Landscape-Scale Environmental and Floristic Variation in Costa Rican Old-Growth Rain Forest Remnants

Steven E. Sesnie[1,2,3], **Bryan Finegan**[2], **Paul E. Gessler**[1], and **Zayra Ramos**[2]

[1]Department of Forest Resources, University of Idaho, Moscow, Idaho 83844-1133, U.S.A.

[2]Departamento Recursos Naturales y Ambiente, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Sede Central 7170, Turrialba, Costa Rica

ABSTRACT

Studies of tropical rain forest beta-diversity debate environmental determinism versus dispersal limitation as principal mechanisms underlying floristic variation. We examined the relationship between soil characteristics, terrain, climate variation, and rain forest composition across a 3000 km^2 area in northeastern Costa Rica. Canopy tree and arboreal palm species abundance and soils were measured from 127 0.25-ha plots across Caribbean lowlands and foothills. Plot elevation, slope, temperature, and precipitation variation were taken from digital grids. Ordination of forest data yielded three floristic groups with strong affinities to foothills and differing lowland environments. Variation in floristics, soil texture, and climate conditions showed parallel patterns of significantly positive spatial autocorrelation up to 13 km and significantly negative correlation beyond 40 km. Partial Mantel tests resulted in a significant correlation between floristic distance and terrain, climate and soil textural variables controlling the effect of geographical distance. Separate comparisons for palm species showed significant correlation with Mg and Ca concentrations among other soil factors. Arboreal palm species demonstrated a stronger relationship with soil factors than did canopy trees. Correlation between floristic data and geographical distance, related to seed dispersal or unmeasured variables, was not significant after controlling for soil characteristics and elevation. Canopy trees and palms showed differing relationships to soil and other environmental factors, but lend greater support for a niche-assembly hypothesis than to a major role for dispersal limitation in determining species turnover for this landscape.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: arboreal palms; canopy trees; Central America; dispersal assembly; environmental factors; niche; tropical rain forest.

DETERMINING FACTORS THAT DRIVE RAIN FOREST BETA-DIVERSITY is fundamental to characterizing the floristic composition of Neotropical landscapes. Rapid deforestation since the 1950s has left dispersed forest fragments over much of Central and South America that are important to maintaining regional floristic diversity (Defries *et al.* 2005, Mayaux *et al.* 2005). Beta-diversity, defined here as the spatial turnover in species composition (Condit *et al.* 2002), is well integrated into temperate zone biodiversity assessment (Scott and Jennings 1998), but has yet to play a prominent role in conservation planning for tropical areas. Floristic variation with respect to environmental differences and geographical location is poorly quantified for wet tropical areas given logistical constraints and challenging taxonomy (Ruokolainen *et al.* 1997). As a result, differences in rain forest composition are broadly characterized by relatively few forest types with wide reaching implications for biodiversity conservation (Tuomisto *et al.* 2003a).

Distinctive floras on poor fertility or inundated sites are well acknowledged aspects of rain forest beta-diversity (Ter Steege *et al.* 1993, Duivenvoorden 1995, Tuomisto *et al.* 1995, Duque *et al.* 2002). Recent quantitative assessments of Panamanian and Amazonian forest plots provide evidence that forest composition on *tierra firme* sites (*e.g.*, nonflooded or less extreme edaphic environments) varies with greater consistency than previously considered (Condit *et al.* 2002; Phillips *et al.* 2003; Tuomisto *et al.* 2003a, b; Chust *et al.* 2006). However, factors accounting for floristic variation contrast between geographical location, scale of analysis, and plant groups

investigated (Ruokolainen and Tuomisto 2002, Phillips *et al.* 2003). For example, Condit *et al.* (2002) found that tree species similarity for Panamanian forest plots was as low as 1 percent at 50 km distance, but showed consistent similarities of 30–40 percent up to 100 km apart for Amazonian plots.

Contemporary points of view distinguish between niche and dispersal assembly as principal mechanisms for variation in rain forest composition (Hubbell 2001, Jones *et al.* 2006). From as early as Gleason (1927) and Whittaker (1967), niche theory posits that plant species show nonrandom distributions that vary according to environmental conditions. Environmental determinism and competitive interaction are assumed to mediate plant community organization and are frequently the basis for models of floristic patterns (Franklin 1995, Austin 2002). A growing number of tropical studies reveal that soil, climate, and topographic differences are significantly related to rain forest tree, fern, and palm species distributions at local (< 1 km^2; Ruokolainen *et al.* 1997, Vormisto *et al.* 2004a, Poulsen *et al.* 2006, John *et al.* 2007), meso-scale (1–100 km^2; Clark *et al.* 1995, 1999, Jones *et al.* 2006), landscape-scale (100–10,000 km^2; Tuomisto *et al.* 1995, 2003a, b, c, Pyke *et al.* 2001, Phillips *et al.* 2003), and continental scale ($> 100,000$ km^2; Ter Steege *et al.* 2006).

