

# Microhabitat specialization in a species-rich palm community in Amazonian Ecuador

JENS-CHRISTIAN SVENNING

Department of Systematic Botany, Institute of Biology, University of Aarhus, Herbarium, build. 137, Universitetsparken, DK-8000 Aarhus C., Denmark

## Summary

**1** Relationships between microhabitat variables (altitude, inclination, topographic position, drainage, canopy height) and the distribution and abundance of palms and palm-like plants in 50 ha of old-growth terra firme rain forest in the Yasuní National Park, lowland Amazonian Ecuador, were examined using 118 20 × 20 m plots laid out in a stratified random design.

**2** If microhabitat niche differentiation is important for maintaining the species richness of the community, then (i) the distribution of the palms will be strongly influenced by microhabitat heterogeneity and (ii) palms of similar growth form will show antagonistic microhabitat relationships.

**3** Mantel and cluster analyses showed that palm species distributions were strongly structured by topography. The main difference in species composition was between plots in the bottomland and plots on the upper slopes and hill tops.

**4** Logistic and logit analyses showed that 20 of the 31 palm and palm-like taxa analysed had distributions that were significantly related to the microhabitat variables measured, mainly to topography but also to drainage and canopy height.

**5** Spatial autocorrelation in the overall community structure was not explained by the microhabitat variables. Analyses of distributions or abundances of single species showed neighbourhood effects for seven taxa.

**6** Antagonistic patterns of microhabitat preferences were recognizable among some species pairs of small palms, medium-sized palms and palm-like plants, but not among canopy palms.

**7** It is concluded that microhabitat specialization is an important factor in maintaining the diversity of this palm community, while mass effects might also be important.

*Keywords:* edaphic specialization, maintenance of biodiversity, mass effects, niche differentiation, topography

*Journal of Ecology* (1999) **87**, 55–65

## Introduction

Tropical lowland rain forests are known for their extremely high richness of woody plant species. The highest observed species richness of trees in small plots has been recorded in western Amazonia (Gentry 1988; Valencia *et al.* 1994). The mechanisms by which this diversity is maintained are a source of ongoing debate (Janzen 1970; Hubbell 1979; Gentry 1988; Condit *et al.* 1992, 1994; Tilman 1994; Duivenvoorden 1995; Grubb 1996; Vásquez & Givnish 1998) and the many hypotheses can be divided into equilibrium

and non-equilibrium categories depending on whether or not they predict that species composition will remain constant (Connell 1978). An important equilibrium hypothesis states that species coexist by occupying different niches (the niche diversification hypothesis; Connell 1978). A more restricted version that has been much debated in tropical plant community ecology proposes that coexistence is a result of habitat or microhabitat specialization (Denslow 1987; Gentry 1988; Welden *et al.* 1991; Clark *et al.* 1993) and that much of the tropical plant diversity therefore depends on habitat and microhabitat heterogeneity. Microhabitat refers to environmental conditions that vary at scales less than 10<sup>3</sup> m, e.g. treefall gaps or local topographic variation. Habitat refers to strong environmental discontinuities, usually

at larger scales, such as floodplain vs. terra firme or white sand vs. clay soils. There is evidence for a diverse, fine-scale mosaic of habitats and microhabitats in western Amazonia (Poulsen & Balslev 1991; Tuomisto & Ruokolainen 1993; Duivenvoorden 1995, 1996; Tuomisto *et al.* 1995; Lips & Duivenvoorden 1996), and microhabitat specialization with regard to topography or soil factors has been shown to be important for several plant groups, including tropical trees, melastomaceous shrubs, herbs and pteridophytes (Lieberman *et al.* 1985; Denslow 1987; Poulsen & Balslev 1991; Ashton 1992a, b; Basnet 1992; ter Steege *et al.* 1993; Tuomisto & Ruokolainen 1993; Tuomisto *et al.* 1995; Clark *et al.* 1998). However, according to Duivenvoorden (1995, 1996) most trees of the well-drained upland habitat in Colombian Amazonia are likely to be soil generalists rather than specialists, which would limit the importance of microhabitat specialization for maintaining tree species richness here. Habitat specialization with regard to soil factors has been documented for tropical trees, lianas, melastomaceous shrubs and pteridophytes (Gentry 1988; Duivenvoorden 1995; Tuomisto *et al.* 1995).

Mass effects, whereby species establish in sites where populations cannot be self-maintaining as a result of continued propagule influx from adjacent, more favourable areas (Shmida & Wilson 1985), may also be important in maintaining a locally high species richness in tropical rain forests (Gentry 1988). Although mass effects, rather than microhabitat specialization, could be the major determinant of local species richness (as first proposed by Shmida & Wilson 1985) this is unlikely for trees in the uplands of Colombian Amazonia (Duivenvoorden 1995, 1996), where relatively low levels of soil heterogeneity are associated with low tree beta diversity. In contrast, Vásquez & Givnish (1998) suggest that beta diversity is highest in lowland tropical forests.

Palms are one of the most diverse and prominent families in neotropical lowland rain forests (Gentry 1988; Kahn & de Granville 1992; Henderson 1995; Scariot 1999), whose abundance of large arborescent palms distinguishes them from most palaeotropical forests (Gentry 1988; Kahn & de Granville 1992). Palms are especially diverse in the western Amazon, perhaps due to higher rainfall (Gentry 1988; Kahn & de Granville 1992; Henderson 1995).

Several studies have shown that habitat specialization is important for maintaining high palm diversity in the Neotropics. It is well documented that Amazonian palm communities differ in species composition among major habitat types, e.g. floodplain and terra firme forest (Kahn & de Castro 1985; Balslev *et al.* 1987; Kahn & de Granville 1992; Peres 1994), but it is less clear whether palms are specialized on particular microhabitats within these major habitat types. In Costa Rica the distributions of five of seven subcanopy and canopy palms were related to top-

ography and/or edaphic factors (Clark *et al.* 1995), and several studies have also shown or suggested that treefall gaps are an important ecological factor for palms (Vandermeer *et al.* 1974; Richards & Williamson 1975; Chazdon 1986; Kahn 1986; Piñero *et al.* 1986; De Steven 1989; Kahn & de Granville 1992). Welden *et al.* (1991), however, found that canopy height was unimportant for the two palm species included in their study. To the author's knowledge, no study investigating microhabitat specialization for all the palm species in a palm community has yet been published.

