THE PALM COMMUNITY IN A TERRA FIRME TROPICAL RAIN FOREST IN THE BOLIVIAN AMAZON AND FACTORS STRUCTURING ITS BETA DIVERSITY

Introduction

The rain forests of the Neotropical lowlands are known for their extreme species richness being among the richest in the world (Losos and Leigh 2004, Friis and Balslev 2005). Palms play an important role in the diversity and structure of these forests (Gentry 1988). The highest species richness of palms is found in the hot and humid areas of the Americas, the Chocó area being the richest, followed by the Mesoamerican Isthmus (Panama and Costa Rica) and the western part of the Amazon Basin in the northern part of Peru together with a long corridor along the eastern slopes of the tropical Andes (Bjorholm et al. 2005). In these forests, palms are diverse, abundant, and often even dominant and they include a range of life forms from small shrubs growing in the understory of the forests to tall trees rising to the canopy and lianas (Kahn and de Granville 1992, Henderson 1995, Scariot 1999). In the major habitat types of the tropical Amazonian rainforests, palm communities differ in species composition, having very high levels of palm species and genus richness in *terra firme* forests while in the flooded and swamp forests the palm flora seems to be less diverse, even though the contribution of palms to the structure of the forests can be dominant (Kahn and de Castro 1985, Balslev et al. 1987, Kahn and de Granville 1992, Normand et al. unpublished, Sanjines et al. unpublished). The occurrence of palm species in the neotropical rain forests is sometimes strongly influenced by environmental conditions (Svenning 2001). Hydrology and topography are main factors that control distribution of palms at local scales (Kahn and de Castro 1985, Kahn 1987, Kahn and de Grandville 1992, Vormisto et al. 2000, Vormisto et al. 2004 a, Normand et al. unpublished), though many palm species exhibit distributions that are strongly influenced by the heterogeneity of the microhabitat, particularly in relation to topography, drainage, height of the forest canopy and/or edaphic factors (Clark et al. 1995, Svenning 1999, Boll et al. 2005, Vormisto et al. 2004). At a continental scale patterns of palm species richness seem to be controlled mainly by water availability (annual precipitation and number of wet days), though soil and unknown large scale factors, maybe historical or geometrical processes are also important (Bjorholm et al. 2005).

Recent studies have demonstrated that both the geographic distance and environmental differences influence beta diversity in the Amazonian *terra firme* forests. Nevertheless, the relative importance of these factors seems to vary, some studies emphasize the first one (Condit et al. 2002, Duivenvoorden et al. 2002, Duque et al. 2002, Vormisto et al. 2004a), while others emphasize the latter (Phillips et al. 2003, Tuomisto et al. 2003a, b). Additionally, it has been suggested that the relative importance of the factors that structure the communities in tropical forests is dependent on scale (Condit et al. 2002, Willis and Whittaker 2002). In the Peruvian Amazon, Vormisto et al. (2004b) have reported that the relative importance of geographic distance and environmental differences as controllers of beta diversity in palm communities in terrace forests is dependent on scale. Environmental differences, notably in soil moisture, are the most important controller of beta diversity of palms at a local scale, while the effect of geographic distance is more important at the regional scale. Normand et al. (unpublished) conclude that not only the local environment, but also dispersal limitation and the biogeographical history may be important controllers of the diversity and composition of local plant communities.

Many studies on beta diversity in Amazonian forests have focused on *terra firme* forests and other forests of the Peruvian Amazon (Condit et al. 2002, Duivenvoorden et al. 2002, Duque et al. 2002, Normand et al. unpublished, Phillips et al. 2003, Tuomisto et al. 2003 a,b, Vormisto et al. 2004 a, Sanjines et al. unpublished). Here we examine the beta diversity of the palm community in a *terra firme* forest in the Madidi region in the northwestern part of the Bolivian Amazon, located at the margins of the Amazonian area joining the eastern slopes of the tropical Andes. This area represents the fourth richest area in palm species (Bjorholm et al. 2005) and also corresponds to the second richest global center of diversity (Barthlott et al. 1996). Across the Americas, palm species richness is highest in humid tropical areas. Species richness declines with latitude even between 10° N to 10° S within the tropical zone. Thus, the highest palm species richness is found in the Chocó region with 83 species per grid square, followed by the adjacent Mesoamerica with 78 species per grid square. The third area in species richness, with a maximum of 69 species per square grid in the western part of the Amazonian Basin in Peru, adjacent to the eastern slopes of tropical Andes, which house 57 species per grid square (Bjorholm et al. 2005).

It is widely accepted that anthropogenic activities threaten the biodiversity of tropical forests (Dirzo and Miranda 1990, Redford 1992, Terborg 1992, Noble and Dirzo 1997, Phillips 1997). This is also the case in our research area, the Madidi region, where increasing colonization with the following enlargement of cultivated areas, cattle raising and overgrazing, added to wood extraction by legally established companies, cause an extensive deforestation and the diminishing of many plant species (Beck et al. 2002). It is known that about 33% of the palm species of the world are considered threatened (Smith et al. 1993). Many palms do not regenerate in open areas and are therefore threatened in areas with extensive deforestation (Pedersen 1994, Moraes et al. 1995). It has been reported that in forests with different levels of human disturbance and in fragmented forests, some palm species are negatively affected, while others benefit (Svenning 1998, Scariot 1999). Several species of useful palms are also negatively affected due to intensive exploitation (Basnet 1992, Balslev 2002, Knudsen et al. unpublished). Approximately 29 species of palms are known from the Madidi region (Moraes et al. 1995) and more than half of these species are used by the local people (Tacanas groups and colonizers) as construction wood, for roof making, fruits eaten as food, drinks, heart of palm, oils, fibers for handicraft products, medicines and handicrafts (Moraes et al. 1995, De Walt et al. 1999). Based on these evidences and knowing the context of the Madidi region, in this study we analyze effects of the human disturbance on the composition and abundance of palm species in a *terra firme* forest with a different level of disturbance along the San Buenaventura-Alto Madidi road. To guide the study we formulated the following questions: (1) Which factors structure the floristic composition of the palm community? (2) Are there differences in the floristic composition, species richness, and diversity in the palm community that occurs on level terrain and that occurs on hilly terrain? (3) Are there differences in the floristic composition, species richness, and diversity in the palm community of a *terra firme* forest with different levels of disturbance? (4) What is the relative importance of the factors in the determination of beta diversity in the palm community? To answer these questions we established transects to make an inventory of the palm community and register environmental variables in forest with different types of terrain and different levels of disturbance, so as to analyze the palm community and the factors that control the variation in the composition of palm species in a *terra firme* forest in the Madidi region.

Methods

Study area

The study took place in a *terra firme* tropical rain forest that is established along the San Buenaventura–Alto Madidi road, main access road to the large towns of San Buenaventura, Tumupasa and Ixiamas[1], in the municipalities of San Buenaventura and Ixiamas of the Abel Iturralde Province, La Paz Department, at the northwest of the Bolivian Amazon. This region is in the buffer zone of the Madidi National Park and Natural Area of Integrated Management, one of the most diverse reserves in the world and part of the hotspot of the tropical Andes, the richest and most diverse in the planer (http://www.biodiversityhotspots.org/xp/Hotspots).

The climate in the area is typically tropical and humid, the annual precipitation is 1927 mm, the rainy season covers the months from October to February and the dry season the months from June to September with a precipitation under 100 mm. The monthly temperature average is 26°C, the highest temperatures are reached in the months from October to January and can reach 33°C. Between the months of March and June cold fronts (southerns) appear. These determine a temperature descent to below 10°C and a sudden increase in humidity due to slight precipitations (SNAP 2001). The altitude varies between 150 m and 700 m above sea level. In the Madidi region there is a wide range of diverse ecosystems and varied terrain topography that include a complex of mountain chains, from the last branching of the Eastern Cordillera, showing a gradual change from the mountain chains with steep slopes to undulating hills that end in a large plain or alluvial plain traversed by numerous rivers and brooks. This diversity of terrains determines the presence of various types of vegetation that correspond to the foothill forests on the hills and slopes, lowland humid forests, riverside forests, flooded forests and

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[1] From Ixiamas, the road that connects with the region of Alto Madidi narrows markedly making transit for cars and other small motor vehicles very difficult, especially during the rainy season.

terrace forests. The substrate presents special characteristics determined by the types of forest, topography, and climate. The soils vary from sandy and shallow on the steep slopes, to franco -sandy with acid pH on the plains (Beck et al. 2002). In areas that are adjacent to the main road that joins the larger towns, secondary vegetation develops constituted mainly of rice fields (*Oryza sativa*), corn fields (*Zea mays*) and manioc (*Manihot esculenta*), as well as secondary forests, fallows of different ages, and extensive grazing lands dominated by *Attalea phalerata*, *Astrocaryum murumuru*[2] and *Euterpe precatoria* (Beck et al. 2002). Species like *Iriartea deltoidea* and *Euterpe precatoria* have been reported as the most common and dominating in the area (Moraes et al. 1995, Beck et al. 2002).

Design of the sampling

With the help of satellite images we selected places of potential interest for the establishment of transects in the *terra firme* forest that occurs on both sides of the San Buenaventura–Alto Madidi road. In the area we clearly distinguished two important parameters. First, the type of terrain on which the forest develops, one characterized by a flat topography and extending along the east side of the road, and another type characterized by a hilly and undulating topography and extends along the western side of the road. Second, the level of disturbance of the forest. Three levels of disturbance were distinguished: (1) not disturbed forest, that has not been cut recently, is occasionally used, with forest structure (high canopy, stratification, with thick trunks), without cultivated fields or fallows, (2) moderately disturbed forest, that has been cut recently, frequently used, with forest structure (high canopy, stratification, with thick trunks), without cultivated fields or fallows and (3) highly disturbed forest, that has been cut in the recent past, affected by the felling of adjacent trunks generating forest clearings, very much used, with an altered forest structure, without cultivated fields or fallows. Taking into account these parameters, six Indigenous villages, both Tacanas and peasant, settled and distributed homogeneously on both sides and along the

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[2] *Astrocaryum murumuru* was identified with the key in the book Flora de Palmeras de Bolivia (Moraes 2004) The Field Guide to the Palms of the Americas (Henderson et al. 1995). There are, though, other studies that suggest that *A. murumuru* is a complex of species (Kahn and Millán 1992). In the region of Madidi, *A. murumuru* was different from the species observed in Peru, and is characterized by being a solitary palm in *terra firme* forests with thicker and smoother trunks. Some individuals did not have spines.

road were chosen for the installation of the transects in areas were the terrain was both level and hilly and in forests with different levels of disturbance.

