (mean = 57%, \pm 12). *Attalea attaleoides* was the second most abundant species in 30 of the 51 clayey plots, accounting for 0 to 28 % of the number of individuals (mean = 14%, \pm 7). *Bactris elegans* replaced *A. attaleoides* as the second most abundant species in 11 plots (0 - 24 % of individuals, mean = 7% \pm 7). In the bottomland (low clay content) plots, the dominant species varied widely among plots, with *Bactris acanthocarpoides*, *Astrocaryum sociale*, *Attalea microcarpa*, *Bactris hirta* pinnated form, *Geonoma aspidiifolia* being the dominant species in 21 plots. The second most abundant species was even more variable than the first (10 species).

Table 3. Standardized regression coefficients and probabilities associated with the null hypothesis (within brackets) for the effects tested in multiple regression models for canopy palm (11 species) or understory palm (32 taxa) composition in 72 plots in Reserva Ducke, Brazil. R^2 is the variance explained by the regression models for the NMDS axes used to represent composition, and VOrd is the variation in community composition captured by NMDS ordinations.

		Slope	Clay content	Base content	R^2	VOrd
Canopy	Quantitative	0.093 (0.262)	0.765 (0.000)	-0.051 (0.541)	0.60	0.76
	Qualitative	0.077 (0.463)	-0.494 (0.000)	0.382 (0.001)	0.32	0.77
Understory	Quantitative	0.098 (0.149)	0.790 (0.000)	-0.351 (0.000)	0.73	0.89
	Qualitative	-0.062 (0.356)	-0.821 (0.000)	0.288 (0.000)	0.73	0.84

How within-habitat fine scale variation affects variation in palm community composition

The understory palm community in bottomlands was non-linearly related to the distance to watercourses, when analysis included all the range of distances from the stream (4 - 276 m), (Fig. 2a). Plots with distances below 50 m spanned a large range of compositional values, and were separated from plots with distances greater than 50 m, which had relatively constant compositional values, except for one plot. This was one “campinarana” plot, which differed from others in the same class, probably because our classification did not take account of the depth to the water-table. However, analysis of plots with distances to watercourses below 50 m (15 plots) showed a strong linear relationship between composition and distance to watercourses ($T = -4.8$, $p < 0.001$, $r^2 = 0.64$; Fig. 2b).

Discussion

Distance or environmental controls?

Geographic distance had only a small influence on palm composition at the scale of 64 km², but environmental factors, in this case soil alone, could predict a large part of the compositional variance (22-68 %). For all other plant groups studied at Reserva Ducke, environmental factors could predict only 15 to 30 % of the compositional variance (Kinupp & Magnusson 2005; Costa et al. 2005). Most studies at larger spatial scales reported percentages of variance explained by pure environmental factors varying from 10 to 20 % (Duivenvoorden et al. 2002; Tuomisto et al. 2003b), even for palms (Vormisto et al. 2004a). A deviation from this pattern was the study of Jones et al. (2006), in which 33 - 49 % of the variance in species composition was accounted for by environmental factors, when the entire range of the soil gradient was analysed. When only