This study reports on the patterns of distribution and abundance in a high diversity palm community in terra firme rain forest in relationship to topography, soil drainage and canopy height at spatial scales of tens to hundreds of metres. In addition to true palms, common species of palm-like growth forms (palmoids) belonging to Bromeliaceae, Cyatheaceae, Cyclanthaceae and Myrsinaceae were included. I tested two predictions, which follow from the niche diversification hypothesis if it is further assumed that coexistence is due to habitat and microhabitat specialization.

**Prediction I:** The distribution of palms will be strongly influenced by microhabitat heterogeneity. If particular palms are specialized on different values of the microhabitat variables assessed, their distributions should be related to these variables.

**Prediction II:** Palms of similar growth form should show antagonistic microhabitat relationships. If species in the palm community studied coexist by microhabitat specialization, then antagonistic patterns of microhabitat preferences should be present. Among the potential mechanisms that could drive microhabitat niche diversification at the 10–10<sup>2</sup> m scale are competition for pollination and seed dispersal (Armbruster 1995), oligophagic pests attacking close relatives (Wills *et al.* 1997), and competition for specific microsites at scales of just a few metres or less. Examples of such microsites are gaps in the litter layer, sites of slightly elevated light availability, or areas of low rooting density (Grubb 1996). These interactions (and thus niche differentiation) are likely to be strongest among species of similar adult size and growth strategy, as these species compete for the same space throughout their life cycles, present flowers and fruits in the same stratum of the forest, appear more similar to pests, and relatively often are close relatives.

It is also discussed whether or not the results of this study support that mass effects could be important for maintaining the palm species diversity in the study site.

## Materials and methods

### STUDY SITE

Field work was carried out from October 1994 to June 1995 at the Yasuni Scientific Station (0°40'S,

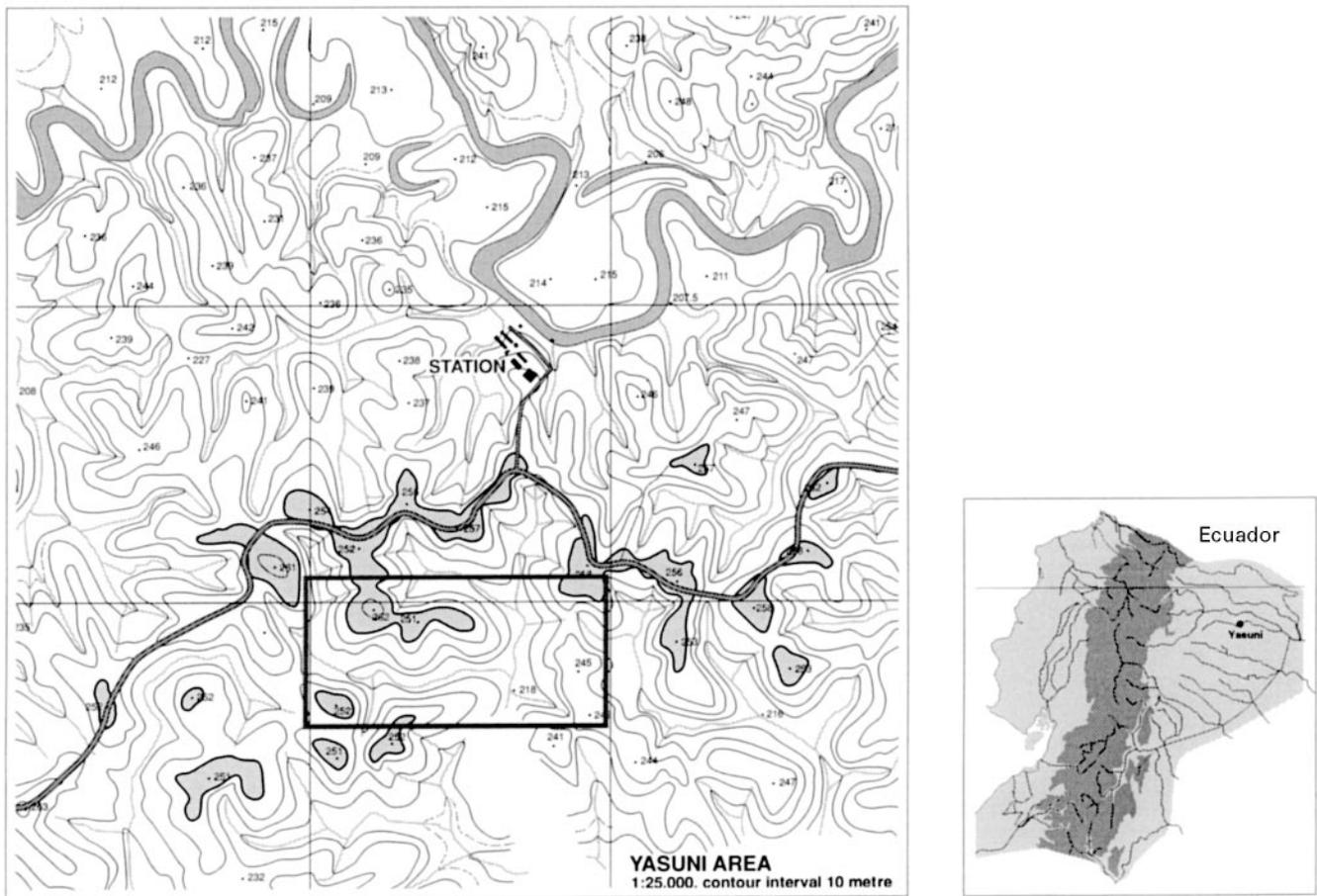
76°23'W) of P. Universidad Católica del Ecuador in the Yasuní National Park in lowland Amazonian Ecuador (Fig. 1). In the vicinity of the field station three major habitat types occur: floodplain, swamp and terra firme. Most of the forest is old-growth (*sensu* Clark 1996) but there are small areas recently disturbed by oil exploration. The fauna is rich and little hunting occurs. The study site was the Yasuní Forest Dynamics Project (YFDP) 50-ha (1.0 × 0.5 km) plot, located about 0.5 km south of the station (Fig. 1). This plot was established in 1995 and a 20-m grid was surveyed by a team of topographers who recorded the altitude (metres above sea level) of each grid point. The plot is located on terra firme and includes three hills and a central bottomland that is generally unflooded except for a few small swampy areas (Fig. 2). The soils are oxisols on the hills, with brown or grey alluvial covers in the bottomland. Thirty-nine species and varieties of palms and palmoids were found within the YFDP 50-ha plot (Table 1). Nomenclature for palms follows Henderson (1995). Four species occurred as two varieties (Table 1), but since they were readily distinguishable at any size and intermediates were never encountered, each variety

was treated as a distinct species. Vouchers were deposited in Herbario QCA in Quito, Ecuador and in Herbarium AAU, Aarhus, Denmark.

