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Abstract: The mechanisms that maintain palm species diversity in tropical rain forests are still debated. Spatial variation in forest structure produces small-scale environmental heterogeneity, which in turn can affect plant survival and reproductive performance. An understanding of how palms respond to variation in forest heterogeneity may help to explain the diversity and structure of their assemblages. We used multivariate ordination statistics and multiple linear models to analyse how palm assemblages are affected by forest structure and landscape features in central Amazonia. In 72 (250×4 m) forest plots distributed over an area of 64 km², we recorded all seedling and adult palms, and measured topographic and soil variables, and components of forest structure and tree abundance. We found 16 976 adults and 18 935 seedlings of 46 palm species and five varieties including two morphological forms making a total of 50 botanical entities. Results show that landscape features (altitude, slope, proportions of soil sand and clay) and various components of forest structure (such as degree of forest openness, abundance of forest trees, logs and snags, and leaf litter mass), influence spatial variation in richness, abundance and species composition of palms, creating ecological gradients in palm community composition. Despite the statistically significant effects of environmental variables, most species occurred throughout the full range of the ecological gradients we studied, indicating that there is either relatively weak niche specialization in the palms, or that the competition between the species is mediated by diffuse demographic processes that cannot be evaluated only through studies of species distributions.

Key Words: Amazonia, forest spatial heterogeneity, palm richness, palm species composition

INTRODUCTION

The mechanisms maintaining high diversity and multi-species coexistence in tropical rain forests remain debated (Couvreur *et al.* 2011, Leibold 2008, Ricklefs 1977, Wright 2002). The regional species pool influences local plant diversity (Kristiansen *et al.* 2011, Vormisto *et al.* 2004), environmental and ecological factors also influence plant communities at local and regional geographical scales (Kristiansen *et al.* 2011). But understanding plant distribution patterns also requires consideration of microhabitat-scale distribution (Fowler 1988). How microhabitat variation explains local distribution and/or whether plant assemblages are influenced by ecological and environmental factors has been largely overlooked in tropical rain forests (Leibold 2008).

Some studies propose tropical forest species diversity results mainly from stochastic events (Condit *et al.* 1992). Others consider meso-scale environmental heterogeneity operating via ecological niche diversification (Clark *et al.* 1999, Russel & Schupp 1998, Svenning 1999, 2001a, b) and density-dependent mortality (Terborgh *et al.* 1996) to be key.

Environmental heterogeneity at both small and intermediate spatial scales is considered important in tropical rain-forest palm assemblage ecology and diversification (Eiserhardt *et al.* 2011, Svenning 1999). It can favour local coexistence of species-rich assemblages via niche differentiation, and is probably an important factor in palm evolutionary diversification (Svenning 2001b).

Palms are one of the most abundant and diverse Neotropical rain-forests plant groups (Balslev *et al.* 2011, Guèze & Paneque-Gálvez 2013, Scariot 1999) in the tropics, and nearly 90% in tropical rain forests (Couvreur

et al. 2011). They are found in almost all forest strata, from the understorey to the canopy, in all types of soil and topography, and exhibit many growth forms (Kahn & Castro 1985).

Studies on palms have reported assemblage composition being influenced by local topography (Costa *et al.* 2008, Kahn 1987), soil type (Emilio *et al.* 2014, Kristiansen *et al.* 2011, Peres 1994), light intensity and leaf litter depth (Cintra & Horna 1997, Cintra *et al.* 2005, Scariot *et al.* 1989), climate, soil, hydrology, regional topography and habitat stability (Eiserhardt *et al.* 2011, Kristiansen *et al.* 2011), plus such mutualistic interactions as seed dispersal effects (Losos 1995).

Few analyses discriminate adults from seedlings, probably because field identification of seedlings is not easy. Consequently, most information on palm assemblages focuses on how environmental and ecological factors affect adult distribution. To our knowledge, our study is the first to investigate the effects of the ecological variables on palm-seedling assemblages at the mesoscale (10–100 km).

We studied palm species abundance, composition and richness in the Reserva Ducke (RFAD), central Amazonia, Brazil. A central plateau divides RFAD into two halves, resulting in two drainage basins. Of similar size, these have significant differences in water type (eastern basin streams have crystalline transparent water; western basin ones have black water), forest tree biomass and herb communities (Castilho *et al.* 2006, Drucker *et al.* 2008). Therefore, we hypothesized differences in palm species assemblage will exist between basins due to greater tree biomass in the eastern basin (Castilho *et al.* 2006). This may create more niche resources and enhance opportunities for palm seed dispersal and seedling survival.

Our prediction was that the natural spatial variation in forest structure and landscape features will influence variation in palm assemblage structure. We investigated the effects of these variables on palm species richness, abundance and composition. We tested the hypothesis that, both for seedlings and adult palm assemblages, spatial variation in species composition will be influenced by spatial variation in both abiotic (landscape and soil) and biotic variables (forest structural components).

MATERIALS AND METHODS

Study area

Sampling occurred from April 2006 to October 2007 in the Reserva Ducke (RFAD) of the Instituto Nacional de Pesquisas da Amazônia (INPA). The RFAD is particularly well-suited for general studies investigating tropical forest heterogeneity, because it has a RAPELD grid of 18 8-km

trails covering an area of 64 km^2, allowing access to the entire reserve (Figure 1a, b). RAPELD is a method for rapid biodiversity surveys in long-term ecological research sites (Magnusson *et al.* 2005).

The RFAD, a 10 000-ha forest reserve, is located 30 km north of the city of Manaus (2º55′–3º01′S, 59º53′–59º59′W RFAD coordinates for corner points), in the Brazilian State of Amazonas (Figure 1a). Although the outskirts of Manaus have reached the southern and western boundaries of RFAD in recent years, the reserve is still connected to continuous forest on its eastern side. The reserve has eastern and western drainage basins separated by a central plateau oriented north-south. Streams in the eastern side of the reserve drain into tributaries of the Amazon River, whereas those on the western side drain into tributaries of the Rio Negro. The dominant vegetation in the reserve is primary terra firme forest, never inundated by large rivers (Ribeiro *et al.* 1999). The soils are predominately oxisols, and small streams are abundant in the area, resulting in an undulating terrain of lowlands, interspersed with plateaux that reach an altitude of up to 140 m asl (Ribeiro *et al.* 1999). Mean precipitation for the area is ~2300 mm y^{-1}, with most rainfall falling between November and May, and a dry season between June and October.

Experimental design and data collection

Palm surveys and measurement of forest structural variables were undertaken in 72 plots (250 × 20 m) uniformly distributed along nine 8-km trails (in a grid of 18 8-km trails) and covering almost the entire 64 km^2 area of the RFAD (Figure 1b). Trails are marked every 100 m. Eight plots that followed altitudinal contours were placed along each of the nine east-west trails. Soil conditions were relatively homogeneous within plots, since soil characteristics tend to vary with altitude (Chauvel *et al.* 1987). Using such thin plots along altitudinal contours maximizes between-plot vegetational variation and reduces within-plot topographic variation (Magnusson *et al.* 2005). The 72 plots were located at least 1 km from one another, and at least 1 km from the reserve borders, reducing possible edge effects (Figure 1b). Palms were sampled in 250 × 4-m subplots, logs/snags in 250 × 20-m subplots and live trees in 250 × 40-m plots.