In contrast, dispersal assembly challenges whether environmental factors are principal drivers of the present variation in old-growth rain forest composition (Hubbell *et al.* 1999, Hubbell 2001, Condit *et al.* 2002, Chust *et al.* 2006). Hubbell *et al.* (1999) noted that small-scale disturbance accommodates opportunistic establishment by individuals from the surrounding meta-community, rather than by species with a competitive advantage. In the event that

disturbances, common to Neotropical rain forest (Hartshorn 1980, Hubbell *et al.* 1999), and seed dispersal are highly random occurrences, tree species similarity is expected to decline logarithmically with increasing geographical distance (Hubbell 2001, Condit *et al.* 2002). Thus, an alternative hypothesis is that distance dependent processes significantly influence forest composition, above that from environmental factors.

Chust *et al.* (2006) conclude that geographical distance related to seed dispersal was a stronger predictor of tree species composition than precipitation or elevation variables from plots across the Panama Canal Watershed, consistent with a dispersal limitation hypothesis. However, no data were available to assess soil differences related to forest composition, as noted by the authors (Chust *et al.* 2006). Amazonia forest plots further suggest that geographic distance and dispersal limitation are more strongly related to differences in palm species abundance than soil and environmental factors at the landscape-scale (Vormisto *et al.* 2004b, Normand *et al.* 2006). In contrast to these studies, soil nutrient status and physical characteristics have shown significant correlation with tree, palm, and fern species on rain forest plots at multiple spatial scales (Duque *et al.* 2002, Phillips *et al.* 2003, Jones *et al.* 2006, Poulsen *et al.* 2006, John *et al.* 2007). Environmental factors can show strong covariance patterns with vegetation at increasingly distant sample locations (Legendre & Fortin 1989). In the case where multiple factors are correlated with floristic composition, spatial autocorrelation among variables can add greater importance to observed relationships than is actually warranted (Wagner & Fortin 2005).

The present study evaluates relationships between rain forest composition and environmental factors on *tierra firme* sites in northern Costa Rica. We sought to clarify quantitative relationships between forest composition, soil, and climate factors for a 3000 km^2 Caribbean forest landscape accounting for the effect of spatial autocorrelation. Our objectives were to: (1) quantify floristic and environmental differences among old-growth forest remnants at a landscape-scale; (2) assess the degree of spatial autocorrelation for floristic data and environmental variables at increasingly distant sample locations; and (3) compare statistical relationships between niche and geographical factors, such as dispersal limitations, random disturbance, and metapopulation dynamics, relevant to principle theories associated with rain forest beta-diversity.

Plots were established to measure floristic composition of mid- to upper-canopy trees and arboreal palms (Arecaceae) and ferns (Cyatheaceae) in old-growth forest remnants that were the focus of data collection and analyses. Several studies suggest that spatial variation sometimes differ among plant groups (*e.g.*, tree vs. palm species) and the environmental factors evaluated (Ter Steege *et al.* 1993, Vormisto *et al.* 2004a, Jones *et al.* 2006, Poulsen *et al.* 2006). With this study, partial mantel tests using distance matrices from trees and palms together and palms separately were evaluated to distinguish among different plant groups occupying forest canopies and mechanisms related to patterns of abundance. The logarithm of geographical distance from spatially referenced plot locations was used to approximate seed dispersal and distance related processes following Hubbell (2001). If species abundance correlates strongly with geographic distance after controlling for significant environmental factors, we would expect to see evidence for dispersal-assembly as a dominant process related to forest beta-diversity. Alternatively, strong environmental control over species abundance would indicate greater importance of niche factors after controlling the affect of geographical distance.

METHODS

FIELD MEASUREMENTS.—Tree and soil measurements were taken from old-growth forest remnants across northeastern Costa Rica (Fig. 1a). A majority of the plots were located in the San Juan–La Selva Biological Corridor, which is one the largest forest aggregations remaining outside national parks in Costa Rica (Watson *et al.* 1998). The corridor area is a portion of the Mesoamerican Biological Corridor that connects protected areas in Costa Rica's Central Mountain Range to protected rain forest in southern Nicaragua (Fig. 1A). Human settlement in the area since the 1950s has reduced forest cover to dispersed remnant patches situated between pasture and croplands (Butterfield 1994).