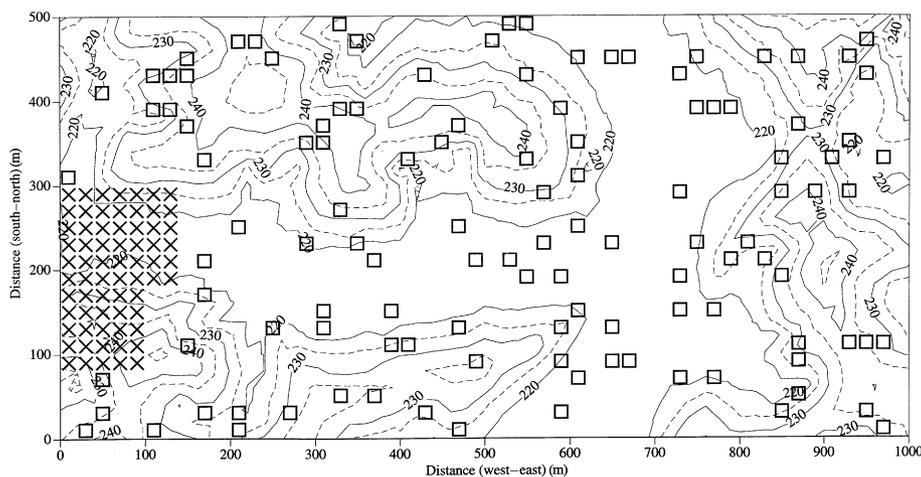
#### FIELD MEASUREMENTS

The YFDP 50-ha plot was divided into 25 subplots of 200 m by 100 m, each composed of 50 quadrats (20 × 20 m). Five quadrats were selected from each subplot using a table of random numbers. Exclusion of 2.68 ha, which represented an area of secondary forest surrounded by a buffer zone of a least one undisturbed quadrat (Fig. 2), allowed data to be collected from 118 quadrats.

Topographic position (TOP) was recorded as hill top or upper third of slope (1), TOP = 1, lower two thirds of slope (2) or bottomland (3). Occurrence of poor drainage (PD), as indicated by the presence of slight depressions without herb layer vegetation or small streams (SM), was recorded as present (1) or absent (0). A combined drainage index (PDSM) was used in the logistic and logit analyses such that when poor drainage and/or streams occurred PDSM = 1; if neither occurred PDSM = 0. Estimated average



**Fig. 1** The location of the Yasuní Scientific Station (STATION) and the Yasuní Forest Dynamics Project 50-ha plot (large rectangle). The topographic map was supplied by MAXUS-ECUADOR Inc. and is based on aerial photographs. Discrepancies between this map and the maximum altitude shown in Figs 2 and 3 is due to the lower precision of the methods used for this larger scale survey. Ecuador map: dark shaded area indicates land  $\geq 1200$  m a.s.l.



**Fig. 2** The location of the 118 quadrats within the YFDP 50-ha plot (crosses indicate the excluded area). Even number contours (220, 230 and 240 m a.s.l.) are shown by full lines, while odd number (225, 235 and 245 m a.s.l.) are shown by dashed lines.

canopy height (MC) was recorded as less than or equal to 20 m (0), or more than 20 m (1). Heights were checked using a clinometer in borderline cases. The altitude of a quadrat (ALT) was defined as the average of the four corners of the quadrat, and the inclination (INC) as the inclination of the plane defined by the average vector between two corners for each pair of parallel sides of the quadrat. Altitudinal data were provided by YFDP.

Each quadrat was surveyed for palm and palmoid species (Table 1). All palms and six common palmoid species were included in the study (Table 1). Only individuals with stems taller than 0.10 m and/or leaf length more than 0.50 m were considered. Abundance was recorded as absent (0), present but not abundant (1), or abundant [2, defined as a quadrat having (i) at least two individuals with stems taller than 2.5 m or leaves longer than 4 m, or (ii) if clonal, at least five separate clones, or (iii) if non-clonal, at least 10 individuals of any size].

Each species was assigned to one of five growth form categories based on adult size and growth strategy: (1) small palms, average adult height (to top of crown) less than 2.5 m; (2) medium-sized palms, average adult height 2.5–10 m; (3) large palms, average adult height taller than 10 m; (4) palm lianas; (5) palmoids, average adult height (to top of crown) less than 2.5 m.

#### STATISTICAL ANALYSES

The Mantel test was used to assess correlations between five distance matrices constructed for the 118 quadrats. (i) A topography matrix was calculated from altitude, inclination and topographic position using Gower's symmetrical similarity coefficient (Legendre & Legendre 1983). (ii) A drainage matrix was computed from the stream and poor drainage variables using the simple matching coefficient (Legendre

& Legendre 1983). (iii) A canopy matrix was calculated from canopy height using the simple matching coefficient (Legendre & Legendre 1983). (iv) A spatial distance matrix (space) consisted of Euclidean distances among the plots. (v) A palm composition distance matrix was computed from the presence–absence of palm species using the Jaccard similarity index (Legendre & Legendre 1983). Palmoids and *Attalea* juveniles were excluded; the first because they are not palms, and the latter because of the confounding of two species. All probabilities of Mantel  $r$ -values were obtained using 500 permutations. For partial Mantel tests, the Smouse, Long & Sokal method was used (Legendre & Fortin 1989).

The cluster analysis reported was a non-hierarchical clustering by the  $k$ -means algorithm (Legendre & Fortin 1989). The clustering was based on a set of the 15 principal coordinates from the same palm composition distance matrix as used in the Mantel analysis. The analysis was restricted to the classification of the plots into two groups. Several initial configurations were used. Two were based on an initial classification by agglomerative hierarchical classification methods (UPGMA and proportional linkage clustering with 0.5 connectedness) as suggested by Legendre & Fortin (1989). Sixty others were created randomly.