Palm surveys

Seedlings and adults of all palm species were recorded within each of the 72 plots. Palms were identified by Ocírio Pereira who has worked with palms of central Amazonia for more than 15 y. We also used a field guide to plants of
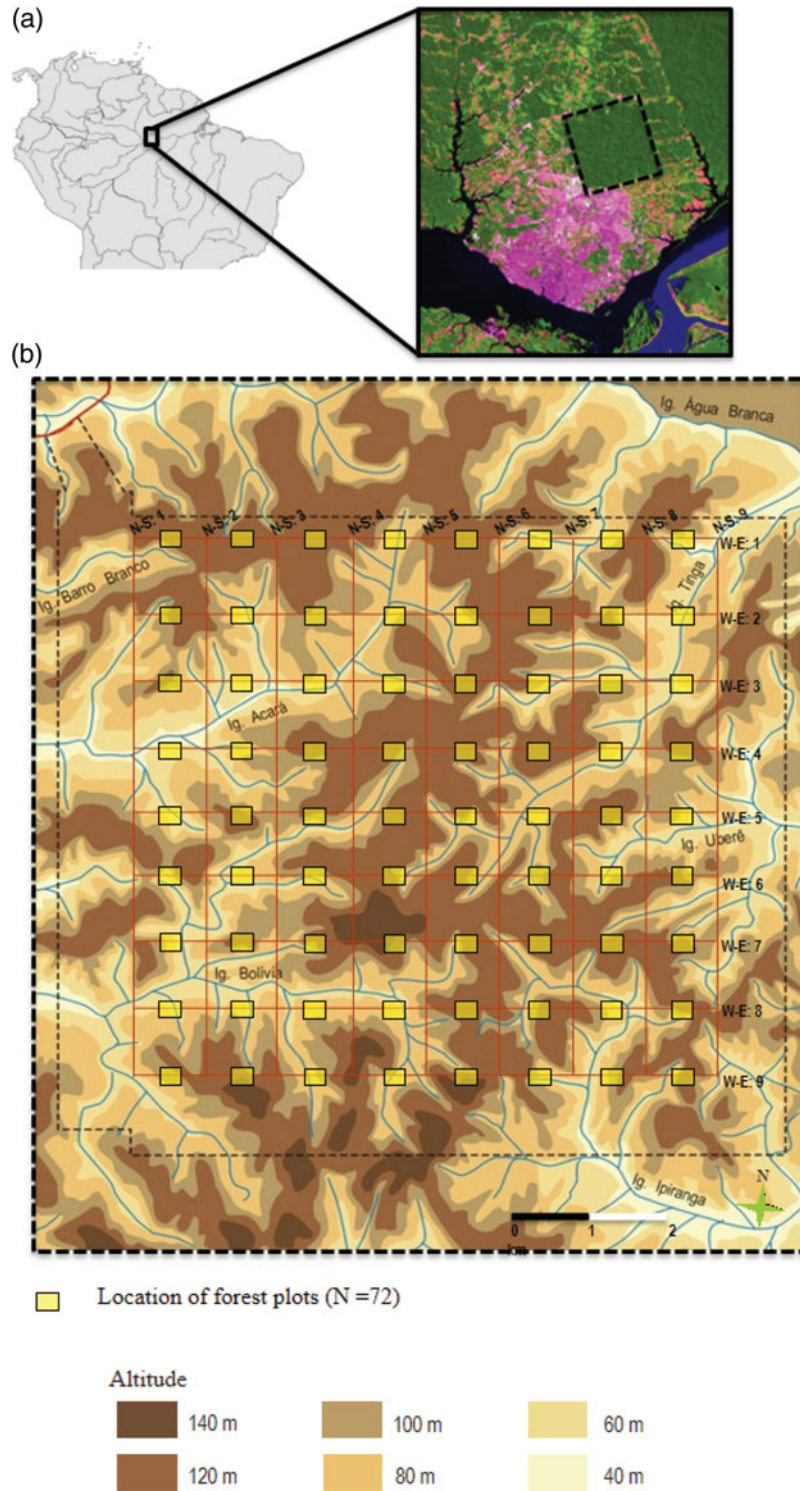
Figure 1. Map (a) of South America and location of study area, Reserve Ducke (the large square) near Manaus. Spatial location (b) of the 72 sampled plots (squares) within the study area at Reserva Ducke, central Amazon.

Reserva Ducke (Ribeiro *et al.* 1999). All individual palms were counted after subdividing the 4-m-wide subplot with a 2-m pole and surveying on each side, covering the entire area of the 250 × 4-m subplot. Clonal palms are rare in the reserve, but any clumps of clonal palm stems were counted as a single individual. Palms of the same age can have different sizes and architecture depending on the amount of light incident in its microhabitat (i.e.

whether they grew close to or far from a tree-fall gap). For example, *Astrocaryum* seedlings yearly surveyed across 6 y in the Peruvian Amazon varied between 22 and 42 cm depending on light conditions, and some plants may remain small for many years (Silman *et al.* 2003). Consequently, plants categorized as seedlings (palms with a maximum of two leaves and no more than 45 cm in height) may have been much more than 1 y old. Seedlings taller than 45 cm were not surveyed in our study. We considered palms as adults according to both: (1) their height or (2) by the number of leaves for acaulescent palms, following specialized literature (Henderson 1995, Lorenzi *et al.* 2010), for example: *O. bataua* (18 m), *Euterpe precatoria* (10 m), *Iriartella setigera* (3 m), *Geonoma aspidiifolia* (1 m) and *Attalea attaleoides* (eight leaves).

Recording the forest structural components

Forest canopy openness. We recorded forest-canopy openness using a spherical crown densiometer (Concave – Mode C – Robert E. Lemon, Forest Densiometer – Bartlesville, OK, USA). Measurements were obtained from four readings (north, south, east and west) at each of six positions (0 m, 50 m, 100 m, 150 m, 200 m and 250 m) along each 250-m plot. Following factory recommendations, we multiplied each reading by 1.04. Forest densiometers are easy to use and relatively accurate to estimate forest canopy openness, and are less affected by variation in cloud cover than other instruments (Englund *et al.* 2000).

Leaf litter mass. We used a wooden frame (50 × 50 cm) placed on the ground on the left and right side (two samples) of each sampling point (0 m, 50 m, 100 m, 150 m, 200 m and 250 m) along each 250-m plot. To minimize the effects of absence or concentration of leaf litter in a certain point, these two samples were mixed into one sample/point and then brought to the laboratory and oven dried for 72 h. The dry weight mean values from the six sampling points per plot were used in the statistical analysis.