The position of the transects was selected by walking between 1 and 2 hours from the community in the direction indicated by the local field helpers and stopping when the forest showed the required criteria.

Collecting the data

Twenty five linear transects, 500 m long by 5 m wide (each one subdivided in subunits of 5 x 5 m) were established in the *terra firme* forest. Thirteen transects in forest with level terrain and twelve transects in forest with hilly terrain (Figure 1). Of the total of 25 transects, seven were installed in highly disturbed forest, twelve in moderately disturbed forest, and six in not disturbed forest (Table 1).

In each subunit, along each transect, all individual palms, including seedlings, juveniles and mature individuals, were registered. For species with clones and multiple stems, each stem was counted as a separate individual, so the concept for an individual is “ramet” and not “genet”. Representative voucher specimens of the species which could be assigned a taxon with certainty were collected. The species are deposited in the herbaria of Aarhus (AAU) and La Paz (LPB). The nomenclature in this work follows the names assigned to the palms by Henderson et al. (1995). For each subunit we registered the canopy opening, amount of organic matter on the forest floor, gap conditions, soil moisture, presence of trails, and fallen trees (Table 2). The canopy opening was measured with a “canopy scope” (graduated from 0 to 25 points, Brown et al. 2000), while the other variables were measured visually with different scales (Table 2).

Numerical methods

To be able to analyze the change in the composition of the palm community in the *terra firme* forest and the potential factors that could be determining such a change, we examined the patters of the community at the transect level (2500 m^2) using Non-metric Multidimensional Scaling, NMS (McCune and Grace

2002), Indicator Species Analysis (Dufrene and Legendre 1997, McCune and Grace 2002) and Multi-Response Permutation Analysis, MRPP (McCune and Grace 2002).

We used NMS to analyze the most important floristic gradients of species palms data of 25 transects (McCune and Grace 2002). NMS is an iterative method of ordination that search for the best position of the samples on *k* dimensions (axes), so that the order range of the distances ends up being as similar as possible to the order range in the original data, minimizing the stress of the k-dimensional configuration (McCune and Grace 2002). The ordinations were made over the data of the species previously transformed to square root (to reduce the effect of the dominant species), using as defined parameters: Sorensen (Bray-Curtis) distance, random number as starting coordinates, 1-6 dimensions (axes), instability criterion of 0.00001, maximum number of iterations de 500, 40 runs with real data and 50 runs with random data (McCune and Grace 2002). The analysis was repeated six times (starting with one dimension and reaching six), until a dimensional solution that provided the largest stress reduction was obtained.

To prove the hypothesis that there is no difference in the forest that becomes established on different types of terrain and the forest with different levels of disturbance, we used MRPP, a non parametric method developed to prove the hypothesis that there are no differences between two or more groups of entities, which are commonly inherent in the sampling design, calculating a *p* value to show the differences among the groups (McCune and Grace 2002). The MRPP was done using Sorensen distance and two environmental categories: type of terrain and level of disturbance.

To relate the occurrence of determined species of palms with the factors that could be determining their distribution, we used Indicator Species Analysis that calculates an indicator value (from 0 = no indicator to 100 = perfect indicator) for each species, based on its relative abundance and relative frequency (Dufrene and Legendre 1997). The statistic significance of the indicator value is estimated by a Monte Carlo test for 10000 permutations. Two environmental categories, type of terrain and level of disturbance in the forest were used in the analysis. NMS ordination, MRPP, and Indicator Species Analysis were made with the program PC-ORD version 4.10 (McCune and Mefford 1999).

Finally, to evaluate the relative importance of the factors that determine the beta diversity in the palm community, we used partitioning the variation, a quantitative statistical method developed by Borcard et el. (1992) for the partition of the variation of compositional data in independent components, using a series of canonical ordinations (partials) (ter Braak 1988, ter Braak and Smilauer 1998). The variation partitioning approach has mainly been applied in delimiting the relative importance of the two or more sets of explanatory variables (Borcard et al. 1992, Borcard and Legendre 1994, Anderson and Gribble 1998) in explaining the variation in species composition. This method allows one to estimate the independent contributions of different (groups of) variables, as well as the covariance between them.

The computer package program CANOCO 4 (ter Braak and Smilauer 1998) involving Canonical Correspondence Analysis (CCA) were used to partitioning the variation of a set of species data in seven components: a pure environmental (E), a pure geographical (G), a pure disturbance (P), pure geographical component of environmental (GE), pure disturbance component of environmental (PE), pure combined disturbance/geographical component (GP) and a combined geographical/disturbance component of environmental (GPE). Four fundamental matrices were used for the analysis; species variables, environmental variables, geographical variables and disturbance variables (Table 2). The environmental variables were: Canopy, Moisture, Gap, Organic layer and Terrain Type. Variables as “Trail” and “Fallen tree” were not included in the analysis because they do not represent natural environmental variables. The five environmental terms were then included in a procedure of “forward selection” using CANOCO. This procedure is useful for ranking environmental variables in their importance for determining the species data. The statistical significance of five selected variables was judged by a Monte Carlo permutation test (ter Braak and Smilauer 1998). Then the variables with statistical significance were included in the analysis. The geographical coordinates (latitude and longitude) X’ and Y’ were considered for the analysis as in the NMS analysis. Disturbance effects on palms distribution and abundance were considered at three quantitative variables: (1) highly disturbed forest (2) moderately disturbed forest (3) not disturbed forest. One first step was done involving a CCA of species matrix, constrained by environmental, geographical and disturbance matrices to obtain the total variation explained by a set of explanatory variables, that is the sum of all canonical eigenvalues. Subsequently, a series of steps involving simple and/or partial CCA were done in the analysis (Table 7, Appendix 2).

Results

Diversity of palms in a terra firme forest

A total of 19760 individuals of 24 species of palms were registered in 25 transects (6.25 ha) in a *terra firme* forest (Appendix 1, Table 3). The species with largest density were: *Geonoma brevispatha*, *Iriartea deltoidea, Geonoma deversa*, *Astrocaryum murumuru*, *Euterpe precatoria* and *Socratea exorrhiza*, which constituted one fourth of the total of individuals. Species with densities under 100 added up to the rest (Table 3). *Euterpe precatoria*, *Iriartea deltoidea* and *Socratea exorrhiza* were the most common species in all the studied transects (Appendix 1).

The diversity of palms found in the *terra firme* forest on level terrain was larger than that found in forest in hilly terrain. Of the total reported species, twenty two were found on level terrain, with six species that were unique to this type of terrain: *Phytelephas macrocarpa*, *Mauritia flexuosa*, *Chamaedorea angustisecta*, *Bactris gasipaes*, *Geonoma* sp. and *Attalea butyracea*, while eighteen were found on hilly terrain, with two unique species: *Geonoma stricta* and *Bactris simplicifrons*. Finally, sixteen species were shared by both types of terrain (Table 3). *Astrocaryum murumuru*, *Euterpe precatoria*, *Iriartea deltoidea* and *Socratea exorrhiza* were the most common species in level terrain transects (Appendix 1), where the species with higher density were *Iriartea deltoidea, Geonoma deversa*, *Geonoma brevispatha*, *Astrocaryum murumuru*, *Euterpe precatoria*, *Socratea exorrhiza* and *Oenocarpus mapora*, adding up to more than 97% of the total of individuals registered on this type of terrain (Table 3). On the other side, *Euterpe precatoria*, *Socratea exorrhiza* and *Iriartea deltoidea*, were the most common species in the transects on hilly terrain (Appendix 1), and *Geonoma brevispatha, Geonoma deversa*, *Iriartea deltoidea*, *Euterpe precatoria*, *Geonoma interrupta* and *Oenocarpus bataua* were the species with highest densities, adding up to more than 80% of the total of individuals registered on hilly terrain. The abundance of *Euterpe precatoria* and *Socratea exorrhiza* was similar on both types of terrain (Table 3).

We found difference in the number of species registered in forest with different levels of disturbance. The highly disturbed forest (1.75 ha) was the richest in palm species with twenty one reported species, eighteen species for moderately disturbed forest (3 ha), and thirteen species for not disturbed forest (1.5 ha). Twelve species were shared by the three types of forest (Table 3). The density of palms also varied between forests with different levels of disturbance and was clearly larger in not disturbed, diminishing in the moderately disturbed forest, until the highly disturbed forest where the smallest density of palms was found. Species like *Geonoma brevispatha*, *Iriartea deltoidea*, *Geonoma deversa*, *Euterpe precatoria, Oenocarpus mapora* and *Oenocarpus bataua*, showed a notorious decrease in their densities in the highly disturbed forest, while *Astrocaryum murumuru*, *Socratea exorrhiza* and *Attalea phalerata* showed a clear increase in their densities in the highly disturbed forest. Species like *Geonoma interrupta*, *Chamaedorea pinnatifrons* and *Geonoma brogniartii* were also less abundant in the highly disturbed forest. On the other side, *Bactris maraja* and *Bactris simplicifrons*, start to appear in the moderately disturbed forest and increase their density in the highly disturbed forest. *Geonoma stricta, Bactris concinna*, *Chamaedorea angustisecta*, *Bactris gasipaes*, *Phytepephas macrocarpa* and *Attalea butyracea*, were reported only in highly disturbed forest (Table 3).