Logistic and ordinal logit regression was used to analyse the relationship of the distribution of individual taxa to the microhabitat variables. Logistic regression was done for the presence–absence of all palm and palmoid species with at least 10 presences and at least 10 absences ( $n = 29$ ). Ordinal logit regressions of abundance were done for species that were abundant in at least five quadrats and with at least 10 presences and 10 absences ( $n = 5$ ). Species that were abundant in a least 10 quadrats but did not have 10 absences were analysed dichotomously as abundant vs. not abundant using logistic regression

**Table 1** Palms and common palmoids in the YFDP 50-ha plot. Growth form codes: L = large palm, M = medium-sized palm, S = small palm, Li = liana, W = woody palmoid, H = robust herbaceous palmoid, (c) clonal, (s) usually no aerial stem, and (r) stilt-rooted. The number of quadrats in which a species was present and in which it was abundant are given. B = Bromeliaceae, C = Cyclanthaceae, TF = tree fern (Cyatheaceae). Regarding the vouchers, J refers to Jens-Christian Svenning, while HB refers to Henrik Balslev. \**Attalea insignis* and *A. maripa* could not be distinguished as stemless juveniles and these were recorded as *Attalea* indet

Species name	Voucher	Growth form	Present	Abundant
<b>Palms</b>				
<i>Aiphanes ulei</i>	J182	M	75	5
<i>Astrocaryum chambira</i>	HB6330	L	31	3
<i>A. murumuru</i> var. <i>urostachys</i>	J183	M (c)	63	11
<i>Attalea insignis</i> *	HB6105	M (s)	4	1
<i>A. maripa</i> *	HB6095	C	0	0
<i>Attalea</i> indet.*	–	–	67	11
<i>Bactris corossilla</i>	J172	M (c)	13	0
<i>B. maraja</i> var. <i>juruenensis</i>	J181	S (c)	19	0
<i>B. maraja</i> var. <i>maraja</i>	J144	M (c)	11	1
<i>B. simplicifrons</i> var. 1	–	S (c)	0	0
<i>B. simplicifrons</i> var. 2	J102	S (c)	16	0
<i>Chamaedorea pauciflora</i>	J142	S	10	0
<i>C. pinnatifrons</i>	J177	S	28	0
<i>Desmoncus giganteus</i>	J54	Li (c)	8	0
<i>D. mitis</i> var. <i>mitis</i>	HB6343	Li (c)	2	0
<i>D. polyacanthos</i>	HB6360	Li (c)	1	0
<i>Euterpe precatoria</i> var. <i>precatoria</i>	J122	L	11	0
<i>G. cf. aspidifolia</i>	J105	S (c)	64	20
<i>Geonoma brongniartii</i>	J145	S	4	0
<i>G. macrostachys</i> var. <i>macrostachys</i>	J170	S (s)	117	40
<i>G. macrostachys</i> var. nov.	J165	S (s)	65	7
<i>G. maxima</i>	J175	M (c)	21	0
<i>G. stricta</i> var. <i>piscicauda</i>	J140	S (c)	3	0
<i>G. stricta</i> var. <i>stricta</i>	J168	S (c)	75	2
<i>G. triglochis</i>	J161	S	33	0
<i>Hyospathe elegans</i>	J174	S (c)	15	2
<i>Iriarteia deltoidea</i>	J108	L (r)	111	79
<i>Mauritia flexuosa</i>	–	L	2	2
<i>Oenocarpus bataua</i> var. <i>bataua</i>	HB6090	L	93	31
<i>O. mapora</i>	HB6103	M (c)	0	0
<i>Phytelephas tenuicaulis</i>	J176	M (c)	42	7
<i>Prestoea schultzeana</i>	J115	S (c)	80	15
<i>Socratea exorrhiza</i>	HB6336	L (r)	12	1
<i>Wettinia maynensis</i>	J109	L	36	1
<b>Palmoids</b>				
<i>Aechmea</i> sp. (B)	J171	W (c,s)	21	1
<i>Asplundia</i> cf. <i>alata</i> Harling (C)	J106	H (s)	103	4
<i>Cyclanthus bipartitus</i> Poit. (C)	J160	H (s)	90	0
<i>Cybianthus</i> ( <i>Weigeltia</i> ) sp.	J157	W	22	0
<i>Alsophila cuspidata</i> (Kunze) Conant (TF)	J190	W	25	0
<i>Cyathea laesiosora</i> (Kunth) Domin (TF)	J162	W	45	1

( $n = 2$ ). A stepwise model selection procedure was used for these analyses [Appendix 1, see *Journal of Ecology* archive on the World Wide Web (WWW); for address, see cover of this issue]. To avoid zero cells, the two variables SM and PD were collapsed (to PDSM) for these analyses. The independent variables were not analysed for interactions as this would require the absence of zero cells in the table of the response variable and all independent variables in the interaction term (Hosmer & Lemeshow 1989). Presence of one zero cell in a two-way crosstab was allowed in the logit analyses, as it should not cause

any problems (A. Agresti, personal communication). The value of the response variable in the nearest neighbouring quadrat was included as an explanatory variable (NN). If several quadrats qualified as the nearest neighbour, NN was assigned the highest value for the response variable in any of these quadrats.

## Results

### MICROHABITAT CHARACTERISTICS

The range and variation in microhabitat characteristics for the studied quadrats are given in Table 2.

**Table 2** Microhabitat composition of the study quadrats

Microhabitat characteristic	Number of quadrats (proportion)
Upper hill (TOP = 1)	32 (27%)
Lower hill (TOP = 2)	49 (42%)
Bottomland (TOP = 3)	37 (31%)
Poor drainage (PD = 1)	28 (24%)
Stream (SM = 1)	22 (19%)
Canopy < 20 m (MC = 0)	48 (41%)
Canopy > 20 m (MC = 1)	70 (59%)
Microhabitat characteristic (unit)	Mean (SD) Range
Altitude (m a.s.l.)	226 (7.89) 216–243
Inclination (°)	11 (7.6) 0–31

Drainage and canopy height were correlated with topography and with each other (Table 3). Topography, but not drainage or canopy height, was found to be positively spatially autocorrelated by the Mantel analysis. The partial correlations showed that none of the correlations among topography, drainage, canopy height or space were due to indirect correlation to another of the variables.

#### PALM COMMUNITY CHARACTERISTICS

Ten species of palms and two species of palmoids occurred in more than 50% of the quadrats (Table 1). *Iriartea deltoidea* and *Geonoma macrostachys* var. *macrostachys* occurred in more than 90% of the quadrats and were also the two most abundant species (Table 1). Seven palm species occurred in less than five quadrats.

#### COMMUNITY STRUCTURE

Palm composition was most strongly correlated with the topography (Table 4). Indirect correlations due to spatial autocorrelation or canopy height only affected the primary correlation negligibly or not at all. Palm composition and canopy height were weakly but significantly correlated, even when accounting for topography. Palm composition and drainage were not correlated. There was a positive spatial autocorrelation component of the palm community structure that was not explained by the microhabitat variables.

All 62 configurations used in the cluster analysis gave the same result. The two types of palm community composition recognized were characteristic of upper hill and bottomland, respectively, with both types found on lower hill (Fig. 3).