Abundance of logs and snags. We recorded all logs and snags (standing dead trunks minimum of 1 m length and dbh $\geq$ 10 cm) within the 250-m plots. To measure their diameter we used a diameter tape (Forestry Suppliers, model 283D, precision $\pm$ 1 mm). The total number of logs and total number of snags were used as indices of abundance in the analysis.

Abundance of forest trees. All non-palm forest trees present in the plots were counted. Individuals $\geq$ 30 cm dbh were recorded within an area of 1 ha (40 × 250 m) in each plot

and their diameters measured with the diameter tape. The total number of trees per plot was used in the analysis as an index of abundance. We used trees > 30 cm dbh, because larger trees may be stronger competitors with palms for space. In the same area, most dead trees < 22 cm dbh and 48 cm dbh died standing, while trees between 22 and 48 cm dbh uprooted or snapped (Toledo *et al.* 2013).

Topographic variables. Two topographic variables, altitude and slope, were determined by Albertina Lima and a professional surveyor using a theodolite. The slope across the plot was measured perpendicular to the contour with a clinometer every 50 m along each plot, totalling six measurements per plot. The mean of the six measurements was used to represent the slope of the plot.

Soil texture. Values for soil variables were obtained from a composite sample of six topsoil (0–5 cm) cores taken every 50 m along the centre line of each 250-m plot. Samples for each plot were oven-dried and passed through a 2-mm sieve. The hydrometer method was used to estimate per cent clay and sand (<0.002 and 0.05–2 mm, respectively) (Mathieu & Pieltain 1998). Soil textural analyses were conducted at INPA. Soil data were provided by the PPBio Research Program in Biodiversity (MCTI–INPA).

Statistical analyses

To compare species composition among the 72 plots, we analysed both quantitative (abundance data) and qualitative (presence/absence data) matrices using Non-metric Multidimensional Scaling ordination analysis (NMDS), implemented in PC-ORD. This analysis summarizes more information in one to two dimensions than other indirect ordination techniques, and is more robust for non-linear effects (Minchin 1987). We used the Bray-Curtis distance measure to obtain values of dissimilarity between sites (McCune & Grace 2002). The resulting NMDS-scores were used as dependent variables in models of multivariate analysis of variance (MANOVA) and multiple linear models. We used two NMDS axes in the analyses, as in general, these explain most of the variance in the original variables for quantitative and qualitative data. We used an a posteriori Pillai-Trace test to analyse differences among sites in relation to the topographic gradient (plateau, slopes, lowlands), drainage basins (western and eastern sides of the reserve) and climatic seasonality. When evaluating the effects of drainage basins, we excluded plots located on the central plateau that divides the two basins.

The Pillai-Trace statistic has been shown to be less sensitive to deviations from assumptions than other multivariate statistics (Borg & Groenen 1997). We also

used multiple linear models followed by Pillai-Trace to evaluate the effects of the forest structural components on qualitative and quantitative community composition of seedling and adult palms across the reserve. These analyses were performed using GLM in Systat 12.0 version. A Pearson correlation matrix was constructed to verify correlation significance among forest structural components and landscape variables (independent variables). In those cases where independent variables were significantly correlated, these were used in different statistical models.

To detect for heteroscedasticity, we also used partial residual plots available in R (http://www.r-project.org). We also used R to verify possible linear relationships among predictor variables, estimating the variance inflation factor, which calculates the level of multicollinearity (Fox 2002).

We used qualitative (presence/absence data) and quantitative (abundance data) species composition matrices in the multivariate analyses. We used multiple linear models for qualitative and quantitative data, using NMDS axes as response variables in the models. The NMDS axes were regressed against the forest structural components as independent variables (forest trees abundance, canopy openness, fallen log abundance, snag abundance (all with dbh $\geq$10 cm); leaf-litter biomass, altitude, slope, % clay and % sand).

RESULTS

Palm surveys

We recorded 46 species and 50 botanical entities in a total of 16 976 adults and 18 935 seedlings (Appendix 1). The varieties of *Bactris acanthocarpa* and *Geonoma maxima* and the two morphological forms of *Bactris hirta* (pinnate- and bifid forms) were counted separately and considered as separate botanical entities in the analysis. Because not all palm taxa were represented in both the seedling and adult palm surveys (Appendix 1), we have included only 43 species both in the qualitative and quantitative matrices considered in the statistical analysis.

The most abundant palm in terms of adult individuals was *Astrocaryum sociale*, while *Astrocaryum sciophilum* and *Oenocarpus bacaba* had the highest abundance of seedlings. None of the palm species was found in all plots. However, *Oenocarpus minor* and *Astrocaryum gynacanthum* were present in more than 90% of the plots both as seedlings and adults. *Oenocarpus bataua*, *Oenocarpus bacaba* and *Astrocaryum sciophilum* also occurred in over 90% of plots, but only as seedlings (Appendix 1).

Forest structural components

There was variation within and among plots for almost every parameter measured, showing a high heterogeneity for our 72-plot sample. The mean abundance of forest trees per plot was 118 (range = 56–218 trees), that of fallen logs was 36 (range = 14–78), and of snags was 7.4 (range = 1–19). Mean leaf-litter biomass was 41 g and ranged from 24.0 to 64.4 g per plot. Mean percentage of canopy openness was 3.6% (range = 1.99–7.80%). Mean altitude was 76.2 m asl (range = 40.4–110 m), and mean slope was 9.9° (range = 0.7–27°). Mean percentage of sand in the soil was 49.1% (range = 8–98.1%) and that of clay was 47.4% (range = 1.62–87.7%).

The results of Pearson correlation analysis revealed that the only variables with very strong and significant correlation were % sand and % clay in the soil (r = −0.998; P < 0.001), % sand and altitude (−0.944; P < 0.001), and clay and altitude (r = 0.944; P < 0.001). Therefore, % sand and % clay were analysed in separate multiple linear models.

Palm richness and abundance

There was variation among the 72 plots for adult palm richness (mean = 14.7; SD = 3.02; range = 4–20) and abundance (mean = 235; SD = 70.6; range = 95–448); and seedling palm richness (mean = 17.3; SD = 3.55; range = 8–25) and abundance (mean = 263; SD = 129; range = 68–732).

Number of NMDS axes used in the analyses

Throughout this study, we used two NMDS axes for quantitative data and two axes for qualitative data as dependent variables. We found that two NMDS axes captured most of the variance in the original variables for presence/absence data in the seedling palm matrix (cumulative proportion of total variance, C_{PV} = 0.88), and two NMDS axes were also enough for the quantitative data matrix (C_{PV} = 0.93). Similarly, for the adult palm data, two axes captured most of the variance for presence/absence data (C_{PV} = 0.90), and two axes served for quantitative data (cumulative proportion of total variance, C_{PV} = 0.95).