The physical environment is influenced by elevation that ranges from sea level to > 3000 m in the Central Volcanic Range (Lieberman *et al.* 1996). Lowland terrain is a mixture of alluvial terraces, swamplands, and steep hills reaching 400 m elevation (Fig. 1B). Soils are mainly Pleistocene aged Ultisols derived from andesitic parent material with evidence of ash falls > 500 m asl (Grieve *et al.* 1990, Sollins *et al.* 1994) and Inceptisols derived from alluvial and colluvial deposits overlaying old lava flows (Hartshorn & Peralta 1988, Sollins *et al.* 1994). Temperatures average near 24°C in the lowlands that decreases to as low as 10°C at the highest elevations (Lieberman *et al.* 1996) with greater seasonal variation in the lowlands (Fig. 1C, D). Annual precipitation ranges from 4500 mm in the foothills (Hartshorn & Peralta 1988, Grieve *et al.* 1990) to 3000 mm in western lowland sites according to meteorological station records and precipitation grids described below (Fig. 1E). The eastern lowlands and the foothills have consistently high monthly rainfall ≥ 150 mm throughout the year. Annual precipitation decreases with distance from the Caribbean Coast and lower monthly precipitation occurs during March in western lowlands averaging < 100 mm rainfall (Fig. 1F).

A total of 127 0.25-ha plots (50 × 50 m) were established at 40–1200 m elevation (Fig. 1B), avoiding extreme site conditions (*e.g.*, palm and forested swamps). A minimum of two plots were located in forest remnants that range in size from 40 ha to more contiguous forest patches > 1000 ha. Plots were positioned following a compass line from an accessible point for a minimum distance of 150 m from a forest edge and at least 300 m from another plot. Areas with tree harvest, wind, or other evidence of recent disturbance were avoided during sampling. Interplot distances range from 0.3 to 61 km. On each plot, a stem dbh (1.37 m above base) and species name was recorded for all trees ≥ 30 cm dbh and arboreal palms and ferns (Cyatheaceae) ≥ 10 cm dbh. Tree species were recorded on site by field taxonomists or sample material was taken to National Institute for Biodiversity (INBio) Herbarium in San
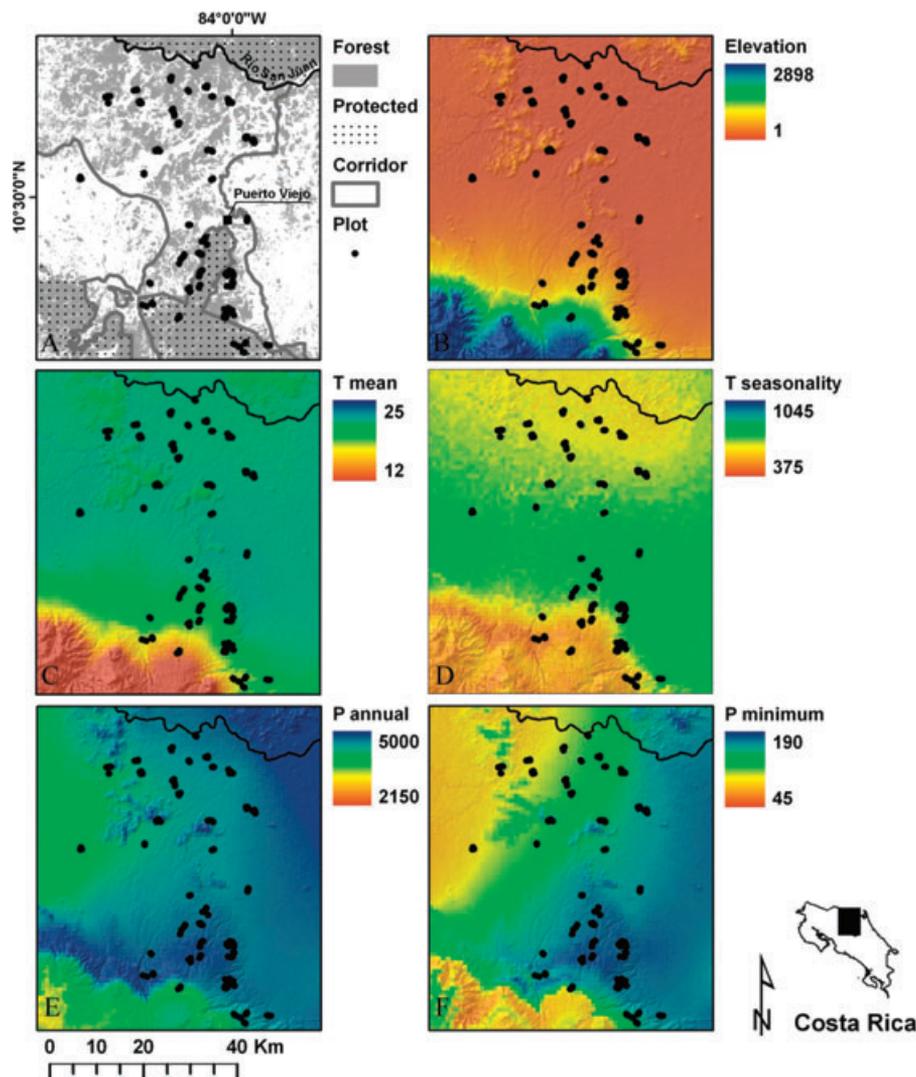
FIGURE 1. Plot locations between the Caribbean lowlands and foothills of the Central Mountain Range (lower left) in northeastern Costa Rica. Figures are: (A) forest (gray) and nonforested areas (white), (B) elevation, (C) mean annual temperature (T), (D) temperature seasonality, (E) total annual precipitation (*P*), and (F) minimum monthly precipitation.