The NMS ordination resulted in one 2-dimensional solution that explains the variation in the composition of palm species, reflecting floristic differences between forest on level terrain and forest growing on hilly terrain and between forests with a different level of disturbance. The floristic gradients recognized can be interpreted in terms of geographic position, soil moisture, and gap condition (Figure 2). The ordination (Figure 4), showed differences in the composition of palm species between forest on level terrain and forest on hilly terrain. The majority of species that are placed on the left side of the ordination, such as

Astrocaryum murumuru, *Iriartea deltoidea, Attalea phalerata*, *Phytelephas macrocarpa*, *Bactris concinna*, *Mauritia flexuosa* and *Chamaedorea* sp., are more related to the forest on level terrain, while species like *Geonoma interrupta*, *Geonoma stricta*, *Bactris simplicifrons*, *Bactris maraja*, *Oenocarpus bataua* and *Wettinia augusta*, seem to be more related to forest on hilly terrain. *Euterpe precatoria*, *Socratea exorrhiza*, *Geonoma deversa*, *Chamaedorea pinnatifrons* and *Oenocarpus mapora* occur on both types of terrain and do not seem to exhibit preference for either habitat.

We find variation in the composition of palm species in forests with different levels of disturbance (Figures 3 and 5). Species like *Bactris maraja*, *Bactris simplicifrons* and *Bactris concinna* showed more relation to the highly disturbed forest, which would be very strongly related to the presence of gaps. The moderately disturbed forest appears to be more related to the factors geographic position and soil moisture. The species that are more related to this forest were *Geonoma stricta* and *Wettinia augusta*. The not disturbed forest appeared as two groups, one corresponding to forest on hilly terrain, located in the central lower part of the diagram and the other corresponding to the forest on level terrain, located on the upper left side of the diagram. Both seem to be related to the geographic position. The species most related to this type of forest was *Chamaedorea* sp. The result of the MRPP allowed us to reject the null hypothesis of no difference between the forest on level terrain and the one on hilly terrain (p = 0.029) and that of no difference between forests with different levels of disturbance (p = 0.00046).

Indicator Species Analysis confirmed that some species showed a distribution that was favored by the type of terrain, *Astrocaryum murumuru*, *Attalea phalerata* and *Iriartea deltoidea* were palms characteristically found on level terrain forest, while *Geonoma interrupta*, *Bactris simplicifrons* and *Oenocarpus bataua*, showed statistically significant values for forest on hilly terrain (Table 4). In the same way, some species showed a distribution that was favored by the level of disturbance of the forest: *Bactris maraja*, *Bactris concinna*, *Phytelephas macrocarpa* and *Bactris simplicifrons* were significant in highly disturbed forest, *Geonoma deversa*, *Wettinia augusta* and *Geonoma stricta* in the moderately disturbed forest, and *Chamaedorea* sp. and *Geonoma brevispatha* in the not disturbed forest (Table 4). A complementary Indicator Species Analysis showed that the distribution of some palm species, en relation to the level of disturbance of the forest, varied between the two types of terrain: *Attalea phalerata*, *Bactris concinna*, *Phytelephas macrocarpa*, and *Socratea exorrhiza,* showed preference for the highly disturbed forest on level terrain and *Bactris maraja* and *Chamaedorea pinnatifrons* were restricted to the highly disturbed forest on hilly terrain. On the other side, *Geonoma deversa* was characteristic of moderately disturbed forest on level terrain, while *Geonoma stricta* and *Wettinia augusta* were characteristic of moderately disturbed forest on hilly terrain. Finally, *Chamaedorea pinnatifrons*, *Chamaedorea* sp. and *Iriartea deltoidea* were characteristic of not disturbed forest on level terrain, while *Geonoma brevispatha* and *Geonoma interrupta* had preference for not disturbed forest on hilly terrain (Table 5).

Relative importance of the factors that structure the palm community of terra firme forests

For 24 species of palms, forward selection and Monte Carlo permutation test of five environmental variables resulted in two significant variables; Terrain type and Moisture which were included in the analyses. The other variables, Canopy, Gap and Organic layer have no statistical significance.

The sum of all eigenvalues in a correspondence analysis of the species matrix was 1.031. The total variation explained by the three sets of explanatory variables combined (sum of all canonical eigenvalues), that are environmental, geographical and disturbance variables, was 0.511 ($p = 0.0001$). Thus, the percentage of the total variation of the species matrix accounted for by each step (1) to (12) of the analysis (Table 6) was obtained by multiplying the sum of canonical eigenvalues by 100 and dividing it by 0.511. These percentages of explained variation are showed in the Table 7, which also shows the calculated probabilities (p) obtained from Monte Carlo tests of significance for each CCA, with 9999 permutations done for each step. The calculations of the values of each component of variation are shown in Table 8 (See also Annex 2).

Permutation tests showed that environmental, geographical and disturbance variables, when considered separately, each contributed significantly to explaining variation in the species data (Table 7 [1], [2] and [3]). Pure environmental and geographic components explained a significant portion of the variation, when the other components were partialled out of analysis (Table 7: [6] and [9]). In contrast, when the geographical and environmental variables were partialled out of analysis, disturbance variables no longer explained a significant percentage (Table 7: [12]). The greatest variation in the palm data was explained by the pure environmental component (34.83%), followed by pure geographical component (22.50%), with the pure disturbance component accounting for much less of the variation in the species data (7.63%). There was also a large variation fraction that accounted for the mixed geographical/disturbance component (22.9%), while the other mixed components showed a low percentage of variation explained (Table 8, Figure 6).

Discussion

Community of palms in a terra firme forest

In our research area in the Madidi region, the palms were diverse and abundant in the *terra firme* forest. These results support previous studies where palms were found to be very abundant in rain forests of the Amazonian lowlands (Kahn and de Granville 1992), even though their densities can vary greatly between places (Normand et al. unpublished, Vormisto et al. 2004b, Vormisto 2002). However, the palm community here studied was less diverse, with 24 species in 6.5 ha, than the palm communities studied in the western Amazonian Basin, where recent studies (Normand et al. unpublished, Sanjines et al. unpublished) reported 37 species in 2.5 ha and 28 species in 3 ha in the terrace forests of the Pastaza Fan (Abanico de Pastaza) in the Peruvian Amazon.

We found that the palm community in the *terra firme* forest consisted mainly of common and widely distributed tree canopy species, such as *Euterpe precatoria*, *Iriartea deltoidea* and *Socratea exorrhiza* which all have a wide Neotropical or Amazonian distribution (Henderson 1995) and possibly have more generalized ecological requirements (Ruokolainen and Vormisto 2000). These species were among the most common and abundant in the palm community of western Amazonia (Normand et al. unpublished, Sanjines et al. unpublished). Species like *Astrocaryum murumuru*, *Oenocarpus bataua* and *Oenocarpus mapora*, also with wide Amazonian distribution (Henderson 1995), were common and characterized the tree storey of the forest, while the shrub layer was characterized by smaller species belonging to the genera *Geonoma*, *Bactris* and *Chamaedorea*. *Geonoma* was the most species rich genus and *Geonoma brevispatha* and *Geonoma deversa* were especially abundant. In general, the majority of the species that were found in the *terra firme* forest in the Madidi region are widely distributed in the lowland rainy forests up to the premontane forests of the Neotropics (Henderson 1995).

The type of terrain was one of the factors that conditioned the differences in the composition and abundance of palm species within the *terra firme* forest. Even though more than half of the total number of species was shared by both types of terrain, other species showed greater preference for a particular type of terrain. The greatest palm species richness was found in forest on level terrain, where common species such as *Iriartea deltoidea* and *Astrocaryum murumuru* were most abundant in relation to the forest on hilly terrain. Both species seem to show preference for humid forest areas on level terrain. These results support previous studies where *Iriartea deltoidea* showed hydrological and topographical preferences (Duivendoorden 1995, Kahn and de Castro 1985, Svenning and Balslev 1999, Vormisto et al. 2004b), while other studies (Clark et al. 1995, Svenning 1999) reported that this species did not present either topographical or hydrological preferences within terrace forests. *Astrocaryum murumuru* preferred humid areas in the *terra firme* forest, which agrees with previous studies where this species showed preference for valley bottoms in the *terra firme* forest in Ecuador and Peru (Svenning 1999, Vormisto et al. 2004 b). On the other hand, six palm species were unique to the forests on level terrain: *Maurita flexuosa,* with a wide Amazonian distribution was found growing in humid areas of the forest on poorly drained soils. *Phytelephas macrocarpa*, was found only in seasonally flooded forest areas close to creeks, while *Attalea butyracea*, *Bactris gasipaes*, *Chamaedorea angustisecta* and *Geonoma* sp., showed preference for disturbed forest areas in forest on level terrain. Species like *Socratea exorrhiza*, *Euterpe precatoria*, *Attalea phalerata* and *Attalea butyracea* were more associated with this type of terrain and were found growing in flooded areas and swamps. All of them have also been associated with flooded plains and swamps in the Amazon (Henderson et al. 1995, Kahn and de Castro 1985, Kahn and Mejia 1990, Scariot et al. 1989, Normand et al. unpublished, Sanjines et al. unpublished).

The community of palms on hilly terrain was characterized by the abundance *Geonoma brevispatha* and *Geonoma deversa* both of which preferred less disturbed areas growing on shadowy slopes of the understory. At the tree storey level *Iriartea deltoidea* and *Euterpe precatoria* were the most dense canopy palms. *Geonoma stricta* was restricted to this type of terrain and occurred principally in slopes with well drained soils. *Bactris simplicifrons* was found particularly in areas were there was human disturbance. Also, Henderson et al. (1995) report this species as growing on non flooded soils and also in partially open areas. *Wettinia augusta*, a species with subandean biogeographic affinities and restricted to premontane forests along the eastern slopes of the Andes (Henderson 1995, Henderson et al. 1995) was found in the village of Santa Rosa de Maravilla, approximately 150 km south of the distribution area cited by Moraes (2004), being this one the southernmost record for this species. This species was found mainly on slopes, though it was also found but in very low densities, in flooded areas close to creeks in the forest on level terrain. Other species such as *Geonoma brevispatha* and *Geonoma deversa* were more abundant and seemed to show preference for shaded slopes without forest clearings.