Effects of forest structural components on palm richness and abundance

We found significant relationships between the parameters of the forest structural components, the number of palm species (richness) and of individuals

(abundance). Seedling palm abundance was only influenced by (and negatively related to) log abundance (multiple linear model, $R^2 = 0.163$, T = −2.27, P < 0.027), and not to any other forest component. Seedling palm richness increased with increasing altitude ($R^2 = 0.251$, T = 3.46, P < 0.001), and slope ($R^2 = 0.251$, T = 2.48, P < 0.016), decreased as log abundance increased ($R^2 = 0.251$, T = −2.36, P < 0.022) and was not influenced other forest components. Seedling palm richness increased significantly with an increasing soil sand % (simple linear model, $r^2 = 0.277$, N = 72, P = 0.019) and decreased with an increase in clay % ($r^2 = 0.269$, N = 72, P = 0.019).

Adult-palm abundance decreased with increase in tree abundance (multiple linear model, $R^2 = 0.551$, T = −6.62, P < 0.0001), log abundance ($R^2 = 0.551$, T = −3.04, P < 0.0001), leaf-litter mass ($R^2 = 0.551$, T = −2.87, P < 0.006) and an increasing amount of clay in the soil ($r^2 = 0.265$, N = 72, P = 0.025). But, adult abundance increased with increase in snag abundance ($R^2 = 0.555$, T = 3.01, P < 0.004) and with an increased % sand (simple linear model, $r^2 = 0.273$, N = 72, P = 0.020). Adult palm species richness decreased with increasing leaf-litter biomass (multiple linear model, $R^2 = 0.189$, T = −2.45, P < 0.017), but was not influenced by the other forest components.

Palm species distribution in relation to ecological gradients

Palm community composition was significantly influenced by altitude, % sand and log abundance (Figure 2a, b, c). However, in all cases, few species were strongly associated with the limits of the gradients, and most species occurred across the entire gradients of altitude, % sand and log abundance.

Effects of forest structural components on changes in palm-species composition

The variation in composition (qualitative data) for seedling palms was significantly related to altitude, tree abundance, leaf-litter mass, log abundance, % sand and % clay (Table 1, Figure 3). When assemblage similarity was evaluated using individual abundance (quantitative data), changes in species composition of seedlings were also correlated with altitude, slope, tree abundance, leaf-litter biomass, log abundance, % sand and % clay (Table 1, Figure 3). However, variation in species composition of seedlings was unrelated to variation in canopy openness, no matter if qualitative (presence/absence) or quantitative (abundance) data were used (Table 1).

With qualitative data, variation in species composition of adults was significantly related to altitude, slope, tree abundance, canopy openness, % sand and % clay in the soil, but not to leaf-litter mass, log abundance or canopy openness (Table 1, Figure 4). When the abundance of individuals was added to the community data (quantitative data), variation in species composition was also related to altitude, tree abundance, leaf-litter mass, log abundance, % sand, % clay and canopy openness (Table 1, Figure 4).

Changes in palm species composition between the two drainage basins

We found significant differences in adult palm composition between the two drainage basins (eastern and western sides of the RFAD) based on qualitative (presence/absence) data (MANOVA, Pillai-Trace test = 0.203; $F_{4,138} = 3.90$; P < 0.005), and quantitative (abundance) data (MANOVA, Pillai-Trace test = 0.237; $F_{4,138} = 4.65$; P = 0.002) (Figure 5a, b). We also found significant differences in species composition of seedlings between the two basins using qualitative (presence/absence) data (MANOVA, Pillai-Trace test = 0.236; $F_{4,138} = 4.61$; P < 0.002) and quantitative (abundance) data (MANOVA, Pillai-Trace test = 0.271; $F_{4,138} = 5.41$; P < 0.0001) (Figure 5c, d).

DISCUSSION

The study indicated that palm assemblage composition varies considerably at this spatial scale (64 km^2) in terra-firme forest in central Amazonia. This study also adds to the increasing evidence that suggests that the natural heterogeneity found within tropical forests affects the local composition of plant and animal communities. There are several examples of this with other taxa from the current study site (Banks & Cintra 2008, Castilho *et al.* 2006, Cintra & Naka 2012, Cintra *et al.* 2005, Costa *et al.* 2008, Kinupp & Magnusson 2005, Mendonça *et al.* 2005, Menin *et al.* 2007).

We found that some of the analysed variables were associated with recorded number of palm species (richness), of individuals (abundance), and changes in palm species composition, and found significant relationships between these and altitude, tree abundance, leaf-litter mass and log abundance. We also found that changes in palm composition can, in part, be attributed to a topographic gradient (plateau-slope-valley), physical soil properties and basin identity.

Most palm species occur throughout the RFAD and the central plateau, which does not represent a geographic barrier. Therefore, we believe our results indicate that palms are tracking differences in the landscape, and in those structural elements of the forest that vary between watersheds.
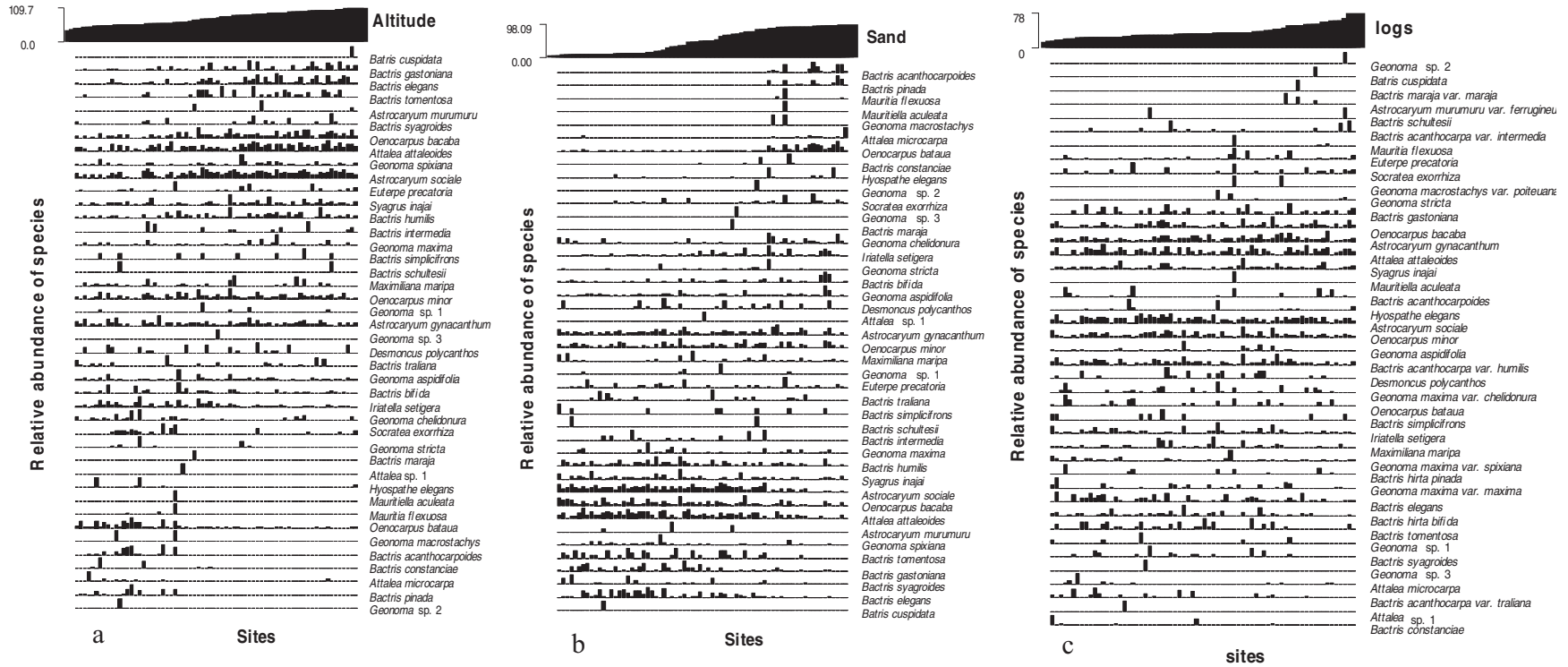
Figure 2. Palm species recorded in each of the 72 plots, quantitative data for adult palms (species abundance), in relation to gradients of altitude (a), % sand in the soil (b), and abundance of logs (c) in terra firme forest, central Amazon. Plots at the base of the graph in an increasing order from left to right (i.e. lower areas are to the left of the x axis). Bars represent the abundance of each species in a given plot. Bars give relative abundance within species but are not comparable between species because the number of individuals varied among species (Appendix 1). Numbers in the top of figure represent the range values of the response variable.