José, Costa Rica, for identification by Nelson Zamora. All plots were geo-referenced from a canopy gap using a global positioning system with an estimated horizontal error of *ca* 12 m.

To assess soil conditions, a 40-cm soil sample was collected at plot center using a 7-cm diameter Dutch-type auger. Soil depth and presence of a high water table were determined with a 1.5-m metal probe, though forest plots were not established on sites with evidence of consistently saturated soil (*e.g.*, water present or strong gleying). Organic material was cleared from the top 1–2 cm of each site prior to auguring. Soil was placed in a labeled plastic bag and transported to the soils laboratory at the Centro Agronómico Tropical de Investigación y Enseñnza (CATIE) in Turrialba, Costa Rica. Samples were air-dried in a screened drying room before laboratory analysis.

Soil chemical and physical properties selected for laboratory analysis were those likely to affect tree growth and rain forest composition (Sollins 1998). Soil pH in water was measured and extractable K and P were measured using Modified Olsen extractions with a 0.5 M sodium bicarbonate ($NaHCO_3$) solution at a pH of 8.5 (Olsen and Sommers 1982). Extractable Ca, Mg, and total acidity extractions were done in a 1N suspension of potassium chloride (KCl) using methods documented by Diaz Romeu and Hunter (1978). Percent soil organic matter (OM) was measured using the total combustion method following Nelson and Sommer (1996) with pretreatment to eliminate carbonates. Soil texture (percent sand, silt, and clay) was determined by the Bouyoucos method (Bouyoucos 1936). Textural classes were assigned following methods from the USDA Soil Survey Staff (1975). Total acidity

was used as an indicator of potential aluminum (Al) toxicity and soil textural features as indicators of drainage and water retention that potentially affect tropical tree species distribution (Lieberman *et al.* 1985, Faber-Langendoen & Gentry 1991, Sollins *et al.* 1994, Sollins 1998).

Climate and terrain variables for geo-referenced plots were taken from digital data layers in a geographic information system. Plot elevations were taken from a 90-m digital elevation model (DEM) obtained from the U.S. Geological Survey Shuttle Radar and Topography Mission (SRTM) data set (http://edc.usgs.gov/products/elevation.html). Percent slope was estimated from the DEM using the Spatial Analyst extension in ArcMap v. 9.1 (ESRI 2005).

Average annual temperature and precipitation values for plot locations were taken from WorldClim 30 arc-second grids (*ca* 1-km resolution) for comparisons with forest composition (Fig. 1C, E). The WorldClim bioclimatic data set is designed for niche modeling of plant and animal species (http://www.worldclim.org/). Digital surfaces of annual and seasonal climate cycles are derived from local weather station records of monthly temperature and precipitation, latitude, longitude, and SRTM elevation data. A description of interpolation methods is found in Hijmans *et al.* (2005). Coefficients of variation (CV) and minimum monthly precipitation values were also used as indices of rainfall seasonality for statistical comparison with floristic data. Metrics for seasonal temperature variation used were the average temperature of the coldest month and monthly temperature standard deviation × 100 that are potentially related to rain forest composition at this scale (Pyke *et al.* 2001).

STATISTICAL ANALYSES.—Modified *t*-tests and Pearson's correlations (Pearson's *r*) were used to determine significant relationships (*P* < 0.05) between soil, climate, and terrain variables (*e.g.*, elevation and slope). Modified *t*-tests account for the degree of spatial autocorrelation among variables measured from plot locations using corrected degrees of freedom to assess statistical significance following Dutilleul *et al.* (1993).

Statistical comparisons between forest composition and environmental factors were made using distance matrices. Sørensen (Bray–Curtis) distance matrices were computed for tree and palm species abundance combined and palm abundance separately for comparisons with environmental and geographical distance matrices. A matrix for palm species included 117 plots containing at least one individual of the four most abundant species (*Iriartea deltoidea* Ruiz & Pav., *Euterpe precatoria* Mart., *Socratea exorrhiza* (Mart.) H. Wendl, and *Welfia regia* Mast). Soil and environmental variables were log transformed and a separate Euclidean distance matrix was derived for each one. Geographical distance among plots was log transformed to approximate the effect of random species dispersal (Hubbell 2001).