Disturbance of the forests and its effect on the palm

In our study area the Madidi region, we found a disturbance gradient of the forest which was directly related to the geographical distance between the town of San Buenaventura and the villages farther away in the direction of the road that connects with the Alto Madidi region. Thus, the highly disturbed forest was found in the villages of San Isidro and Buena Vista, 10 and 16 km northwest of San Buenaventura respectively, on the road to Alto Madidi. The moderately disturbed forest was found in the villages 25 de Mayo, San Silvestre and Santa Rosa de Maravilla, 30, 52 and 70 km from San Buenaventura respectively. Finally, the not disturbed forest was found in the village of Alto Satariapo, 120 km away from San Buenaventura, on the road adjacent to Alto Madidi (Figure 1, Table 1). This meant that the nearer the forest is to the village of San Buenaventura, it is more used and thus more disturbed, while from the opposite side the farther away the forest is to the larger towns, it is less used and thus less disturbed, such as the forest in Alto Satariapo.

We also found differences in the palm species richness between forests with different levels of disturbance. The highly disturbed forest was the richest in palm species while the not disturbed forest had fewer species. The higher species richness in the disturbed forest could be due to the increased heterogeneity of the habitat, mainly as a consequence of human activity, but also due to natural disturbances such as periodical flooding in areas of the forest close to the rivers, and the formation of clearings in the forest due to tree felling. According to Svenning (2002), the diversification of the niches in function of small changes in the light conditions in the understory, could be an important factor in maintaining the very high local species richness in the tropical rain forests. Thus, the new habitats formed are being rapidly occupied by secondary taxa species (Scariot 1998).

On the other hand, some species of palms showed preference for forests with a different level of disturbance. *Bactris maraja* and *Bactris simplicifrons* seemed to be particularly favor the disturbed forest on hilly terrain with non flooded soils (Henderson et al. 1995, Scaritot 1999). Both form the two large species complexes that are still poorly understood taxonomically and could eventually be divided in several species, subspecies, or varieties. *Bactris concinna* was the most abundant in the disturbed forest on level terrain that is close to the banks of the river Beni. According to Henderson et al. (1995) the genus *Bactris*, which is distributed over the Amazon Basin is the most abundant in the lowland rainy forests, especially along river margins and disturbed areas. The formation of dense populations of *Phytelephas macrocarpa* found only in disturbed forest on level terrain could possibly be favored by periodical disturbances due to the temporal flooding of these forests (Kahn and de Granville 1992).

At the same time, in our study area in the Madidi region several useful palms species exhibited an increase or decrease in their densities in disturbed forests. The density of *Attalea phalerata* was notoriously favored in the disturbed forest and *Bactris gasipaes* which has only been reported from this type of forest, both are cultivated species and used mainly because of its edible fruits (Moraes et al. 1995, Paniagua et al. unpublished). *Attalea phalerata* is the palm with the highest number of uses in the region, especially because of its edible fruits, and is particularly abundant in cultivated fields, grazing lands and home gardens (Paniagua et al. unpublished). The presence of these species in a semi wild state in the disturbed forest would be related to the anthropogenic influence on the forest. Borchsenius et al. (1998), find this species occurring in a semi domestic state, associated with human settlements. *Astrocaryum murumuru* and *Socratea exorrhiza*, also showed an increase in their density in the disturbed forest, probably because of the fact that the adult palms are preserved when the forest is felled (Kahn and de Granville 1992), in addition, *Socratea exorrhiza* is one of the first species that germinates in open areas (Kahn and de Granville 1992).

Other palm species showed a decrease in their densities in the disturbed forest. *Euterpe precatoria* showed the lowest density in the moderately disturbed forest. This palm species is the most used in the Madidi region (Moraes et al. 1995, Paniagua et al. unpublished) and the intensive use could be negatively affecting the population. On the other side, its density increased in the highly disturbed forest, where the adult palms are apparently being preserved for fruit recollection, and for this reason are not felled. *Euterpe precatoria* is also domesticated in cultivated areas close to the villages (Moraes et al. 1995). In the same way, *Oenocarpus bataua* showed the lowest density in the moderately disturbed forest, which could be due to the extensive use that this species has in the region after *Euterpe precatoria* (Moraes et al. 1995, Paniagua et al. unpublished). This palm is usually felled for its fruits and, just as *Euterpe precatoria*, its density increased slightly in the highly disturbed forest where probably some adult individuals are being preserved. *Geonoma deversa*, one of the palms of which the leaves are most used for roof making, also showed a low density in the highly disturbed forest. Moraes et al. (1995) report that, according to the Tacanas population of the region, the groups of *Geonoma deversa* where located farther and farther away from the villages, possibly because of the strong extractivism pressure on this species. At present, the highest density of this species is found only in not disturbed forests that are far away from the villages.

One of the most clear negative effects of the use of palms was found in *Oenocarpus mapora* and *Iriartea deltoidea*. The densities of these palms diminished drastically in the moderately disturbed forest and in the highly disturbed forest. Both species are also among the most used palms in the region. The trunks of *Iriartea deltoidea* are used mainly for house construction, hedges and for palm heart extraction. The trunks and leaves of *Oenocarpus mapora* are used for making walls and roofs respectively, its fruits and oils are also much used (Moraes et al. 1995, Paniagua et al. unpublished). The use of the trunks in both species implies that the felling of individuals affects not only their decrease in the population, but also their natural regeneration. Thus, the intensive use of these species seems to be the determining factor in the decrease of the density of these palms in the forests with more human intervention in the region. This phenomenon has also been reported for *Iriartea deltoidea* that was disappearing from a part of the La Selva Biological Station due to the harvesting of trunks for obtaining heart of palms and for construction wood, this was also true for other tree species in Puerto Rico (Basnet 1992, Clark et al. 1995). In the same way, a negative response to the increased disturbance of the forest has been reported for other species of palms in the understory (Svenning 1998).

Finally, many species of useful palms have a wide distribution, are common, and are apparently capable of surviving in areas cleared for cultivation (Byg 2002), nevertheless, the pressure of extraction shows clearly negative effects on the population of the community of palms, principally on the most important ones, so the establishment of management plans for the useful palms becomes very important in the Madidi region.

Relative importance of the factors that structure the community of palms in the terra firme forest

The largest variation in species composition was explained by the pure environmental component (34.8%) and the pure geographical component (22.5%). The pure disturbance component represented a percentage that was not significant for the explanation of the variation. Nevertheless, when the environmental, geographical, and disturbance variables were considered separately, each one contributed significantly to the explanation of the species variation with 55%, 47% and 29%, respectively. Our results indicate that the relative importance of the environmental differences and the geographic distance as factors that structure the beta diversity, explained the greater variation in the species composition in the community of palms in a *terra firme* forest in the Bolivian Amazon. Similar results were reported in the Peruvian Amazon, where the relative importance of the geographical distance and the environmental differences for the beta diversity explained the major part of the variation in the species composition changes at a regional scale, the first one, and at a local scale, the second one (Normand et al. unpublished). Our results also support other studies in the Amazon Basin, where the environmental factors explained much of the beta diversity at a regional scale (Phillips et al. 2003, Tuomisto et al. 2003 a, b), though at a local scale the environmental differences were also important (Gentry 1988, Tuomisto et al. 1995, 2003 a, b). The importance of the geographic position also supports previous investigations where the geographic distance, at a regional scale, was of great importance for the Amazonian palms and other plants in the *terra firme* forest (Duivenvoorden et al. 2002, Duque et al. 2002, Vormisto et al. 2004 a). The environmental factors, the type of terrain, and the soil moisture were the most important controllers of the distribution of palm species in a *terra firme* forest in the Bolivian Amazon. These results are supported by previous studies where the hydrology and the topography are important for the structuring of the Neotropical palm communities (Kahn 1987, Kahn and de Castro 1985, Kahn and de Granville 1992, Sanjines et al. unpublished, Svenning 1999, Vormisto et al. 2000, 2004 a). Similar data were recently reported by Normand et al. (unpublished) and Sanjines et al. (unpublished) in the terrace forests of the Peruvian Amazon, where the soil moisture and the topography were also the most important factors in the structuring of the palm community. Thus, we support the theory that beta diversity is the deterministic result of changing environmental conditions (Gentry 1988, Tuomisto et al. 1995, 2003a). However, we have to considerer that dispersal limitation and biogeographical history can be important controls of the diversity and composition of local plant communities (Bell 2001, Cornell and Lawton 1992, Hubbell 2001, Normand et al. unpublished, Vormisto et al. 2004 b).

In conclusion, we found that the diversity in the palm community in the *terra firme* forest in the Madidi region was lower than that of the palm community in the *terra firme* forests of the western Amazon. The most common and most abundant palm species in the Madidi region are, in general, widely distributed in the Amazon Basin and probably present more generalized ecological requirements. The palm community was more diverse and dense the forest on level terrain, while in the forest on hilly terrain the diversity was lower. On the other side, the palm diversity in disturbed forest was larger compared to the not disturbed forest even though the greater abundance of species was found in the not disturbed forest. The majority of palm species in the region showed a variation in their densities in forests with a different level of disturbance. In the highly disturbed forest, some useful species were favored in their densities, while other palms, the most used in the region, showed a strong decrease. The graters variation in species composition was explained by the pure environmental component and the pure geographical component. The environmental factors such as the type of terrain and soil moisture were the most important variables that explained the variation in the composition of palm species. The relative importance of the environmental differences and the geographic position as controllers of the beta diversity was determining in the *terra firme* forest in the Madidi region.