Table 1. Results of the multiple regression analyses performed to evaluate the effects of forest structural components on qualitative and quantitative measures of seedling palm and adult palm communities in a Brazilian Amazon terra firme forest (Manaus). The analyses were performed on scores from Multidimensional scaling (NMDS). Because % sand and % clay were significantly correlated to other variables, these two variables were analysed in separate multiple linear models. NMDS-axes were used in both models for quantitative and qualitative analysis. The negative and positive signals within parentheses are given to indicate the directions of the relationships and are not related to Pillai-Trace values.

Variables	Qualitative				Quantitative			
	Pillai-Trace	F	df	P	Pillai-Trace	F	df	P
Seedling palms								
Forest tree abundance	0.15	5.74	2,63	0.005	0.18	6.97	2,63	0.002
Snag abundance	0.01	0.42	2,63	0.655	0.06	1.86	2,63	0.164
Log abundance	0.19	7.34	2,63	0.001	0.18 (-)	6.76	2,63	0.002
Leaf litter biomass (g)	0.07	2.54	2,63	0.087	0.12	4.18	2,63	0.020
% sand	0.30 (-)	15.0	2,69	0.001	0.49	32.8	2,69	0.001
% clay	0.31	15.5	2,69	0.001	0.49	32.9	2,69	0.001
Canopy openness	0.03	0.94	2,63	0.395	0.03	1.13	2,63	0.330
Altitude (m)	0.30	13.5	2,63	0.001	0.57	42.1	2,63	0.001
Slope	0.03	0.97	2,63	0.386	0.13	4.88	2,63	0.011
Adult palms								
Forest tree abundance	0.23	9.60	2,63	0.001	0.33	15.5	2,63	0.001
Snag abundance	0.01	0.36	2,63	0.701	0.01	0.26	2,63	0.775
Log abundance	0.05	1.85	2,63	0.166	0.17	6.58	2,63	0.003
Leaf litter biomass (g)	0.03	0.97	2,63	0.385	0.15 (-)	5.54	2,63	0.006
% sand	0.37 (-)	20.0	2,69	0.001	0.46	29.9	2,69	0.001
% clay	0.37	19.9	2,69	0.001	0.46	29.8	2,69	0.001
Canopy openness	0.25	10.6	2,63	0.001	0.02	0.56	2,63	0.576
Altitude (m)	0.45	26.3	2,63	0.001	0.59	45.8	2,63	0.001
Slope	0.12	4.35	2,63	0.017	0.17	6.58	2,63	0.003

There was a significant response by the palm assemblages to a topographic gradient (plateau-slope-valley), even though the altitudinal range between our plots was only 75 m (39–114 m asl). Although this variation is small, it is enough to create a topographic gradient that includes higher flatter areas (plateaux), low areas (valleys, which often flood on rainy days) and either gentle or steep slopes connecting the two. This topographic gradient has been related to several soil parameters, particularly the proportions of clay and sand in the soil (Chauvel *et al.* 1987), which in turn has been shown to be the best predictor of above-ground tree biomass at RFAD (Castilho *et al.* 2006) and also at other sites in central Amazonia (Laurance *et al.* 2002). This topographic gradient at RFAD has also been shown to affect the distribution of palms (Costa *et al.* 2008, Raupp & Cintra 2011), ants (Oliveira *et al.* 2009), frogs (Menin *et al.* 2007) and birds (Cintra & Naka 2012), and here we show that it also affects the distribution of palm seedlings.

Variation in species composition (qualitative data) was significantly related to spatial variation in landscape, soil properties and forest structural components for seedlings and for adults. In addition, differences in relative abundances (quantitative data) for both adult and seedlings were correlated with most of the same variables. Our results corroborate those of Emilio *et al.* (2014), which indicate that palms and trees are associated with different physical soil conditions. Those authors defended the idea that adaptation of these life forms

is the mechanism that drives their responses to soil structure, and such responses, therefore, are important in shaping the overall physiognomy of Amazonian forest vegetation.

The central plateau divides the RFAD and results in two relatively similar-sized drainage basins that differ significantly in their palm assemblage compositions. Similar results have been found for assemblages of herbs and palms (Costa *et al.* 2008, Drucker *et al.* 2008), fish (Mendonça *et al.* 2005) and birds (Cintra & Naka 2012). Therefore, it is possible that the differences in palm assemblages between basins are due to differences in tree biomass and soil composition, the former being higher in the eastern basin of the RFAD (Castilho *et al.* 2006). Higher tree biomass may result, for both plants and animals, in more niche resources and enhanced opportunities for dispersal and survival, but these indirect relationships remain speculative.

The general trend of a decrease in seedling richness and abundance as the abundance of forest logs increased may be related to the process of plant secondary dispersal and predation by vertebrate frugivores (Cintra 1998, Kiltie 1981, Silman *et al.* 2003).