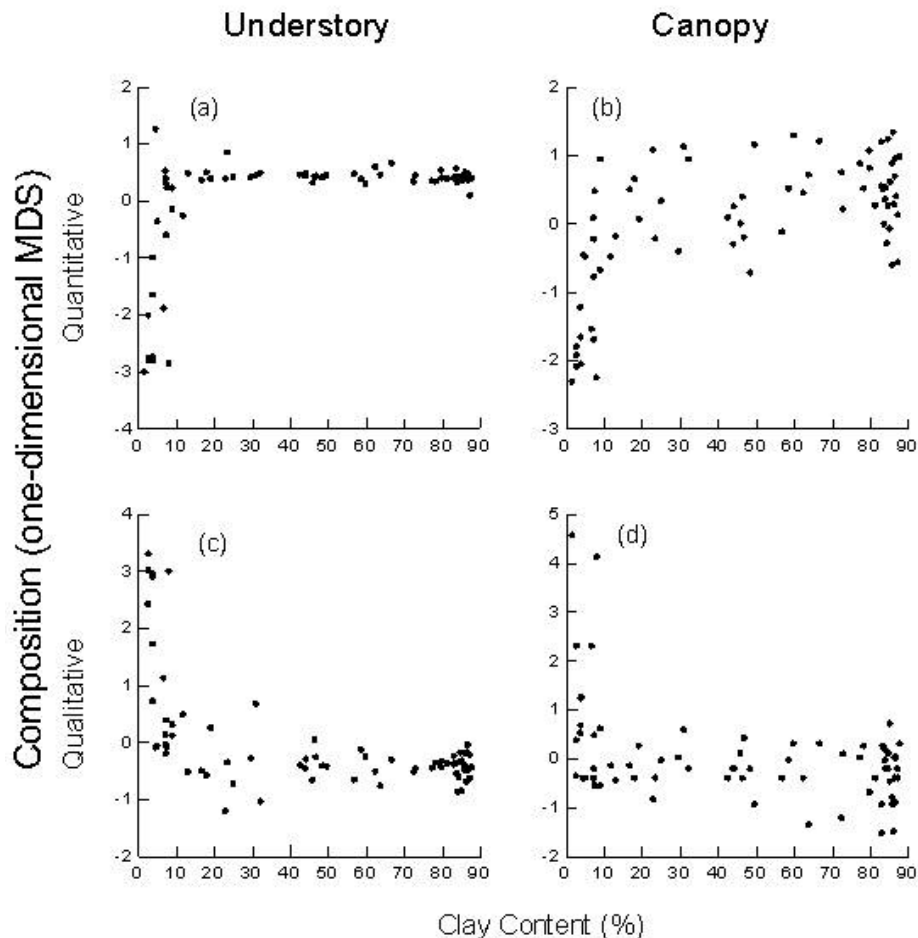


Fig. 1. Relationships between palm composition, based on abundance data (a, b) or presence-absence data (c, d) and summarized by NMDS, with the percentage of clay content in the soil.

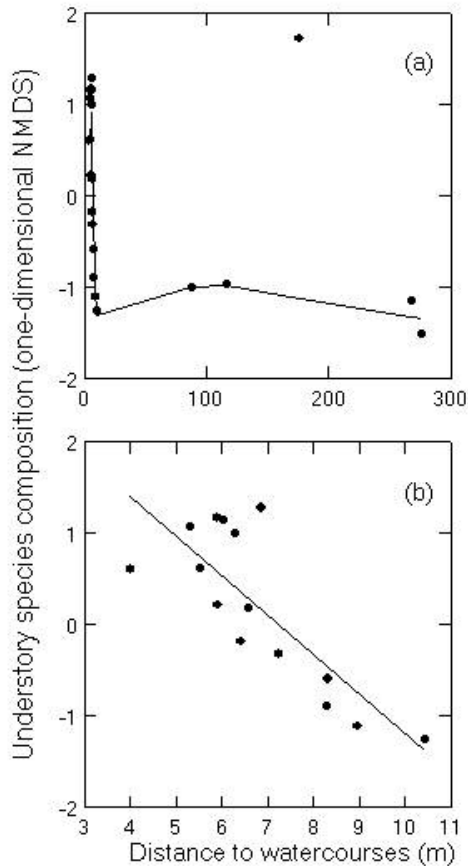


Fig. 2. Relationships between the understory palm composition (summarized by NMDS) and the distance of plots to the nearest watercourse. In (a) the complete set of bottomland plots ($n = 19$), and in (b) only plots with distances to the nearest watercourse lower than 50 m ($n = 15$).

one type of soil was analysed in the plots from Costa Rica (Jones et al. 2006), environmental factors had an importance (10 %) similar to that observed in other studies. The contribution of geographical distances has been much more variable between studies, varying from less than 1 up to 40 % (Duivenvoorden et al. 2002; Tuomisto et al. 2003b; Vormisto et al. 2004a; Jones et al. 2006; Normand et al. 2006).

The empirical pattern emerging from this collection of studies, now spanning spatial scales from 5.7 km² to ca. 80 000 km² suggests that the importance of geographical distance increases with the increase in the spatial scale. However, there is some evidence that the importance of measured environmental factors may depend on the length of environmental gradients sampled, rather than on the geographical scale (Jones et al. 2006).

Restriction of our analysis to plots on clayey soil, which represent 86 % of the length of the clay content gradient, and possibly a fairly homogeneous habitat for

palms, did not shift the relative contributions of geographical and environmental distances as predictors of palm floristic distances. Geographic distance was not a significant predictor or explained a very small portion of the variance. Absence of an effect of geographical distances when the gradient was shortened suggests that dispersal limitation may be leaving detectable signs only at very local scales, since our plots were at least 1 km apart. This is expected from similarity decay curves under the neutral theory (Hubbell 2001), in which the fastest decay is predicted for the smallest distances, typically well below 1 km.