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Appendices

Appendix 1. Palm species found in 25 transects (6.25 ha) in a *terra firme* forest along the San Buenaventura to Alto Madidi road in the northwest of the Bolivian Amazon

	Hilly terrain												**Level terrain**												
	101	**102**	**103**	**107**	**108**	**109**	**116**	**117**	**118**	**119**	**120**	**121**	**104**	**105**	**106**	**110**	**111**	**112**	**113**	**114**	**115**	**122**	**123**	**124**	**125**
Astrocaryum murumuru	0	0	1	7	7	74	42	21	27	17	43	51	284	86	105	144	113	45	1	6	13	117	277	105	199
Attalea butyracea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Attalea phalerata	0	0	0	0	0	0	0	6	0	0	1	0	2	3	1	0	0	0	2	5	0	8	3	25	54
Bactris concinna	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	15	20	56	126
Bactris gasipaes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0
Bactris maraja	0	0	0	0	0	0	0	5	3	6	1	2	0	0	0	0	0	0	0	0	0	1	1	0	0
Bactris simplicifrons	0	0	0	0	0	0	0	1	5	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chamaedorea angustisecta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1
Chamaedorea pinnatifrons	0	0	0	0	1	0	4	4	5	0	1	3	20	4	3	0	1	1	0	0	0	0	2	0	0
Chamaedorea sp	0	0	0	0	0	1	0	0	0	0	0	0	7	5	10	0	0	0	0	0	0	0	0	0	0
Euterpe precatoria	13	9	37	101	23	199	48	39	23	32	111	48	91	146	45	77	65	79	57	62	91	44	80	52	38
Geonoma brevispatha	588	725	692	13	439	46	152	44	55	0	0	4	107	151	151	24	17	51	396	392	399	0	1	1	0
Geonoma brongniartii	0	0	0	1	0	0	5	2	5	2	1	4	13	0	0	0	0	1	0	1	1	0	1	3	0
Geonoma deversa	104	207	352	334	612	201	28	4	0	2	0	0	0	0	0	19	8	93	495	595	523	251	171	0	0
Geonoma interrupta	98	82	145	0	0	0	0	0	1	13	44	76	0	0	0	0	0	0	0	9	0	0	0	0	0
Geonoma sp	0	0	0	46	111	71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geonoma stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Iriartea deltoidea	14	9	29	327	14	273	183	83	51	73	55	129	447	344	449	273	329	290	79	35	121	162	229	194	149
Mauritia flexuosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	8	1	0	0	4	0
Oenocarpus bataua	35	19	39	63	92	34	0	1	15	1	8	62	4	0	1	0	0	7	27	28	9	6	4	16	13
Oenocarpus mapora	49	90	36	7	76	25	8	6	1	0	1	2	34	34	19	9	18	20	124	55	73	0	2	1	7
Phytelephas macrocarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	45	105
Socratea exorrhiza	54	27	53	17	14	10	13	19	52	31	39	36	21	12	17	24	22	17	40	17	32	30	55	80	48
Wettinia augusta	0	0	0	65	38	114	0	0	0	0	0	0	0	0	0	1	0	27	0	0	0	0	0	0	0
Total	**955**	**1168**	**1384**	**981**	**1427**	**1048**	**483**	**235**	**243**	**181**	**307**	**420**	**1030**	**785**	**801**	**571**	**573**	**631**	**1235**	**1213**	**1263**	**641**	**851**	**591**	**743**

Appendix 2. Partitioning the variation

In a CCA of a species matrix, where an environmental (or other) matrix is used to constrain the analysis, the sum of canonical eigenvalues corresponds to the amount of variation in the species data explained by variables in the environmental (or other) matrix. If the analysis includes a matrix of covariables, then these variables are partialled out of the analysis. The total inertia or sum of all eigenvalues, obtained by an unconstrained correspondence analysis (CA) of the species data provides a measure of the total variation in the species data. The sum of canonical eigenvalues obtained by any CCA is a proportion of the total inertia obtained by CA on that data (Borcard *et al*. 1992, Anderson & Gribble 1998). As is recommended by Økland (1999), we change the focus from the total inertia and the “unexplained variation” (see Borcard et al. 1992, Anders & Gribble 1998), to relative amounts of variation explained by different sets of explanatory variables. Thus, the sum of the canonical eigenvalues obtained by any CCA is a proportion of the total variation explained by explanatory variables. One first step was done using CANOCO involving a CCA of species matrix, constrained by environmental, geographical and disturbance matrices to obtain the total variation explained by a set of explanatory variables, that is the sum of all canonical eigenvalues. Subsequently, a series of steps involving simple and/or partial CCA were done in the analysis (Table 6). For each step, the value of the sum of canonical eigenvalues for the analysis was recorded. The proportion of the total variation explained by explanatory variables, that this sum represented, was then calculated and multiplied by 100 to obtain a value for the percentage explained variation for each step. For each step, unrestricted permutation test (with 9999 permutations) were done of the overall trace statistic. The permutation test for this statistics indicates the significance of the effects of constrained variables on the species variables (removing the effects of covariables when present). The values corresponding to the percentage variation for each component of variation of interest were then calculated according to the method proposed by Borcard et al. (1992) and Anderson & Gribble (1998). The pure environmental component, E, is equal to [6]; the pure geographical component, G, is equal to [9]; and the pure disturbance component, D, is equal to [12]. For the other components is necessary to consider some intermediate values. First, total geographically structured environmental variation is calculated as [1] – [4] or [2] - [7]. It is important to note that this estimate still contains some disturbance component. This value will be referred to as GEd to denote that a disturbance component is still in the estimate. In the Figure 6, one can see that this value correspond to GDE + GE, and is the total overlap of the geographical and environmental' circles influence. Thus, GEd = GDE + GE. Total disturbance structured environmental variation DEg = GDE +DE. DEg can be calculated as [1] – [5] or [3] - [10]. Finally there is the total variation geographical/ disturbance variation, which we denote by GDe = GDE + GD and still contains some environmental component. It can be calculated as [2] - [8] or [3] – [11]. The central value that we need to obtain the real estimates of GE, DE and GD is the geographical and disturbance structures environmental variation, GDE. The total variation explained by the geographical variable (Ωg) = G + GE + GD + GAE. We know that GDe = GDE +GD and GEd = GDE + GE, therefore: GDE = G + GDe +GEd – Ωg. Similarly, from total variation explained by the environmental variables (Ωe) or the total variation explained by the disturbance variables (Ωa) we can obtain independent calculations for GDE as: GDE = E + GEd + DEg – Ωe or GDE = D + GDe + DEg – Ωd. The calculations for these three equations in terms of the steps outlined in Table 4 are, therefore:

GDE = (9) + ([2] - [8]) + ([1] - [4]) – [2], GDE = [6] + ([1] - [4]) + ([1] - [5]) - [1], GDE = [12] + ([3] - [11]) + ([3] - [10]) – [3]. Once the value for GAE has been obtained, the calculations for the remaining three components are straightforward: GD= GDe – GDE = [2] – [8] – GDE, GE = GEd– GDE = [1] – [4] – GDE, DE = DEg – GDE = [1] – [5] – GDE.

Legends to figures

Figure 1. The location of 25 transects (5 x 500 m) used to study diversity of the palm community in a *terra firme* forest along San Buenaventura-Alto Madidi road in the northwest of Bolivian Amazon.

Figure 2. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the terrain type variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: 0 = hilly terrain, 1 = level terrain.

Figure 3. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the disturbance variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: 1 = highly disturbed, 2 = moderately disturbed, 3 = not disturbed.

Figure 4. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the disturbance variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: 0 = hilly terrain, 1 = level terrain.

Figure 5. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the disturbance variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: 1 = highly disturbed, 2 = moderately disturbed, 3 = not disturbed.

Figure 6. Representation of the partitioning variation for the species data explained by three groups of explanatory variables. G, D, and E are unique effects of Geography, Disturbance and Environment variables, while GD, GE, DE and GDE are the fractions corresponding to their combined effects.