Palm assemblages clearly responded to graded changes in key ecological factors, but the response was not uniform. There was a gradual substitution of palm species with increasing terrain altitude. We detected three species groups in relation to altitude, that included (1) palm species that occur more frequently on higher areas (the
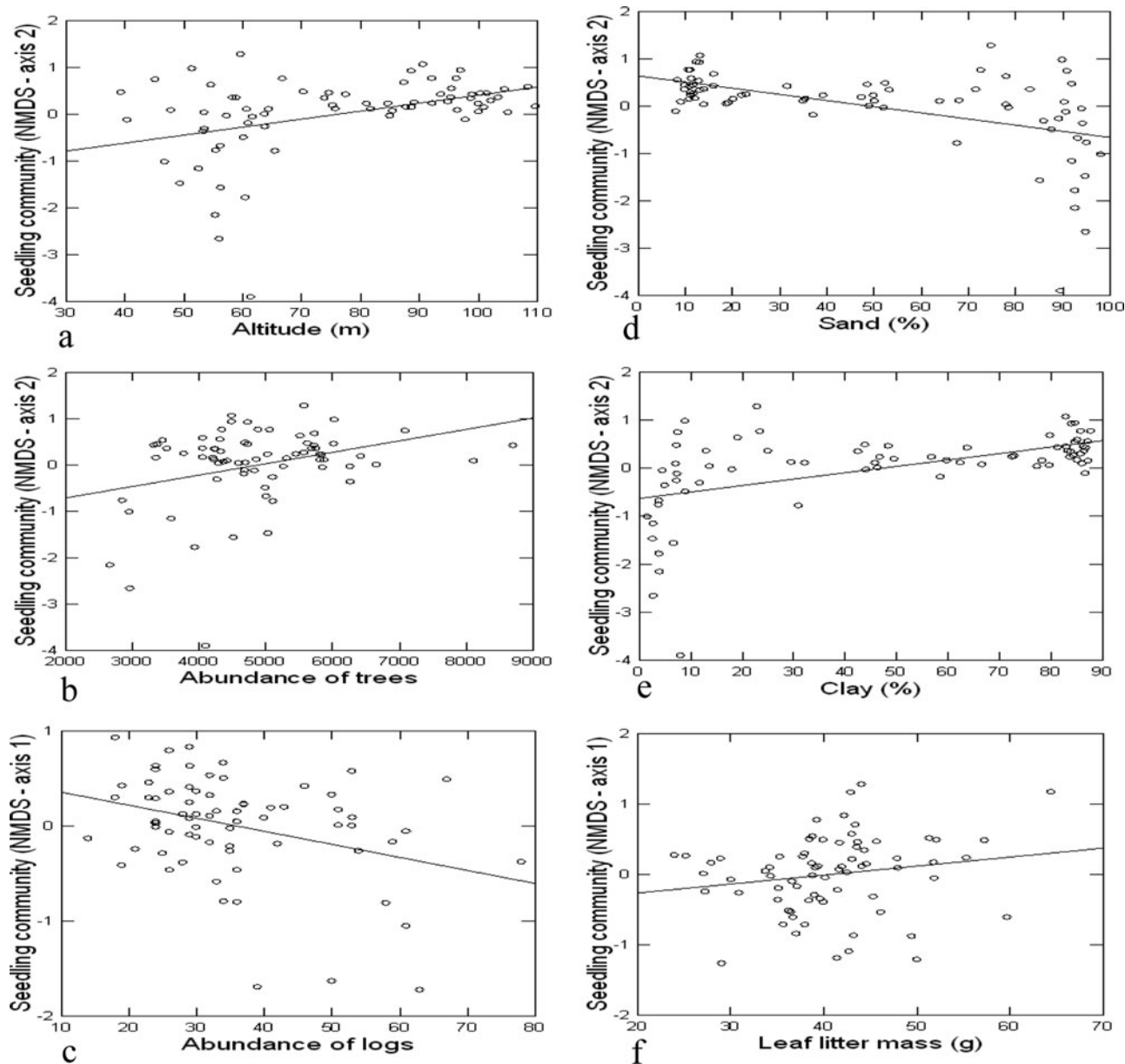
Figure 3. Relationships between NMDS-axes (variation in seedling palm community composition) from qualitative data in relation to altitude (a), tree abundance (b), logs (c), % sand (d) and % clay (e); and an NMDS-axis from quantitative data in relation to leaf-litter mass (f) in Central Amazon.

plateau) and composed mainly of understorey species (e.g. *Bactris cuspidata* to *Bactris syagroides*); (2) palms that occur throughout the topographic gradient in the RFAD independent of altitude composed of both canopy and understorey palms (e.g. *Oenocarpus bacaba* to *Geonoma stricta* var. *stricta*); and (3) palms that occur more frequently in areas with lower altitude (valleys) composed mainly of understorey species, such as *Bactris maraja* var. *maraja* to *Geonoma* sp. 2.

Several palm species were more or less restricted to sandy soils (e.g. *Bactris acanthocarpoides*, *Astrocaryum acaule*, *Mauritia flexuosa*, *Mauritiella aculeata* and *Geonoma macrostachys*) (Figure 2b). Others, such as

Bactris cuspidata and *Astrocaryum murumuru* var. *ferrugineum*, were found mainly in plots with high clay content.