Hierarchical cluster analysis using the Flexible beta linkage method (beta = −0.25) and Nonmetric Multidimensional Scaling (NMS) were used to characterize floristic composition observed from plots. Twenty runs with real data and 50 runs with randomized data were used to evaluate the stability of the final ordination. Pearson correlation coefficients between tree species, environmen-

tal factors, geographical distance (*e.g.*, x and y co-ordinates) and ordination axes were used to interpret NMS results. The PC-ORD statistics package v. 5.01 was used for these analyses (McCune & Mefford 1999).

Mantel correlation comparisons (Mantel's *r*) between matrices were performed using the PASSAGE statistics package v. 1.1 (Rosenburg 2001). The standardized Mantel statistic is similar to a Pearson product-moment coefficient, but is calculated comparing paired distance matrices rather than original variables (Legendre & Fortin 1989). The degree of spatial autocorrelation between floristic composition, environmental variables, and geographical distance was first evaluated via Mantel Corrrleograms (Legendre & Fortin 1989). Mantel correlation coefficients were compared for distance classes ranging from 0–0.5 km to 58–61 km to determine the degree of spatial autocorrelation among variables at increased interplot distances. Distance classes were closely spaced initially at 0.5 km and then at 3-km intervals.

Partial Mantel tests were used to determine relationships between two distance matrices while controlling the effects of a third factor (*e.g.*, environmental or geographical distance). Species and environmental distances were compared after controlling for geographical distance. Geographical distance itself was considered an important variable related to the dispersal assembly hypothesis (Condit *et al.* 2002, Chust *et al.* 2006) and compared with floristic distance after controlling for statistically significant environmental factors. Statistical significance was tested for each comparison using Monte Carlo permutations from 999 matrix randomizations (α < 0.05).

RESULTS

SOIL AND TERRAIN CONDITIONS.—Soils showed a wide range of chemical and physical properties along the gradients sampled (Table 1). Cation concentrations (Ca, K, Mg), pH, and extractable P showed a broad range of values, but had relatively low standard deviations. Greater cation concentrations were found on six plots

TABLE 1. *Summarized soil chemical and physical properties from 0.25-ha old–growth forest plots (N = 127) in northeastern Costa Rica.*

	Mean	Range	SD
Ca (cmol(+)/kg)	0.73	0.06–11.0	1.78
K (cmol(+)/kg)	0.08	0.02–0.28	0.04
Mg (cmol(+)/kg)	0.46	0.82–5.59	0.95
Sum of Ca, K, Mg	1.27	0.19–15.2	2.72
P (mg/kg)	2.70	0.47–15.1	1.92
Total acidity (cmol(+)/kg)	2.88	0.10–7.26	1.23
pH	4.57	3.83–6.40	0.38
Organic matter—OM (%)	8	1.70–23.9	4.15
Sand (%)	37	8–81	21.3
Silt (%)	17	7–42	5.56
Clay (%)	46	4–78	20.7

TABLE 2. *Correlation matrix and Pearson coefficients from Modified t-tests comparing soil and terrain variables from plots. Significant correlations (P < 0.05) in bold were computed with reduced degrees of freedom (effective sample size) corrected for spatial autocorrelation (Dutilleul et al. 1993).*

	Acidity	Ca	K	Mg	P	Sand	Silt	Clay	OM	Slope	Elev
pH	**−0.53**	**0.81**	**0.44**	**0.82**	**0.22**	−0.02	**0.61**	−0.14	−0.20	0.07	0.05
Acidity		−0.29	−0.16	**−0.27**	0.01	**−0.41**	−0.08	**0.45**	**−0.28**	−0.14	**−0.45**
Ca			**0.68**	**0.95**	**0.44**	−0.14	**0.63**	−0.03	−0.26	0.07	−0.11
K				**0.60**	**0.40**	**0.24**	**0.41**	**−0.36**	0.20	0.15	0.23
Mg					**0.53**	−0.18	**0.71**	−0.01	−0.27	0.00	−0.15
P						−0.11	**0.26**	0.04	0.01	−0.18	−0.20
Sand							−0.25	**−0.97**	**0.80**	0.33	**0.87**
Silt								−0.02	**−0.31**	0.07	−0.12
Clay									**−0.74**	−0.36	**−0.87**
OM										0.18	**0.78**
Slope											0.33

measured at low elevation sites contributing to the range observed. Extractable phosphorous (P) was also highest for these plots. Forest soils sampled were commonly acidic (pH 4.57 ± 0.38) and low in bases (Table 1). Significantly positive Pearson correlations between pH and cation concentrations, and P to a lesser degree indicated a relationship between acidity and native soil fertility (Table 2). Total acidity was significantly and negatively correlated with elevation and Mg concentrations, but had low SD across sites (Tables 1 and 2). No significant trend between soil cations and terrain variables elevation and percent slope was observed (Table 2).