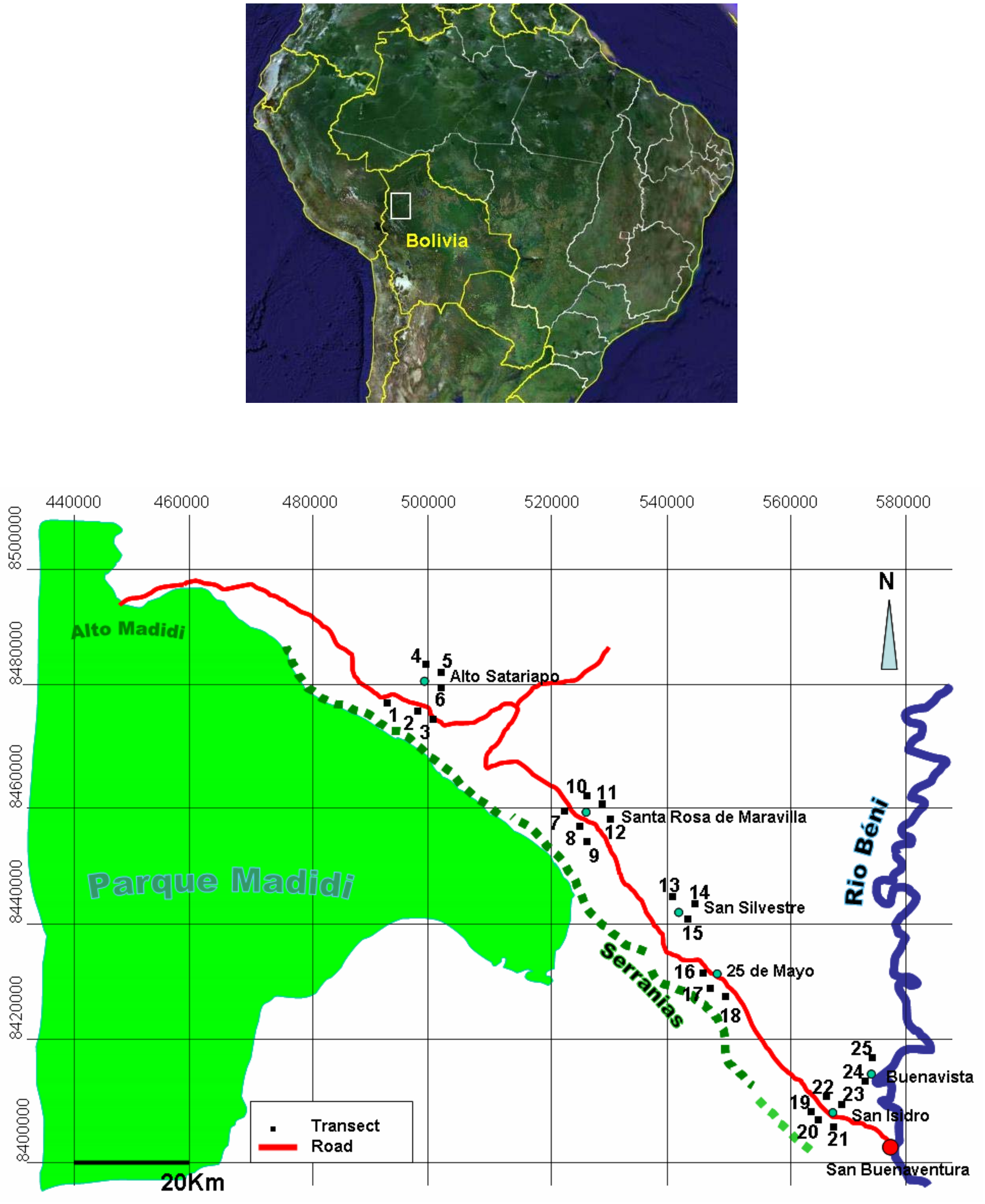

Figure 1. The location of 25 transects (5 x 500 m) used to study diversity of the palm community in a terra *firme* forest along San Buenaventura-Alto Madidi road in the northwest of Bolivian Amazon.

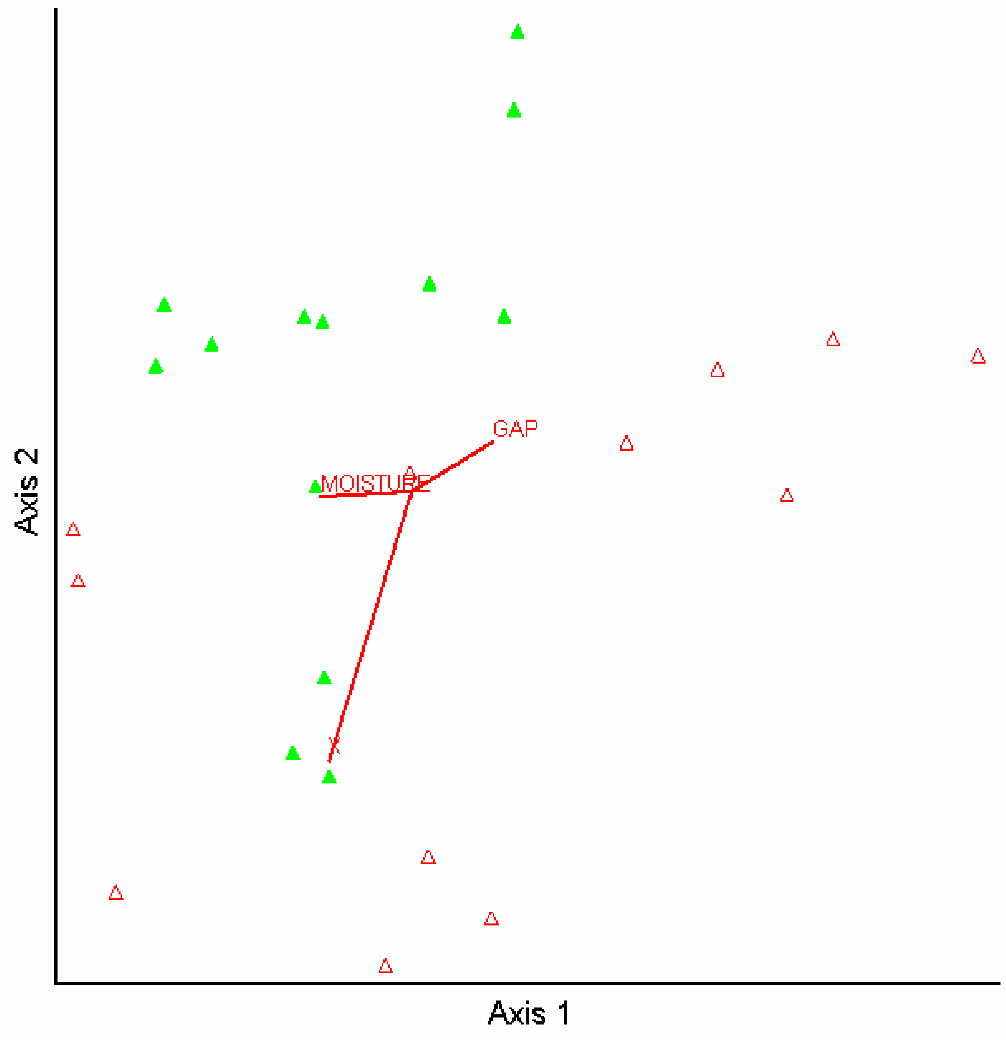

Figure 2. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the terrain type variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: △ = hilly terrain, ▲ = level terrain.

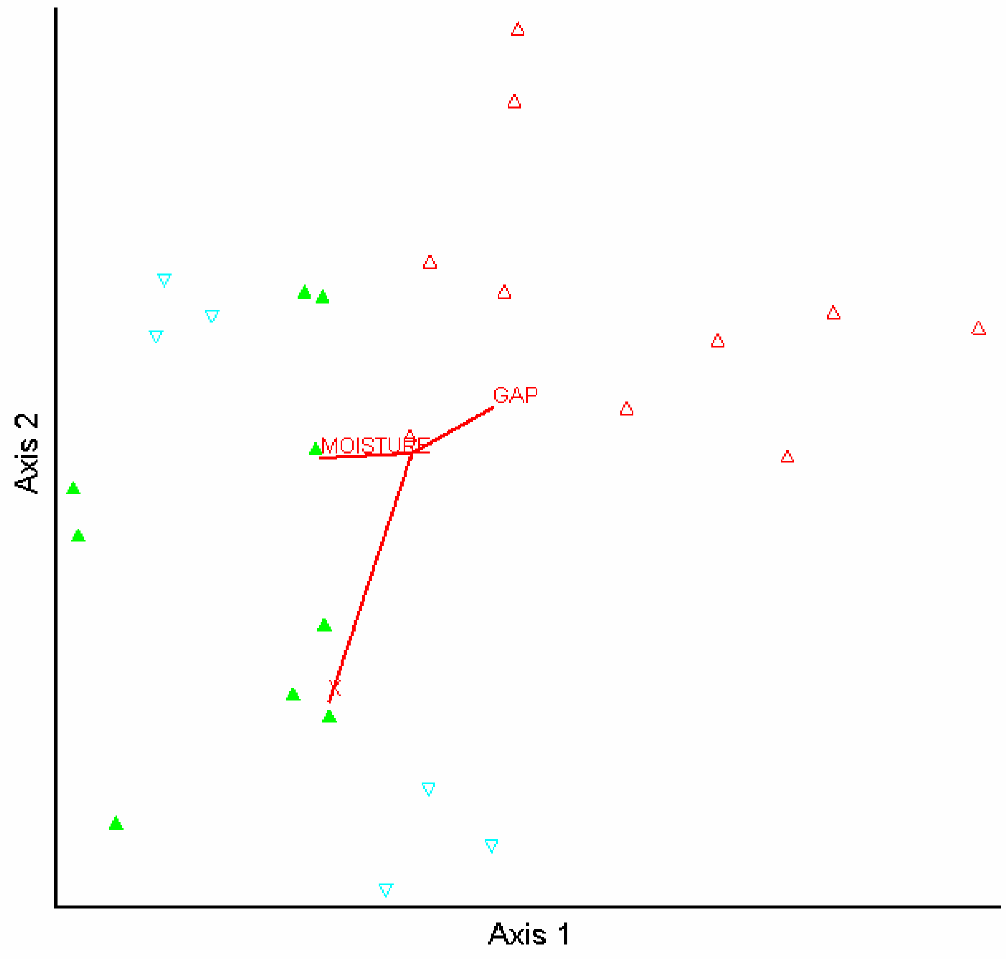

Figure 3. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the disturbance variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: △ = highly disturbed, ▲ = moderately disturbed, ▽ = not disturbed.