#### SINGLE-SPECIES PRESENCE-ABSENCE

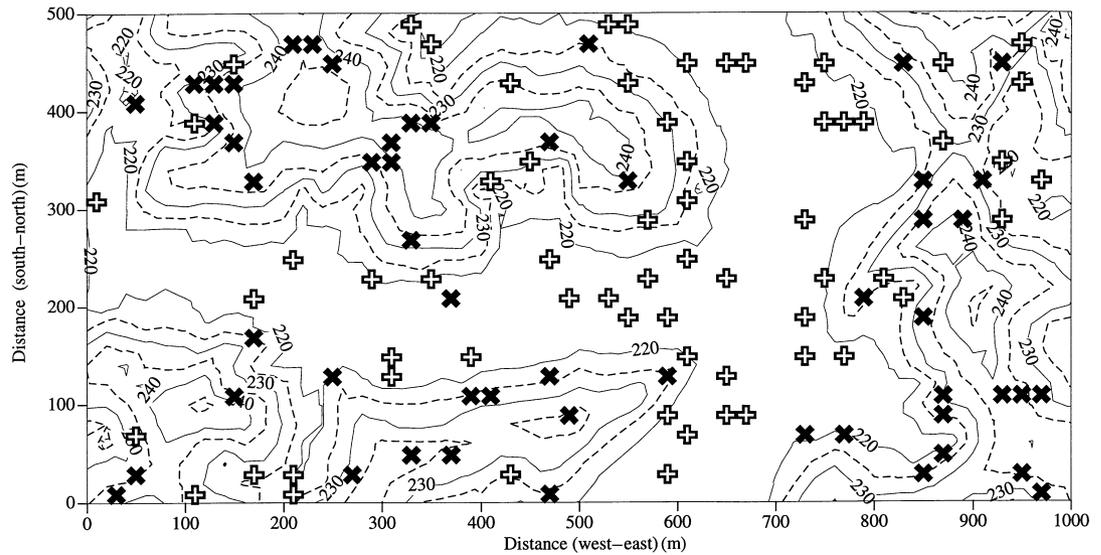
The distributions of 14 of the 23 palm taxa analysed were related to microhabitat variables, especially to

**Table 4** Mantel and partial Mantel correlations of the palm composition similarity matrix with space and microhabitat matrices. Matrix B is the matrix correlated with the palm composition similarity matrix. Matrix C is the matrix whose effect is removed when calculating the partial correlations

Matrix B		<i>r</i>	<i>P</i>
Space		0.09	0.00599
Topography		0.30	0.00200
Drainage		0.03	> 0.1
Canopy		0.05	0.00200
Matrix B	Matrix C	Partial <i>r</i>	<i>P</i>
Topography	Space	0.29	0.00200
Space	Topography	0.07	0.00599
Canopy	Topography	0.03	0.03393
Topography	Canopy	0.30	0.00200

**Table 3** Mantel correlations and partial correlations among microhabitat variables. Matrices A and B are the matrices correlated. Matrix C is the matrix whose effect is removed when calculating the partial correlations

Matrix A	Matrix B		<i>r</i>	<i>P</i>
Topography	Space		0.06	0.004
Drainage	Space		−0.00	> 0.1
Canopy	Space		−0.02	> 0.1
Drainage	Topography		0.12	0.00200
Canopy	Topography		0.07	0.00599
Canopy	Drainage		0.13	0.00200
Matrix A	Matrix B	Matrix C	Partial <i>r</i>	<i>P</i>
Canopy	Drainage	Topography	0.13	0.00200
Canopy	Topography	Drainage	0.05	0.00798
Drainage	Topography	Canopy	0.11	0.00200



**Fig. 3** Location of the two groups of quadrats produced by the cluster analysis of quadrat species composition. The two groups are symbolized by black, tilted crosses and empty, upright crosses. They are located mainly on the upper hill or in the bottomland, respectively. Even number contours (220, 230 and 240 m a.s.l.) are shown by full lines, while odd number (225, 235 and 245 m a.s.l.) are shown by dashed lines.

topographic position (Table 5). The full models are given in Appendix 2 on the WWW; for address, see cover of this issue. Three taxa were related to altitude, two negatively and one positively. Two taxa were related to inclination, one positively, one negatively. Nine, or possibly 10, taxa were related to topographic position: *Hyospathe elegans*, *Euterpe preclatoria* and *Oenocarpus bataua* were preferentially found only on the upper hill, *Geonoma cf. aspidiifolia* and *Geonoma maxima* on both upper and lower hill, *Geonoma macrostachys* var. nov. and *Phytelephas tenuicaulis* only in bottomland, while *Geonoma trigloch*, *Astrocaryum murumuru* and *Attalea* indet. favoured both upper hill and bottomland but avoided lower hill. Three taxa were related to poor drainage, two positively and one negatively. Finally, *Chamaedorea pauciflora* and *Prestoea schultzeana* preferred low canopy, while *Attalea* indet. preferred high canopy.

The distributions of all palmoids except *Cyclanthus bipartitus* were related to the measured microhabitat variables. Two were related to altitude, one positively and one negatively. Three were related to topographic position, one preferring upper and lower hill, two preferring lower hill and bottomland. Two were related to poor drainage, one positively and one negatively. Finally, *Asplundia cf. alata* preferred high canopy, while *Aechmea* sp. preferred low canopy.

The topographic distributions of those taxa that showed preferences are given in Table 6. Note that all of these taxa occurred in all of the topographic positions, including the least preferred.

Neighbourhood effects were present for *Chamaedorea pinnatifrons*, *Phytelephas tenuicaulis*, *Oenocarpus bataua* and *Astrocaryum chambira*. The spatial autocorrelation was positive for the first three species and negative for the last.

#### SINGLE-SPECIES ABUNDANCE

The abundances of all seven taxa analysed except *Iriartea deltoidea* were related to the microhabitat variables (Table 7). The models are given in Appendix 3 on the WWW; for address, see cover of this issue. The three small palms, *Geonoma cf. aspidiifolia*, *Geonoma m.* var. *macrostachys* and *Prestoea schultzeana*, had very different microhabitat preferences, whereas the two medium-sized palms had rather similar preferences. Only one large palm was related to the microhabitat variables measured. Two species were positively and one negatively related to altitude. One species was related (negatively) to inclination. Four taxa were related to topographic position, with one preferring upper hill only, one preferring both upper and lower hill and two preferring both upper hill and bottomland. Two species avoided poor drainage, while one preferred such conditions. One species, *Prestoea schultzeana*, was related to canopy height, preferring low canopy. Neighbourhood effects are present for *Geonoma macrostachys* var. *macrostachys*, *Prestoea schultzeana* and *Attalea* indet., and in all cases represented clumping.