Soil physical properties showed a more substantial difference across the study area (Table 1). A high range in silt content (7–42%) and low SD (± 5.6) was attributed to four plots across a single large forest remnant on lowland flood plains with silty-clay textures that likely developed from intermittent flooding. These plots were also the highest in cation and P concentrations. Soil clay, sand, and organic content differed considerably across the study landscape and were highly and significantly correlated with elevation (Table 2). Soils in the foothills of the Central Volcanic Range were clearly higher in sand and organic material contrasting with clay-rich soils in the lowlands (Fig. S1). Percent slope showed a negative correlation with clay and positive correlation with sand content, but were not significantly related (Table 2).

CLIMATE AND TERRAIN CONDITIONS.—Temperature and precipitation patterns showed notable differences between plots, but did not reflect extreme climatic gradients (*e.g.*, wet to dry tropical environments; Table 3). The largest coefficients of variation for monthly precipitation are approximately half of those found in dry tropical forest environments (data not shown) as characterized by the Holdridge Life Zone system (Holdridge 1967). Mean temperatures were moderately cooler for plots in the foothills (minimum monthly temperature of 15°C) with moderate seasonal differences in the lowlands (Fig. 1C, D). Seasonally lower precipitation was observed for plots in the western lowlands (Fig. 1F) although annual precipitation was generally high across all plots (Table 3). Metrological

station records obtained for the study area generally confirm temperature and precipitation variation in the lowlands observed from interpolated WorldClim grids. A drier period > 1000 m elevation (Fig. 1F) could not be confirmed as weather stations are sparsely distributed in this area however a decline in annual rainfall > 1800 m is reported in Hartshorn and Peralta (1988) for this area.

The elevation range of plots (41–1222 m) was the most important source of variation in terrain and showed a strong negative correlation with temperature seasonality (Pearson $r = -0.64$, $P < 0.001$) and minimum monthly temperature (Pearson $r = -0.98$, $P < 0.001$). No other climate variables were significantly correlated with elevation or slope from Modified *t*-tests. Precipitation did not show a significant correlation with elevation. Complex physiographic conditions across the study area likely reduce covariance patterns as rainfall decreases with distance from the Caribbean coast and increases then decreases at higher elevations in the Central Mountains (Lieberman *et al.* 1996).

FLORISTIC VARIATION AND MEASURED GRADIENTS.—A total of 189 species with > 1 individual encountered on all plots (5066 individuals) were used for statistical analyses. Ninety percent of individuals

TABLE 3. *Summarized climate and terrain attributes associated with forest plots from digital grids.*

	Mean	Range	SD
Elevation (m)	267	41–1222	264
Slope (%)	9	0–53	9
Mean monthly temperature (°C)	25	20–26	1.1
Temperature seasonality (SD × 100)	663	515–762	54
Min. monthly temperature (°C)	20	15–21	1.2
Annual precipitation (mm)	3976	2853–4530	313
Rainfall seasonality (CV)	32	27–59	6
Min. monthly precipitation (mm)	144	51–187	34

were identified to the species level. All others were identified to genus and given a species number that was repeated for individuals with similar morphological characteristics. Tree species accounted for 61 percent of the individuals sampled and 38 percent were four of the most abundant palm species (*I. deltoidea*, *E. precatoria*, *S. exorrhiza*, and *W. regia*). Arboreal ferns $\geq$ 10 cm dbh (*Cyathea spp.* Sm.) and other palms (*Bactris* spp. Jacq. ex Scop.) were measured on plots, but accounted for 1 percent of all individuals. Fewer plots at the highest elevations where arboreal ferns are most common (Hartshorn & Peralta 1988, Lieberman *et al.* 1996) account for the low number of individuals recorded in comparison with palms.

To observe floristic variation among plots, three principle floristic groups resulting from a hierarchical cluster analysis of plots were overlaid on NMS ordinations (Fig. 2). A three dimensional solution was obtained from ordinations with a final stress index of 16.7 that was significantly better than if by chance ($P < 0.05$) from Monte Carlo randomizations. The amount of variance explained was 22, 30, and 30 percent for axis 1, 2, and 3, respectively (82% total).