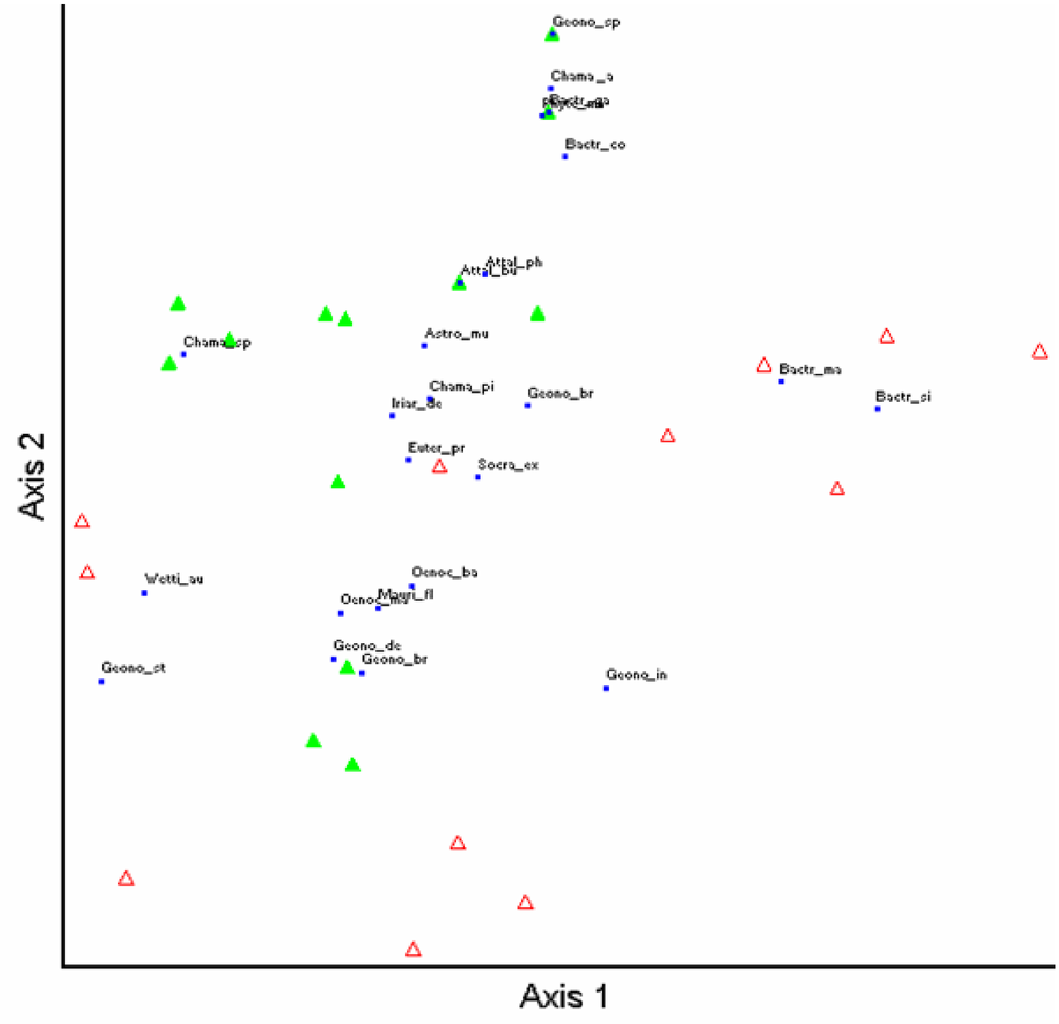

Figure 4. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the disturbance variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: △= hilly terrain, ▲ = level terrain.

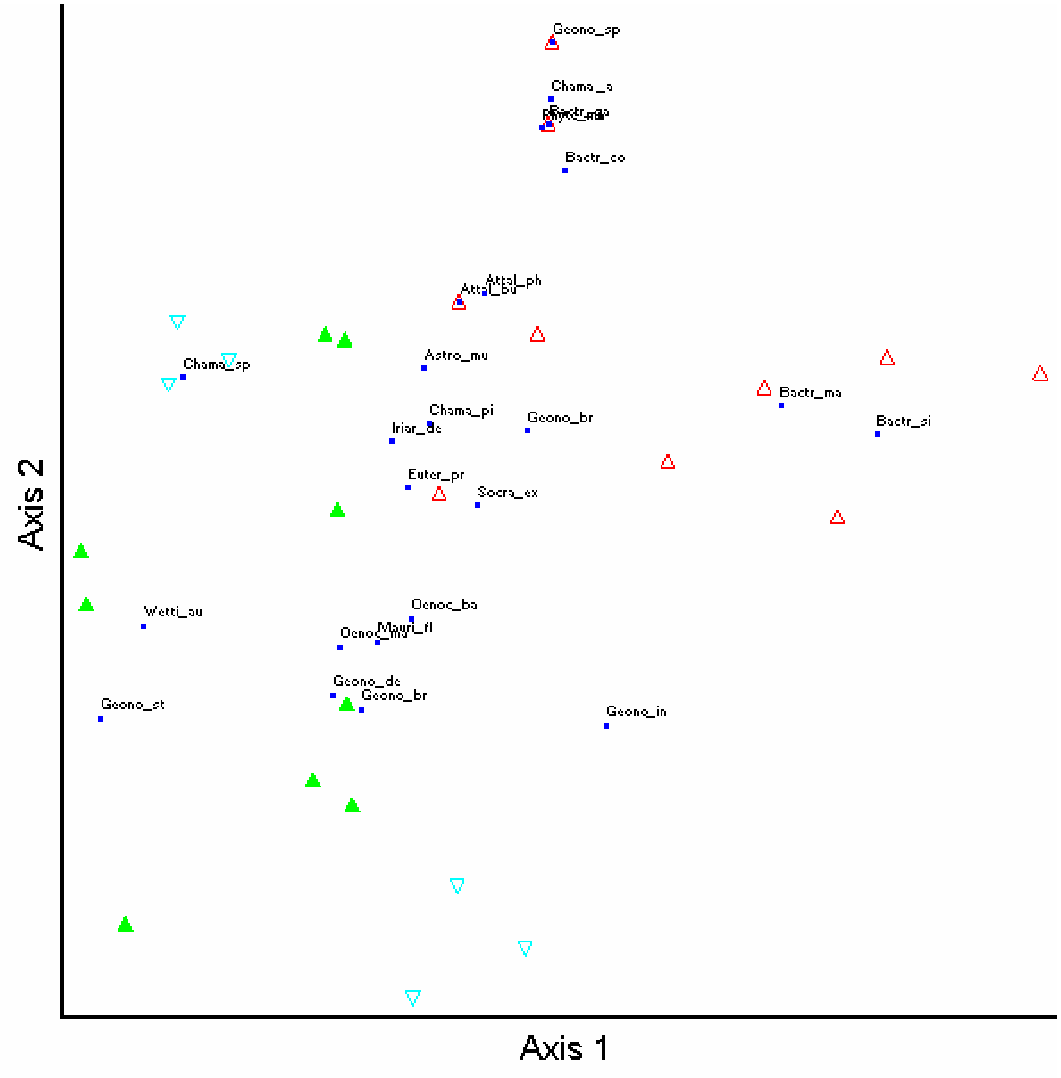

Figure 5. Non-metric multidimensional scaling ordination of palm species composition (using the Sorensen distance on square abundances) in 25 transects (50 x 500 m) for the disturbance variable in a *terra firme* forest in the northwest of Bolivian Amazon. Symbols: △= highly disturbed, ▲ = moderately disturbed, ▽ = not disturbed.

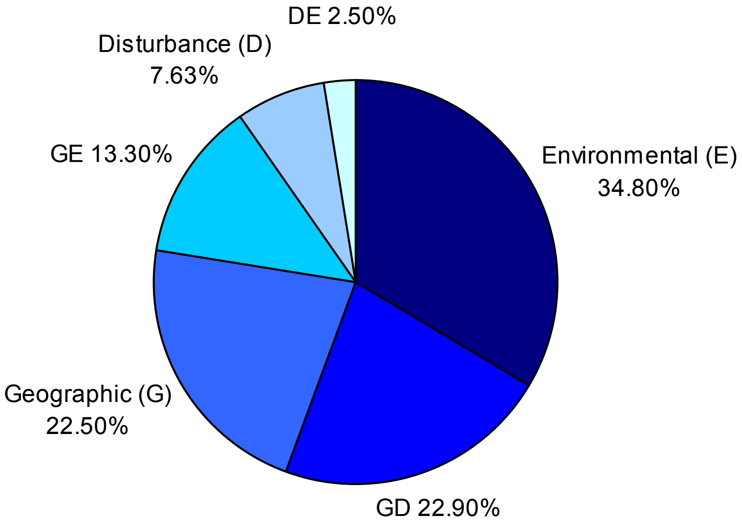

Figure 6. Representation of the partitioning variation for the species data explained by three groups of explanatory variables. G, D, and E are unique effects of Geography, Disturbance and Environment variables, while GD, GE, DE and GDE are the fractions corresponding to their combined effects.

Table 1. Transects established in level and hill terrain and three different levels of forest disturbance in a *terra firme* forest along San Buenaventura-Alto Madidi road in the northwest of Bolivian Amazon

Village	**Transect**	**Longitude West**	**Latitude South**	**Terrain**		**Disturbance**
				Level	**Hilly**	
Alto Satariapo	1	68° 15' 34.8"	13° 46' 56"		+	not
Alto Satariapo	2	68° 15' 46.6"	13° 46' 54.2		+	not
Alto Satariapo	3	68° 15' 48.3"	13° 46' 52.5"		+	not
Alto Satariapo	4	68° 14' 26 "	13° 47' 8.3"	+		not
Alto Satariapo	5	68° 14' 30.8"	13° 47' 2.4"	+		not
Alto Satariapo	6	68° 14' 20.4"	13° 46' 53.7"	+		not
Santa Rosa de Maravilla	7	69° 00' 34"	13° 57' 57.2"		+	moderately
Santa Rosa de Maravilla	8	68° 00' 42.3"	13° 58' 9.8"		+	moderately
Santa Rosa de Maravilla	9	68° 00' 34.6"	13° 58' 14.8"		+	moderately
Santa Rosa de Maravilla	10	67° 59' 35.7”	13° 57' 18.2"	+		moderately
Santa Rosa de Maravilla	11	67° 59' 25.2"	13° 57' 14.4"	+		moderately
Santa Rosa de Maravilla	12	67° 59' 20.2"	13° 57' 28.1"	+		moderately
San Silvestre	13	67° 51' 34.5"	14° 5' 50"	+		moderately
San Silvestre	14	67° 51' 44.6"	14° 6' 1.3"	+		moderately
San Silvestre	15	67° 51' 36.9"	14° 6' 5.3"	+		moderately
25 de Mayo	16	67° 47' 36.3"	14° 12' 53.9"		+	moderately
25 de Mayo	17	67° 47' 43.5"	14° 12' 58.2"		+	moderately
25 de Mayo	18	67° 47' 45.5"	14° 13' 6.4"		+	moderately
San Isidro	19	67° 36' 59.3"	14° 25' 4.5"		+	highly
San Isidro	20	67° 37' 12"	14° 25' 2.9"		+	highly
San Isidro	21	67° 37' 12"	14° 25' 17.8"		+	highly
San Isidro	22	67° 37' 35.4"	14° 22' 52.8"	+		highly
San Isidro	23	67° 37' 35.1"	14° 22' 46"	+		highly
Buena Vista	24	67° 36' 8.1"	14° 21' 37.8"	+		highly
Buena Vista	25	67° 36' 8"	14° 21' 32.6"	+		highly