Spatial variation in soil properties may create a complex series of gradients within the forest in which each palm species is a superior competitor in a particular sub-area along this gradient (Tilman 2004). Therefore, the importance of a given physical or biological resource may be different for each palm species and, even evaluating some of them together, it is still difficult to find and identify in a very complex environment the key factors which form the defining resource for palm niches. We found seedling and adult abundance increased with increases in
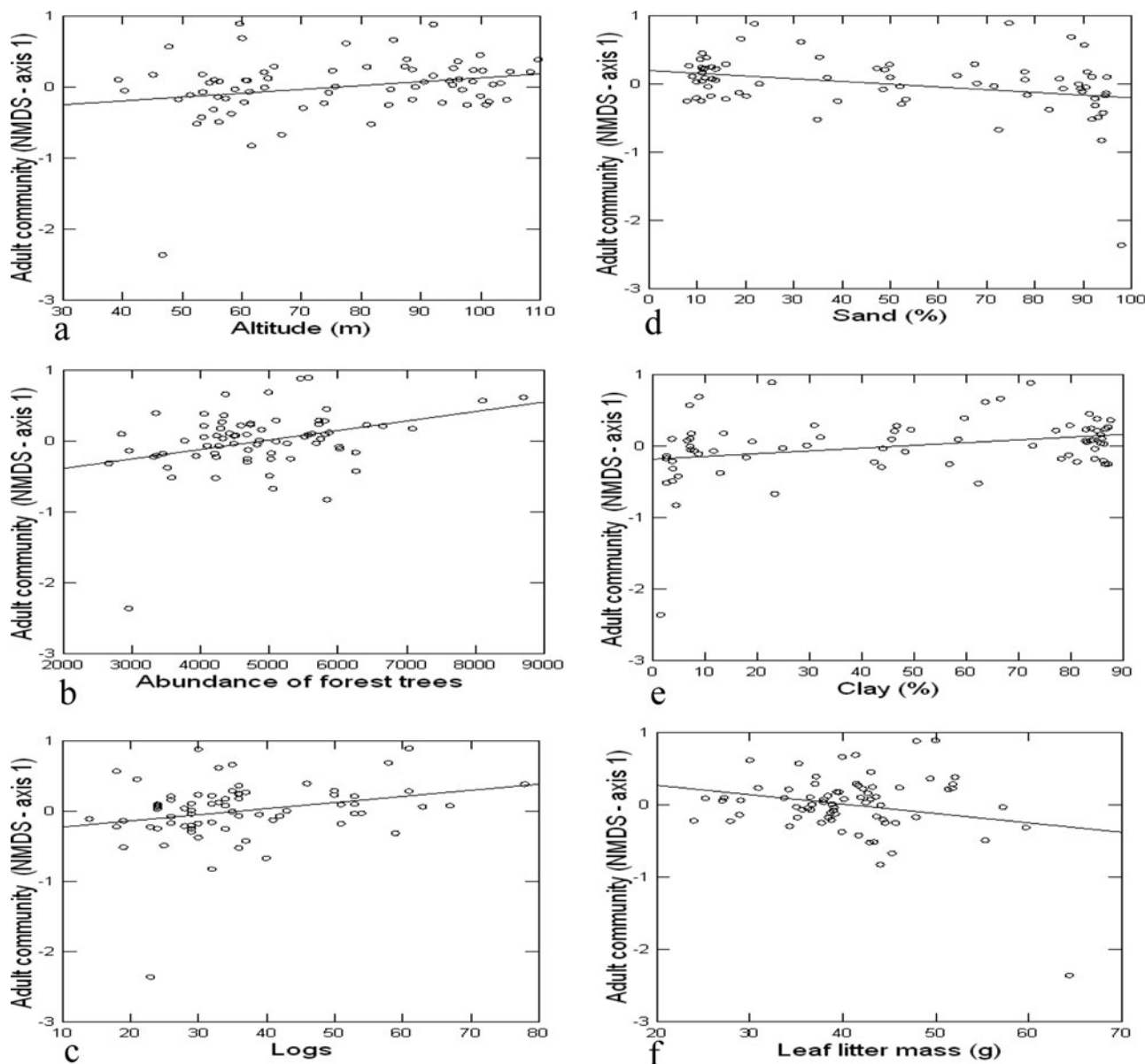
Figure 4. Relationships between NMDS axes (variation in adult palm community composition) from quantitative data in relation to altitude (a), tree abundance (b), logs (c), % sand (d), % clay (e) and leaf-litter mass (f) in central Amazon.

soil sandiness, while seedling species richness increased with higher proportions of soil clay. However, changes in species assemblages of seedlings (for qualitative and presence/absence data) did not follow the same patterns. They showed a trend to decrease with increases in soil sandiness and increase with clay concentration (Figure 3d, e). Again, this pattern may result from species adaptations to a given type of soil.

We expected a greater abundance of palm seedlings in areas with higher leaf-litter mass, because palm seeds would be more protected or less vulnerable to predation and also because of the potentially higher nutrient availability in such areas as a consequence of increased plant matter decomposition (Luizão & Schubart 1987).

However, we found lower seedling palm abundance in such areas, probably because seeds were not able to penetrate the litter during their seedling phase, because they were attacked more often by pathogenic fungi which are more abundant in areas of greater litter accumulation (Augspurger & Kelly 1984), or because the falling leaves covered the seedlings. One of the indirect effects of leaf litter on growth and survival of palm seedlings is to produce changes in the local microclimatic conditions with increasing humidity favouring fungal growth (Cintra & Horna 1997, Cintra & Terborgh 2000, Sork 1983).

The abundance of adult palms was lower in areas with more trees. Although palms are adapted to shady
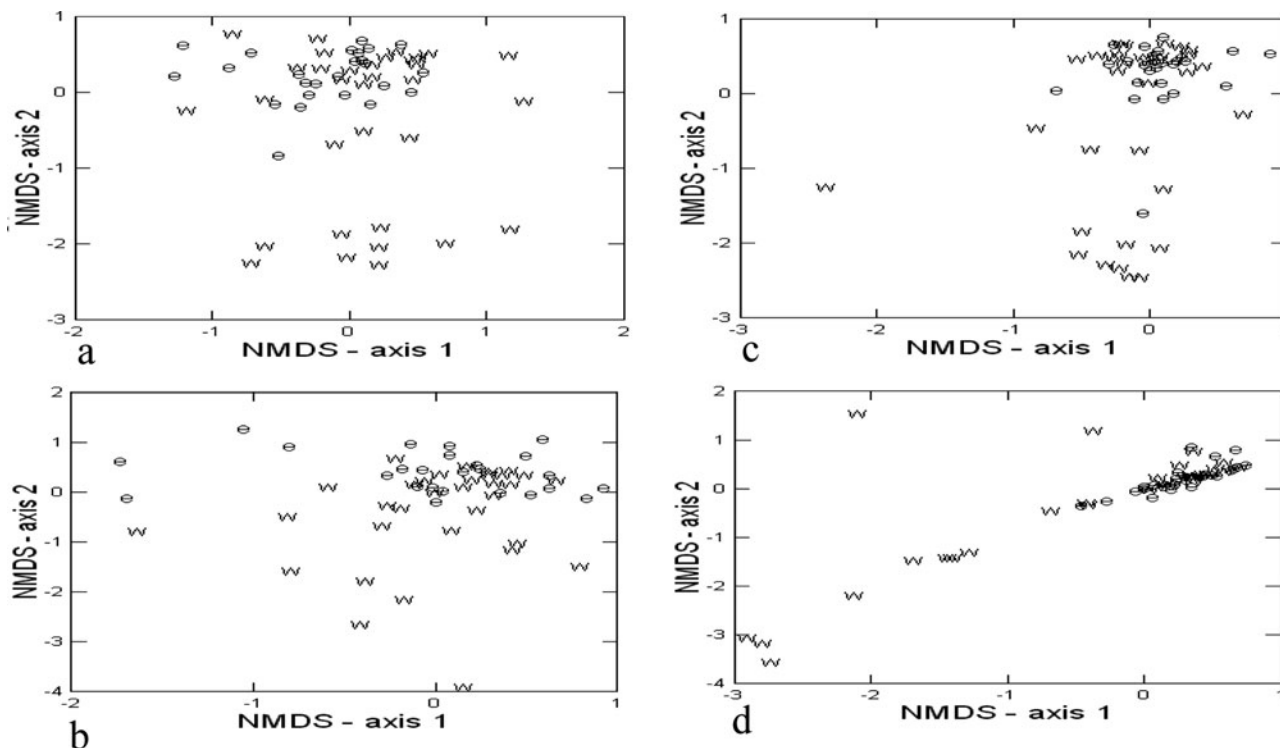
Figure 5. Similarities in palm community composition: qualitative data for seedlings (a), quantitative data for seedlings (b), qualitative data for adults (c), quantitative data for adults (d), between the water basins located on western (w) and eastern (e) sides of central plateau which is oriented north-south and divides the Reserva Ducke into these two drainage systems. Plots from the plateau areas were not included in the analysis.

conditions, they still need a minimum amount of incident light for photosynthesis, as well as water and nutrients for growth. All of these essential resources are likely to be less available in areas with high density of other plants. Also, positive and negative interactions in the survival of seedlings near adults have been documented (Cintra 1997a, b; Ibáñez & Schupp 2001). In the Neotropical rain-forest understorey in Costa Rica, forests seedlings of canopy tree species compete with a well-developed community of shrubs, palms, herbs and treelets (Denslow *et al.* 1991).