#### Discussion

Prediction I, that the distribution of palms in the Yasuni community is strongly influenced by microhabitat heterogeneity, must clearly be accepted. All analyses showed that species composition within this palm community was related to the microhabitat variables. Of the 31 taxa analysed separately, 20 had significant microhabitat relationships. Thus, most of the palm and palmoid species are distributed according

**Table 5** Final logistic models for presence of palm and palmoid species. NN = presence of conspecifics in the nearest neighbouring quadrat; ALT = altitude; INC = inclination; TOP = 1, upper hill; TOP = 2, lower hill; TOP = 3, bottomland; PDSM = 1, poor drainage; MC = 0, low canopy. Independent variables with significant single-effect test are marked with + (positive relationship) or - (negative relationship). Parentheses indicate borderline significance ( $0.05 < P \leq 0.06$ ). One + or - indicate  $0.01 < P \leq 0.05$ , two  $0.001 < P \leq 0.01$ , three  $0.0001 < P \leq 0.001$ , four  $0.00001 < P \leq 0.0001$ , and five  $P \leq 0.00001$ . *U* is the uncertainty coefficient. *P* is the significance of the whole model; NS = not significant. \*All *Desmoncus* spp. pooled. †This relationship could not be evaluated due to zero cells

Taxon	NN	ALT	INC	TOP = 1	TOP = 2	TOP = 3	PDSM = 1	MC = 0	<i>U</i>	<i>P</i>
<b>Small palms</b>										
<i>Aiphanes ulei</i>										NS
<i>Bactris maraja</i> var. <i>juvuensis</i>										NS
<i>B. simplicifrons</i> var. 2										NS
<i>Chamaedorea pauciflora</i>								++	0.10	0.0078
<i>C. pinnatifrons</i>	(+)								0.03	0.0504
<i>Geonoma</i> cf. <i>aspidifolia</i>		+		++	++	--			0.53	<0.0001
<i>G. macrostachys</i> var. <i>nov.</i>				-----	-----	++++	++		0.40	<0.0001
<i>G. stricta</i> var. <i>stricta</i>			-						0.04	0.0121
<i>G. trigloch</i>				(+)	(-)	(+)	-		0.07	0.0198
<i>Hyospathe elegans</i>				++++	-----	-----			0.24	<0.0001
<i>Prestoea schultzeana</i>		-					+++	+	0.36	<0.0001
<b>Medium-sized palms</b>										
<i>Astrocaryum murumuru</i>		-		+++	---	+++			0.17	<0.0001
<i>Attalea</i> indet.				+	-	+		--	0.09	0.0031
<i>Bactris corosilla</i>										NS
<i>B. maraja</i> var. <i>maraja</i>										NS
<i>Geonoma maxima</i>				+++	+++	---			0.14	<0.0001
<i>Phytelephas tenuicaulis</i>	++++			-	-	+			0.30	<0.0001
<b>Large palms</b>										
<i>Astrocaryum chambira</i>	-								0.03	0.0395
<i>Euterpe precatorea</i>				+	-	-			0.11	0.0207
<i>Oenocarpus bataua</i>	+			++	--	--			0.14	0.0008
<i>Socratea exorrhiza</i>	†									NS
<i>Wettinia maynensis</i>										NS
<b>Palm lianas</b>										
<i>Desmoncus</i> spp.*			+						0.06	0.0368
<b>Palmoids</b>										
<i>Aechmea</i> sp.								++	0.09	0.0016
<i>Asplundia</i> cf. <i>alata</i>							--	-	0.20	0.0001
<i>Cyclanthus bipartitus</i>										NS
<i>Cybianthus</i> ( <i>Weigeltia</i> ) sp.				--	++	++			0.09	0.0064
<i>Alsophila cuspidata</i>		+		-	+	+	+		0.14	0.0018
<i>Cyathea laesiosora</i>		-		+++	+++	---			0.12	0.0004

to the microhabitat variables at scales of tens to hundreds of metres.

The microhabitat heterogeneity that had most influence on the distribution of the palms was that related to topography. This result is in accordance with earlier studies on neotropical palms (Kahn & de Castro 1985; Kahn & de Granville 1992; Clark *et al.* 1995). It also agrees with other studies showing that tropical rain forest trees, shrubs, herbs and pteridophytes often have distributions that are related to topographic variation at scales of 10–10<sup>3</sup> m (Clark *et al.* 1998; Lieberman *et al.* 1985; Denslow 1987; Poulsen & Balslev 1991; Ashton 1992a, b; Basnet 1992; ter Steege *et al.* 1993; Tuomisto & Ruokolainen 1993; Tuomisto *et al.* 1995). The result that canopy height also influenced the distributions of some of

the species, but was of much less importance than topography, agrees with similar results for pteridophytes and Melastomataceae (Tuomisto *et al.* 1995). The prominence of topography as a factor structuring tropical rain forest plant communities at local scales could be due to its correlation with both edaphic conditions and forest structure and dynamics (Poulsen & Balslev 1991; Ashton 1992a, b; Poorter *et al.* 1994; Clark *et al.* 1996; Tuomisto & Ruokolainen 1993).

There was positive spatial autocorrelation in the palm community structure that was not explained by the measured microhabitat variables, but this could be due to other, unmeasured microhabitat variables that were autocorrelated, or to disturbance history or regeneration processes (Denslow 1987). Clumping,

**Table 6** The distributions among topographic positions of the taxa that showed preferences in their presence–absence distributions with regard to topographic position. The percentage of quadrats with a certain topographic position in which the taxon was present is given. Sample size for each topographic position is given in parentheses

Taxon	% occurrence in topographic positions		
	Upper hill (32)	Lower hill (49)	Bottomland (37)
<i>Alsophila cuspidata</i>	6	20	35
<i>Astrocaryum murumuru</i>	47	35	84
<i>Attalea</i> indet.	69	43	65
<i>Cyathea laeiosora</i>	56	43	16
<i>Cybianthus</i> ( <i>Weigeltia</i> ) sp.	3	29	19
<i>Euterpe precatorea</i>	22	6	3
<i>Geonoma</i> cf. <i>aspidiifolia</i>	97	65	3
<i>G. macrostachys</i> var. nov.	13	53	95
<i>G. maxima</i>	38	16	3
<i>G. triglochis</i>	38	18	32
<i>Hyospathe elegans</i>	38	4	3
<i>Oenocarpus bataua</i>	97	78	65
<i>Phytelephas tenuicaulis</i>	13	31	62

which is a common phenomenon among tropical tree species (Denslow 1987; Hubbell 1979; Newbery *et al.* 1986), was also shown by the positive neighbourhood effects found for several species. It is noteworthy that the species with the most highly significant neighbourhood effect was the large-seeded *Phytelephas tenuicaulis*, since clumping due to limited seed dispersal has been found in other large-seeded tropical trees (Denslow 1987).