Axis 1 explained less of the total variation among plots and was not strongly correlated with a dominant tree species or floristic group (Fig. 2A). Plots along axes 2 and 3 were divided into floristic groups with a strong affinity toward the foothills ($N = 31$ plots) or differing lowland environments (Fig. 2B). Lowland sites were dominated by *Pentaclethra macroloba* (Willd.) Kuntze ($N = 61$ plots) showing a strong negative correlation with axis 3 (Fig. 2). Composition differences between the two lowland floristic groups were determined by an increased abundance for trees in the Vochysiaceae family (*e.g.*, *Qualea paraensis* Ducke, *Vochysia allenii* Standl. & L.O. Williams, *Vochysia ferruginea* Mart.) that are positively correlated with axis 3 and abundant palm species negatively correlated with axis 2 ($N = 29$ plots; Fig. 2B). Floristic groups were nominally termed foothills, *P. macroloba* and *Q. paraensis* forest in reference to different tree species composition for each group.

Environmental variables resulting in a strong positive or negative correlation with ordination axes are given in order of importance. Floristic differences between the foothills and lowlands along axis 3 were positively correlated with sand content ($r = 0.65$) and plot elevation ($r = 0.69$) and negatively correlated with all temperature variables ($r \geq -0.70$; Fig. 2). Clay content was negatively correlated with axis 3 ($r = -0.63$) in the direction of *P. macroloba* dominated forest at the lower end of this axis. Axis 2 showed positive correlation with elevation ($r = 0.40$) and a negative correlation with soil texture using a ratio of clay to sand ($r = -0.42$). Axis 2 was also negatively correlated with geographical distance ($r = -0.61$) in a south to north direction from plot co-ordinates. Axis 1 was negatively correlated with total annual precipitation ($r = -0.71$) and minimum monthly precipitation ($r = -0.64$) that is likely a result of decreasing precipitation from east to west across both the lowlands and foothills (Fig 1E, F). All other environmental factors showed a weak correlation with ordination axes.

Modified *t*-tests indicate that a number of the factors correlated with ordination axes are intercorrelated with each other such as elevation and clay content (Table 2). These data identify multiple gradients across both the lowlands and foothills that are potentially related to floristic composition.
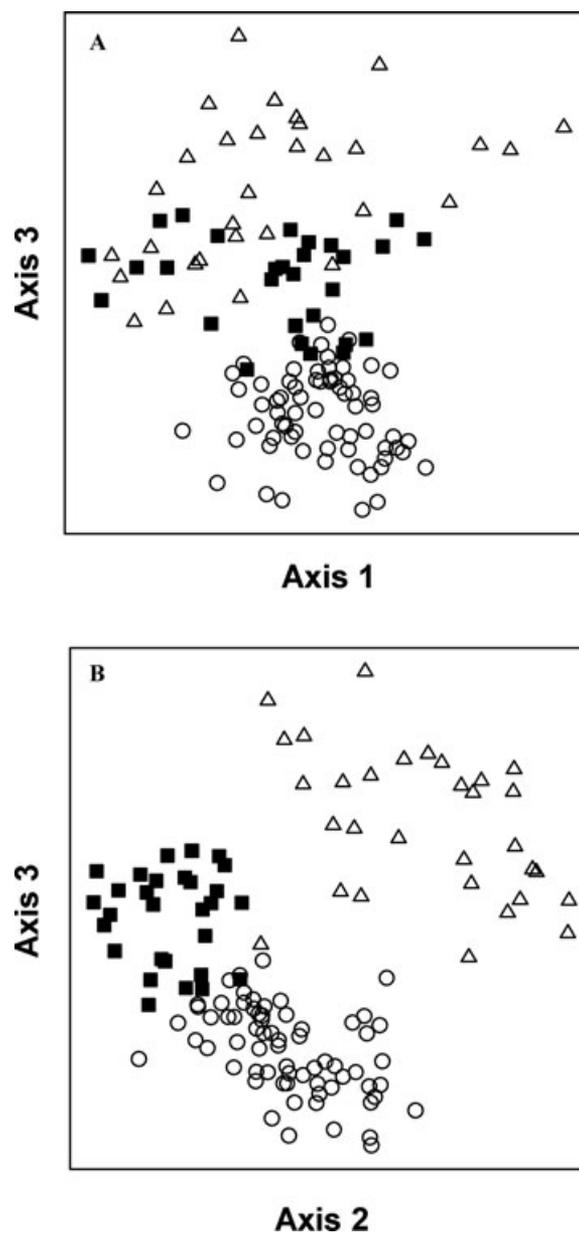

FIGURE 2.   NMS ordinations of plot data along: (A) axes one and three and (B) axes two and three overlaid with floristic groups from cluster analysis. Floristic groups are termed: foothills forest (triangle), and *P. macroloba* (circle) and *Q. paraensis* (square) forest in the lowlands. Ordination axes are principally correlated with tree species *Tapirira guianensis* Aubl. (Pearson $r = -0.40$, axis 1), *Q. paraensis*, *E. precatoria*, *S. exorrhiza*, *W. regia* (Pearson $r > -0.50$, axis 2), *P. macroloba* (Pearson $r = -0.85$, axis 3) and *V. allenii* (Pearson $r = 0.51$, axis 3).