Table 2. Environmental variables recovered in each subunit of 5 x 5 m of 25 transects for the palm communities analyses in a *terra firme* forest along San Buenaventura-Alto Madidi road in the northwest of Bolivian Amazon

Variable	**Category**	**Calculation per transect (2500m^2)**
Canopy openness	Direct canopy scope measure (0-25)	Average
Soil moisture	1: dry 2: ≤ ½ mud 3: > ½ mud 4: ≤ ½ water 5: > ½ water	Average
Gap condition	1: No gap 2: Limit of gap 3: Gap * 4: Gap with dense understory	Average
Organic layer	Measured in cm	Average
Terrain type	0:Hilly 1:Level	Number of subplots in hilly terrain Number of subplots in level terrain
Trail	0: No trail 1: Trail	Number of subplots with trails
Fallen trees	0: No fallen trees 1: Fallen trees	Number of subplots with fallen trees
Forest disturbance	1: highly disturbed 2: moderately disturbed 3: not disturbed	Number of transect in highly disturbed forest Number of transects in moderately disturbed forest Number of transect in not disturbed forest
Geographic coordinates	Initial point in each transect	Intermediate points calculated for each transects

* ≥ 50 m^2

Table 3. Palms density (individual /ha) in 25 transect (6.25 ha), thirteen transects (3.25 ha) in level terrain, twelve transects (3 ha) in hilly terrain, six transects (1.5 ha) in not disturbed forest, twelve transects (3 ha) in moderately disturbed forest and seven transects (1.75 ha) in highly disturbed forest in a *terra firme* forest

Species	**Total**	**Terrain**		**Disturbance**		
		Level	**Hilly**	**Not disturbed**	**Moderately disturbed**	**Highly disturbed**
Geonoma brevispatha	711.7	520	919.3	1609.3	676	3.4
Iriartea deltoidea	694.6	954.2	413.3	861.3	686	566.3
Geonoma deversa	639.8	567.4	718.3	442	970.7	242.3
Astrocaryum murumuru	285.6	460	96.7	317.3	166.7	462.3
Euterpe precatoria	257.6	285.2	227.7	227.3	288	231.4
Socratea exorrhiza	124.8	127.7	121.7	122.7	92.3	182.3
Oenocarpus mapora	111.5	121.8	100.3	174.7	140.7	7.4
Oenocarpus bataua	77.4	35.4	123	65.3	92	62.9
Geonoma interrupta	74.9	2.8	153	216.7	3.3	76
Wettinia augusta	39.2	8.6	72.3	0	81.7	0
Geonoma stricta	36.5	0	76	0	0	1.7
Bactris concinna	35.4	66.8	1.3	0	0	126.3
Phytelephas macrocarpa	25.8	49.5	0	0	0	92
Attalea phalerata	17.6	31.7	2.3	4	4.3	52
Chamaedorea pinnatifrons	7.8	9.5	6	18	5.3	3.4
Geonoma brongniartii	6.4	6.2	6.7	8.7	5.3	6.3
Mauritia flexuosa	4.3	8.3	0	0	7.7	2.3
Chamaedorea sp	3.7	6.8	0.3	14.7	0.3	0
Bactris maraja	3	0.6	5.7	0	2.7	6.3
Bactris simplicifrons	1.8	0	3.7	0	2	2.9
Chamaedorea angustisecta	1	1.8	0	0	0	3.4
Bactris gasipaes	0.6	1.2	0	0	0	2.3
Geonoma sp	0.5	0.9	0	0	76	0
Attalea butyracea	0.2	0.3	0	0	0	0.6
Total species	24	22	18	13	18	21
Total individuals /ha	**3161.6**	**3266.7**	**3047.6**	**4082**	**3301**	**2133.7**

Table 4. Species with statistical significant indicator values for terrain type and disturbance variables in 25 transects in a *terra firme* forest

	Level	**Indicator Value**
Terrain	*Astrocaryum murumuru*	70.1 **
	Attalea phalerata	60.1 **
	Iriartea deltoidea	62.3 **
	Hilly	
	Geonoma interrupta	55.3 **
	Bactris simplicifrons	33.3 *
	Oenocarpus bataua	60.7 *
Disturbance	**Highly disturbed**	
	Bactris maraja	70 ***
	Bactris corosilla	60 **
	Phytelephas macrocarpa	40 *
	Bactris simplicifrons	40 *
	Moderately disturbed	
	Geonoma deversa	59.2 **
	Wettinia augusta	55.6 **
	Geonoma stricta	33.3 *
	Not disturbed	
	Chamaedorea sp	46.2 **
	Geonoma brevispatha	55.6 *

Significance: P ≤ 0.05 *, ≤ 0.01 **, ≤ 0.001***, ≤ 0.0001****

Table 5. Species with statistical significant indicator values for forest disturbance variable in 13 level terrain transects and 12 hilly terrain transects in a *terra firme* forest

Disturbance	Level terrain	Indicator Value	Hilly terrain	Indicator Value
Highly disturbed	*Attalea phalerata*	68*	*Bactris maraja*	86.3*
	Bactris corosilla	100**	*Chamaedorea pinnatifrons*	68.1*
	Phytelephas macrocarpa	100**		
	Socratea exorrhiza	44.3**		
Moderately disturbed	*Geonoma deversa*	66.6*	*Geonoma stricta*	100**
			Wettinia augusta	100**
Not disturbed	*Chamaedorea pinnatifrons*	79.9**	*Geonoma brevispatha*	63*
	Chamaedorea sp	100**	*Geonoma interrupta*	75.6**
	Iriartea deltoidea	43.4*		

Significance: P ≤ 0.05 *, ≤ 0.01 **, ≤ 0.001***, ≤ 0.0001****

Table 6. Steps in the analysis done using CANOCO

Steps	Description
[1]	CCA of species matrix, constrained by the environmental matrix
[2]	CCA of species matrix, constrained by the geographical matrix
[3]	CCA of species matrix, constrained by the disturbance matrix
[4]	CCA of species matrix, constrained by the environmental matrix, with variables geographic treated as covariables
[5]	CCA of species matrix, constrained by the environmental matrix, with variables disturbance treated as covariables
[6]	CCA of species matrix, constrained by the environmental matrix, with geographical + disturbance variables treated as covariables
[7]	CCA of species matrix, constrained by the geographical matrix, with environmental matrix treated as covariables
[8]	CCA of species matrix, constrained by the geographical matrix, with disturbance variables treated as covariables
[9]	CCA of species matrix, constrained by the geographical matrix, with environmental + disturbance matrix variables treated as covariables
[10]	CCA of species matrix, constrained by the disturbance matrix, with environmental variables treated as covariables
[11]	CCA of species matrix, constrained by the disturbance matrix, with geographical variables treated as covariables
[12]	CCA of species matrix, constrained by the disturbance matrix, with environmental + geographical variables treated as covariables

Table 7. Summary of results of constrained and partial canonical correspondence analysis for data of 24 species of palms

Step in analysis	Value in calculations	Sum of canonical eigenvalues	Explained variation (%)	*P*
[1]	Ωe	0.240	46.960	0.0008
[2]	Ωg	0.282	55.180	0.0001
[3]	Ωd	0.150	29.350	0.0009
[4]		0.190	37.180	0.0001
[5]		0.245	47.940	0.0001
[6]	E	0.178	34.830	0.0002
[7]		0.232	45.400	0.0001
[8]		0.183	35.810	0.0009
[9]	G	0.115	22.500	0.0162
[10]		0.155	30.330	0.0003
[11]		0.050	9.780	0.1471
[12]	D	0.039	7.630	0.2026

Ωe = total variation explained by the environmental variables, Ωg = total variation explained by geographical variables, Ωd = total variation explained by disturbance variables. E = pure environmental component, G = pure geographical component, D = pure disturbance component. The analyses corresponding to numbered steps are outlined in Table 6. The percentage of explained variation was calculated as a proportion of the total variation explained by the set of explanatory variables (environmental, geographical and disturbance variables) = 0.511.The significance tests were done using the reduce model permutation method of ter Braak on the overall trace statistic (ter Braak & Smilauer 1998).

Table 8. Summary of calculations for the partitioning of variation where there are geographical, disturbance and environmental variable, including results obtained for the data of 24 species of palm

Component	Calculation	Explained variation (%)
Geographical = G	[9]	22.5
Disturbance = D	[12]	7.6
Environmental = E	[6]	34.8
GD	GDe – GPE = [2] - [8] - GPE	22.9
GE	GEd – GPE = [1] - [4] - GPE	13.3
DE	DEg – GPE = [1] - [5] - GPE	2.5
GDE	GDE = [9] + ([2] -[8]) +([1] - [4]) - [2]	-3.5
Total variation explained		100

The numbers of square brackets refer to the numbered steps in the analysis described in Table 6 and 7. The calculations for GD, GE, DE and GDE are described in Appendix 2.