In our study area, Costa *et al.* (2008) found that dispersal limitation does not explain palm composition at the mesoscale, and that soil and topography can predict a large proportion of palm composition, even though some environmental gradients differ in scale and are nested within others so that they do not necessarily coincide. They concluded that geographical distance was a poor predictor of palm species turnover and should not be used as a surrogate for compositional dissimilarity. However, studies in other areas reached different conclusions (Guèze & Paneque-Gálvez 2013). Considering both seedlings and adults, our results corroborate the findings of Costa *et al.* (2008).

In general, our results corroborate earlier studies about palm ecology in the same and other areas in the Amazon region (Balslev *et al.* 2011, Cintra & Horna 1997,

Costa *et al.* 2008, Raupp & Cintra 2011). We conclude that individuals in more than one demographic stage such as seedling and adults can be similarly affected by soil conditions, forest structure and dynamics both locally (at microsite scale) and in a broader spatial scale (landscape scale) through the changes in the palm species composition produced by ecological gradients.

The patterns of palm species composition following gradients of ecological resources reinforce the idea that niche specialization could be a factor promoting the coexistence of many palm species in tropical rain forests. However, the topographic-edaphic niches of the species we studied overlapped considerably, and many of the species could be found throughout the ecological gradients we studied.

Despite the statistically significant effects of environmental variables, most species occurred throughout the full range of the ecological gradients we studied, indicated that there is either relatively weak niche specialization in the palms, or that the competition between the species is mediated by diffuse demographic processes that cannot be evaluated only through studies of species distributions.

More refined investigations on niche specialization, which not only evaluate ecological factors acting in different spatial and temporal scales but also consider differences in plant species demographic responses (Raupp

& Cintra 2011) may help increase our understanding of the influences of forest structure components and landscape on palm assemblage composition.

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Appendix 1. Palms species abundance (adults and seedlings) and frequency of occurrence on 72 plots at Reserve Ducke, Manaus. Authorities for this entire species list are available in Ribeiro *et al.* (1999). An abundant species in the adult category (*Astrocaryum sociale*) is missing in the seedling category, and also a species in the seedling category (*Astrocaryum sciophilum*) is missing in the adult category. This was due to misidentification during the field surveys as the species have very similar appearances at the seedling stage. We then re-constructed the ordination figures, with the two species (which are also abundant as many others) removed. We found the same distribution pattern of the palm community in relation to the environmental variables (altitude, % sand and logs) as before and do not think this oversight, whilst regrettable, will change the overall results of the study. Codes: AA = adult abundance; AF = Adult frequency; SA = Seedlings abundance; SF = Seedlings frequency.

Taxon

Adults	AA	AF
Astrocaryum sociale	5537	64
Oenocarpus bataua	2231	62
Attalea attaleoides	1392	63
Astrocaryum gynacanthum	1263	68
Iriartella setigera	902	62
Oenocarpus minor	848	65
Bactris elegans	734	49
Attalea microcarpa	551	17
Oenocarpus bacaba	511	59
Bactris acanthocarpoides	449	13
Bactris acanthocarpa var. *humilis*	433	59
Geonoma aspidiifolia	342	54
Bactris hirta (pinnate form)	320	13
Syagrus inajai	285	58
Bactris hirta (bifid form)	275	47
Attalea maripa	131	25
Geonoma maxima var. *spixiana*	121	32
Euterpe precatoria	80	24
Bactris gastoniana	72	33
Geonoma stricta	63	12
Geonoma maxima var. *chelidonura*	57	22
Bactris tomentosa	48	23
Bactris acanthocarpa var. *trailiana*	48	15
Hyospathe elegans	45	9
Socratea exorrhiza	42	16
Geonoma maxima var. *maxima*	40	19
Desmoncus polyacanthos	33	16
Bactris syagroides	26	13
Bactris acanthocarpa var. *intermedia*	24	10
Bactris constanciae	13	5
Astrocaryum murumuru var. *ferrugineum*	12	3
Mauritia flexuosa	12	3
Astrocaryum acaule	10	5
Bactris simplicifrons	9	8
Geonoma sp. 1	9	5

Geonoma macrostachys	2	2
Bactris schultesii	2	2
Geonoma sp. 2	1	1
Bactris cuspidata	1	1
Mauritiella aculeata	1	1
Attalea sp. 1	1	1
Bactris maraja var. *maraja*	1	1
Geonoma sp. 3	1	1

Seedlings	SA	SF
Astrocaryum sciophilum	3996	66
Oenocarpus bacaba	3855	70
Oenocarpus bataua	1983	68
Astrocaryum gynacanthum	1169	68
Iriartella setigera	1114	61
Attalea attaleoides	988	64
Geonoma aspidiifolia	964	61
Bactris hirta (bifid form)	820	56
Bactris elegans	486	52
Oenocarpus minor	451	65
Attalea microcarpa	424	17
Syagrus inajai	389	54
Bactris simplicifrons	381	53
Bactris acanthocarpa var. *humilis*	288	59
Euterpe precatoria	214	50
Socratea exorrhiza	161	38
Bactris tomentosa	159	33
Bactris gastoniana	142	43
Geonoma maxima var. *spixiana*	128	37
Bactris acanthocarpoides	122	17
Geonoma maxima var. *maxima*	109	35
Geonoma stricta	105	25
Bactris sp. 2	70	10
Bactris syagroides	59	18
Bactris sp. 3	58	5
Geonoma sp. 2	41	16
Attalea maripa	41	9
Geonoma maxima var. *chelidonura*	37	15
Hyospathe elegans	30	9
Bactris acanthocarpa var. *trailiana*	29	13
Desmoncus polyacanthos	28	16
Bactris sp. 1	22	8
Astrocaryum murumuru var. *ferrugineum*	14	3
Mauritia flexuosa	13	5
Bactris cuspidata	8	5
Bactris constanciae	8	4
Bactris balanophora	8	3
Geonoma macrostachys	5	3
Bactris killipii	5	2
Bactris schultesii	4	3
Bactris aubletiana	4	2
Geonoma sp. 1	2	2
Astrocaryum acaule	1	1