Environmental responses of palms at the mesoscale

Both canopy and understory palm compositions were strongly related to the soil properties at Reserva Ducke, but slope had no effect on palm stand composition, contrary to the pattern observed for other plant groups in the same area (Costa et al. 2005; Drucker et al. 2008; Kinupp & Magnusson 2005; Garcia 2005). It is possible that one of the main effects of slope on plants is linked to litter thickness, which tends to be smaller as inclination increases. Higher depths of the litter layer generally inhibit small-seeded plants, for which litter constitutes a barrier (Facelli & Pickett 1991). Pteridophytes and the shrubs studied all have small propagules, while palm species found at Reserva Ducke have seeds at least one order of magnitude larger. Absence of restrictions imposed by litter thickness may be the cause of absence of slope effects for palms.

Base content, which can be regarded as part of a fertility gradient, was significantly related to the composition patterns, but explained only a small proportion of the variance. A small amplitude of variation may preclude differentiation of species composition along this gradient, since the range of values of exchangeable bases observed at Reserva Ducke (0.03 – 0.11 cmol.kg⁻¹) is very small compared to most areas where fertility was detected as a significant predictor of plant composition (e.g. Vormisto et al. 2004a; Jones et al. 2006). The texture gradient was a stronger predictor of composition at Reserva Ducke, and probably this is related to the association of texture with soil drainage.

Fine-scale variation in composition

Understory palms showed large variability in composition in areas with clay content below 10%. The separate analysis of these sandy plots showed that part of the variation in composition is associated with fine-scale variation in environmental conditions of plots. Bottomlands are heterogeneous areas, in terms of water retention in the soil and water-table depth (Hodnett et

al. 1997; Drucker et al. 2008), light incidence (Drucker et al. 2008) and flooding patterns (Pazin et al. 2006) and this environmental variability was not incorporated in our analysis. However, distance to watercourses, a descriptor which may aggregate some of these effects, could predict 43% of variation in understory composition in bottomlands. Drucker et al. (2008) documented variation in herb composition in bottomlands that was associated with the distance to the water course margins, and showed that soil water potential changed from the margins to the border of slopes. Therefore, understory palms are probably responding to more subtle gradients which were not measured here. However, Lieberman et al. (1985), who also found higher variability of composition of trees and lianas in bottomlands as compared to higher altitude plots at La Selva, Costa Rica, showed that composition in these lowland areas was not related to the mapped microtopography of plots. Variation in species dominance between bottomland samples may also be linked to dispersal limitation. Bottomlands may act as islands, with limited movement of propagules between them, and therefore the composition of each area could be a function of historical colonization processes. Dominance by a different species in close but isolated islands with the same environmental conditions was predicted by Hubbell (2001), as a function of dispersal limitation. Our evidences suggest that both the environmental and the dispersal explanations may be simultaneously correct. Variation in environmental factors such as susceptibility to waterlogging may be the cause of the largest part of the variation in composition. However, even after considering its effects, through the surrogate 'distance to watercourses', there was still a large amount of unexplained variance in composition, which could be a result of limited dispersal.

Our results suggest that community structure changes not only between broad topographic classes, but is also structured along fine-scale variations inside some of these classes. Partition of microtopographic niches in flooded or permanently humid areas was observed in several studies reviewed by Svenning (2001). Therefore, the potential for niche differentiation along topographical gradients is certainly greater than assumed by Wright (2002).

At Reserva Ducke, as in many terra-firme sites in Central Amazonia predominantly covered by latosols and podzols, water drainage patterns seem to be the major controllers of plant distribution pattern along topographic gradients. Drainage patterns are more variable inside bottomlands, and tend to change less from middle slopes to ridges, what agrees with distribution patterns observed for palms and other plant groups (Costa et al. 2005; Kinupp & Magnusson 2005; Drucker et al. 2008).

Conclusions

This study has shown that both palm assemblages respond to environmental gradients, but the patterns differ between overstory and understory assemblages, and the gradients differ in scale, with some environmental gradients being nested within others. This means that, although all environmental gradients are nested within geographic distances, they do not necessarily coincide. At the mesoscale, geographic distances cannot predict palm composition, suggesting that between 1 and 10 km dispersal limitation does not determine floristic similarity for this group. Within the same biogeographical domain, the amplitude of environmental gradients can be as important as the scale of analysis in determining the relative contributions of environmental and geographical components to community structure. Therefore, future studies should take into account the amount of environmental variability contained within sites to be compared.

The finding that much of the variation in palm species composition can be predicted from soil texture alone, at least in Central Amazonia, has important practical applications. Soil properties are largely coincident with altitude in central Amazonia (Chauvel et al. 1987; Anon. 1982), and fine-resolution altitude data is easily obtained from the SRTM (Shuttle Radar Topographic Mission) bases. With these data, it is possible to roughly establish distribution and abundances of plants with economic interest at the landscape scale, which is an essential first step for management plans. At the scale examined (100 km²), geographical distance was a very poor predictor of species turnover and cannot be used as a surrogate for compositional dissimilarity.

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