Regarding Prediction II, that palms of similar growth form show antagonistic microhabitat relationships, the conclusion for the Yasuní palm community is that it can only be partly accepted. For both small- and medium-sized palms, as well as palmoids, several very different types of microhabitat preferences were recognizable within each group (Tables 5 and Table 7). Six species pairs of small palms (involving five species) as well as two species pairs of medium-sized palms (involving three species) showed anta-

gonistic microhabitat preferences. However, some species were too rare to be analysed, some of those analysed did not show any relation to the microhabitat variables measured, and some showed similar relationships. The majority of the large palm species did not show apparent microhabitat preferences, and the two species that did, *Euterpe precatorea* and *Oenocarpus bataua*, had quite similar microhabitat relationships, both preferring the upper parts of the terrain. Palm lianas (*Desmoncus* spp.) were too rare in the sample for any conclusions regarding differences in microhabitat preferences. Thus, the results provide limited support for coexistence by microhabitat specialization, but only for understory palms and palmoids.

Among the 13 taxa that showed preferences in their presence–absence distributions with regard to topographic position, all also occurred in the least preferred topographic position (Table 6). These patterns

**Table 7** Final ordinal logit models for the abundance of common species. Legends follow Table 5, except NN = 1, conspecifics present but not abundant in nearest neighbouring quadrat; and NN = 2, conspecifics abundant in the nearest neighbouring quadrat. †Presence of zero cells. \*Analysed dichotomously as abundant (2) vs. not abundant (0 or 1)

Taxon	NN = 1	NN = 2	ALT	INC	TOP = 1	TOP = 2	TOP = 3	PDSM = 1	MC = 0	U	P
Small palms											
<i>Geonoma</i> cf. <i>aspidiifolia</i>			+		++†	++†	--†	–		0.40	<0.0001
<i>G. macrostachys</i> var. <i>macrostachys</i> *		++		--						0.16	<0.0001
<i>Prestoea schultzeana</i>	+++†	+++†	(–)		†	†	†	++++	+	0.34	<0.0001
Medium-sized palms											
<i>Astrocaryum murumuru</i>	†	†	–		+++	---	+++			0.15	<0.0001
<i>Attalea</i> indet.	–	+			+	–	+		–	0.10	0.0008
Large palms											
<i>Iriartea deltoidea</i> †											NS
<i>Oenocarpus bataua</i>					++++	----	----	–		0.15	<0.0001

could result from mass effects over scales less than  $10^3$  m. There were also patterns that could have resulted from mass effects over larger scales, among habitats. Five of the rarer species, *Chamaedorea pauciflora*, *Desmoncus polyacanthos*, *Euterpe precatoria*, *Geonoma brongniartii* and *Socratea exorrhiza*, were all much more abundant on the nearby Tiputini floodplain and in some cases also in nearby swamps (J.-C. Svenning, personal observation). Thus, their presence on terra firme might only be maintained by seed dispersal from these habitats. Demographic studies would be necessary to find out whether these distribution patterns are due to mass effects. While the results presented here do not test the importance of mass effects for maintaining tropical plant species diversity at small scales ( $10\text{--}10^3$  m), in contrast to Duivenvoorden (1995, 1996) they indicate that this phenomenon could be important, as has also been suggested by Gentry (1988) and Tuomisto *et al.* (1995).

In conclusion, the species composition of this highly diverse palm community appeared to be structured by the microhabitat variables studied, especially topographic position, at scales less than  $10^3$  m. Many of the palms and palmoids had distributions strongly influenced by microhabitat heterogeneity. The presence of antagonistic patterns of microhabitat preferences among some species pairs of small- and medium-sized palms as well as palmoids supports the hypothesis that coexistence by microhabitat specialization is important in maintaining the local species richness of these groups. There is no evidence that canopy palms coexist by microhabitat specialization. Mass effects might be important for maintaining the palm diversity both at the habitat and at the microhabitat level. Overall, the results of this study suggest that topographic and other microhabitat heterogeneity could be important factors in the maintenance of the high local plant species richness in tropical rain forests.

### Acknowledgements

I thank Henrik Balslev, Pamela Hall and Else Magård for invaluable assistance with this project, and Renato Valencia, Richard Condit and Robin Foster of the Yasuní Forest Dynamics Project for allowing me to use the 50-ha plot and to use the altitudinal data. I acknowledge INEFAN for research permits, and Pontificia Universidad Católica del Ecuador for scientific and practical assistance. I am grateful to the Faculty of Natural Sciences, University of Aarhus and Statens Naturvidenskabelige Forskningsråd (grant number 11-0390 to the Centre for Tropical Biodiversity) for economic support. Thanks to Flemming Nørgaard for making Fig. 1. Finally, I wish to thank David B. Clark, Carlos Peres and Tony Davy for review comments.

### References

- Armbruster, W.S. (1995) The origins and detection of plant community structure: reproductive versus vegetative processes. *Folia Geobotanica et Phytotaxonomica*, **30**, 483–497.
- Ashton, P.M.S. (1992a) Establishment and early growth of advance regeneration of canopy trees in moist mixed-species forest. *The Ecology and Silviculture of Mixed-Species Forests* (ed. M. J. Kelty), pp. 101–122. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Ashton, P.S. (1992b) The structure and dynamics of tropical rain forest in relation to tree species richness. *The Ecology and Silviculture of Mixed-Species Forests* (ed. M. J. Kelty), pp. 53–64. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Ashton, P.S. & Hall, P. (1992) Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology*, **80**, 459–481.
- Balslev, H., Luteyn, J., Øllgaard, B. & Holm-Nielsen, L.B. (1987) Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica*, **92**, 37–57.
- Basnet, K. (1992) Effect of topography on the pattern of trees in tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. *Biotropica*, **24**, 31–42.
- Chazdon, R.L. (1986) Light variation and carbon gain in rain forest understorey palms. *Journal of Ecology*, **74**, 995–1012.
- Clark, D.A. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315–344.
- Clark, D.B. (1996) Abolishing virginity. *Journal of Tropical Ecology*, **12**, 735–739.
- Clark, D.B., Clark, D.A. & Read, J.M. (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology*, **86**, 101–112.
- Clark, D.B., Clark, D.A. & Rich, P.M. (1993) Comparative analysis of microhabitat utilization by saplings of nine tree species in neotropical rain forest. *Biotropica*, **25**, 397–407.
- Clark, D.B., Clark, D.A., Rich, P.M., Weiss, S. & Oberbauer, S.F. (1996) Landscape-scale evaluation of understorey light and canopy structure: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research*, **26**, 747–757.
- Clark, D.A., Clark, D.B., Sandoval, M., R., Castro, C. & M.V. (1995) Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology*, **76**, 2581–2594.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *The American Naturalist*, **140**, 261–286.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1994) Density dependence in two understorey tree species in a neotropical forest. *Ecology*, **75**, 671–680.
- Connell, J. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.
- Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, **18**, 431–451.
- De Steven, D. (1989) Genet and ramet demography of *Oenocarpus mapora* ssp. *mapora*, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology*, **77**, 579–596.
- Duivenvoorden, J.F. (1995) Tree species composition and rain forest-environment relationships in the middle Caquetá area, Colombia, NW Amazonia. *Vegetatio*, **120**, 91–113.
- Duivenvoorden, J.F. (1996) Patterns of tree species richness

- in rain forests of the middle Caquetá area, Colombia, NW Amazonia. *Biotropica*, **28**, 142–158.
- Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1–34.
- Grubb, P.J. (1996) Rainforest dynamics: the need for new paradigms. *Tropical Rainforest Research – Current Issues. Vol. 74. Monographiae biologicae* (eds D. S. Edwards, W. E. Booth & S. C. Choy), pp. 215–233. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Henderson, A. (1995) *The Palms of the Amazon*. Oxford University Press, Oxford, UK.
- Hosmer, D.W. & Lemeshow, S. (1989) *Applied Logistic Regression*. John Wiley & Sons, New York, NY.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Janzen, D.H. (1970) Herbivores and the numbers of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.
- Kahn, F. (1986) Life forms of Amazonian palms in relation to forest structure and dynamics. *Biotropica*, **18**, 214–218.
- Kahn, F. & de Castro, A. (1985) The palm community in a forest of central Amazonia, Brazil. *Biotropica*, **17**, 210–216.
- Kahn, F. & de Granville, J.-J. (1992) *Palms in Forest Ecosystems of Amazonia*. Ecological studies Vol. 95. Springer-Verlag, Berlin, Germany.
- Legendre, L. & Legendre, P. (1983) *Numerical Ecology*. Elsevier Scientific Publishing Company Inc., Amsterdam, the Netherlands.
- Legendre, P. & Fortin, M.-J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.
- Legendre, P. & Vaudor, A. (1991) *The R Package: Multidimensional Analysis, Spatial Analysis*. Département de Sciences Biologiques, Université de Montréal, Montreal, Canada.
- Lieberman, M., Lieberman, D., Hartshorn, G.S. & Peralta, R. (1985) Small-scale altitudinal variation in lowland wet tropical forest vegetation. *Journal of Ecology*, **73**, 505–516.
- Lieberman, M., Lieberman, D., Peralta, R. & Hartshorn, G.S. (1995) Canopy closure and the distribution of tropical tree species at La Selva, Costa Rica. *Journal of Tropical Ecology*, **11**, 161–178.
- Lips, J.M. & Duivenvoorden, J.F. (1996) Regional patterns of well drained upland soil differentiation in the middle Caquetá basin of Colombia Amazonia. *Geoderma*, **72**, 219–257.
- Newbery, D.M.C., Renshaw, E. & Brüning, E.F. (1986) Spatial pattern of trees in kerangas forest, Sarawak. *Vegetatio*, **65**, 77–89.
- Peres, C.A. (1994) Composition, density, and fruiting phenology of arborescent palms in an Amazonian terra firme forest. *Biotropica*, **26**, 285–294.
- Piñero, D., Martínez-Ramos, M., Mendoza, A., Alvarez-Buylla, E. & Sarukhán, J. (1986) Demographic studies in *Astrocaryum mexicanum* and their use in understanding community dynamics. *Principes*, **30**, 108–116.
- Poorter, L., Jans, L., Bongers, F. & Van Rompaey, S.A.R. (1994) Spatial distribution of gap along three catenas in the moist forests of Taï National Park, Ivory Coast. *Journal of Tropical Ecology*, **10**, 385–398.
- Poulsen, A.D. & Balslev, H. (1991) Abundance and cover of ground herbs in an Amazonian rain forest. *Journal of Vegetation Science*, **2**, 315–322.
- Primack, R.B. & Hall, P. (1992) Biodiversity and forest change in Malaysian Borneo. *Bioscience*, **42**, 829–837.
- Richards, P. & Williamson, G.B. (1975) Treefalls and patterns of understorey species in a wet lowland tropical forest. *Ecology*, **56**, 1226–1229.
- Scariot, A. (1999) Forest fragmentation effects on palm diversity in central Amazonia. *Journal of Ecology*, **87**, 66–76.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman and Company, New York, NY.
- ter Steege, H., Jetten, V.G., Polak, A.M. & Werger, M.J.A. (1993) Tropical rain forest types and soil factors in a watershed area in Guyana. *Journal of Vegetation Science*, **4**, 705–716.
- Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.
- Trexler, J.C. & Travis, J. (1993) Nontraditional regression analyses. *Ecology*, **74**, 1629–1637.
- Tuomisto, H. & Ruokolainen, K. (1993) Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of Vegetation Science*, **4**, 25–34.
- Tuomisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W. & Rodriguez, Z. (1995) Dissecting Amazonian biodiversity. *Science*, **269**, 63–66.
- Valencia, R., Balslev, H., Paz y Miño, C. & G. (1994) High tree alpha-diversity in Amazonian Ecuador. *Biodiversity and Conservation*, **3**, 21–28.
- Vandermeer, J.H., Stout, J. & Miller, G. (1974) Growth rates of *Welfia georgii*, *Socratea durissima* and *Iriartea gigantea* under various conditions in a natural rainforest in Costa Rica. *Principes*, **18**, 148–154.
- Vásquez, G., J.A. & Givnish, T.J. (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *Journal of Ecology*, **86**, 999–1020.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 35–50.
- Whitmore, T.C. (1989) Canopy gaps and two major groups of forest trees. *Ecology*, **70**, 536–538.
- Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Science of the USA*, **94**, 1252–1257.

Received 13 March 1998

revision accepted 1 June 1998