SPATIAL AUTOCORRELATION AMONG VARIABLES.—Multivariate Mantel Correlograms indicate that distance decay relationships were similar for environmental conditions and forest composition across the study area (Fig. 3). Floristic and environmental variables were significantly autocorrelated up to the 10–13 km class (Fig. 3). A decline in floristic similarity with geographical distance was steepest up to the 4–7 km class in parallel with elevation and climate
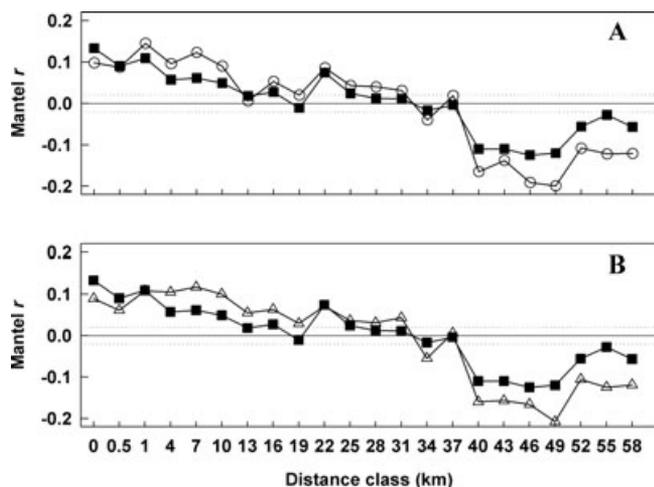
FIGURE 3. Spatial autocorrelation coefficients of forest plot pairs for 22 geographic distance classes. The x-axis shows the minimum geographic distance in each class. Mantel comparisons are from distance matrices of: (A) floristic composition (square), and elevation, temperature seasonality, and minimum monthly precipitation combined (circle), and (B) floristic composition (square) and clay and sand combined (triangle). Symbols above (+) and below (−) the dotted lines are significant correlations ($P < 0.05$).

factors (Fig. 3A). Soil physical properties, sand and clay, were significantly correlated with geographical distance for the 22–25 km class (Fig. 3B). A significant positive spatial autocorrelation in floristic composition at the 22–25 km distance class was related to plot pairs located in similar foothills and lowland environments (*e.g.*, *cerros* or hills) at this distance (Fig. 3). Significantly negative spatial autocorrelation for floristic distance after 40 km showed a pattern consistent with environmental Correlograms that was evident at most geographic distance intervals (Fig. 3). Significant negative correlations indicate that there are few or no species in common on plots > 40 km distant which were also negatively correlated with soil and climate conditions.

COMPARISONS OF FLORISTIC, ENVIRONMENTAL AND GEOGRAPHICAL VARIABLES.—The above comparisons provided a basis for testing the null hypothesis of no relationship between floristic and environmental distances once accounting for spatial autocorrelation (geographical distance). Alternatively, geographical distance is significant factor related to dispersal assembly processes and floristic variation after controlling the effect of significant environmental variables.

Simple Mantel tests comparing a matrix of tree and palm species with soil factors resulted in significant correlations for sand, clay and organic matter (Table 4). Partial Mantel tests showed no loss of significance after controlling for the effect of geographical distance. Similar trends were observed for palm species analyzed separately although silt content was also a significant factor (Table 4).

From here, only the results of Partial Mantel tests are presented unless a loss of significance was observed between simple and partial tests. No significant relationships were found between soil chemical properties and canopy tree and palm species combined (Table 4). Results likely reflect a broad distribution of principle canopy trees over soils with a low deviation in the chemical properties examined. Conversely, comparisons with a matrix of the four most abundant palm species showed significant relationships with differences in Ca and Mg concentrations (Table 4). Soil pH and total acidity and were also significantly related to palm distributions that are significantly correlated with soil cation concentrations (Table 2). Silt was weak, but significantly correlated with palm species abundance likely due to a few lowland plots showing high silt content.

Terrain variables, elevation and slope, were also significant factors for trees and palms combined, but slope was not a strong variable (Table 4). These results were not surprising as elevation covaries with significant soil physical properties (Table 2) and temperature variables. Slope was a weak, but significant variable likely due to the scale of the elevation data used. Plots (50 × 50 m) were generally established on sites with a consistent slope position however available elevation data at a 90-m grid-scale limits modeling local hillslope variation. Palm species were not significantly related to percent slope from separate comparisons possibly due to the above limitation.

Climate factors showed moderate seasonal and annual variation among plots (Table 3), but were significantly related to forest composition (Table 4). Coefficients of variation and minimum month precipitation were not significantly correlated with palms after controlling for geographical distance. No large turnover in palm species composition was observed on plots in the lowlands. Significant correlation between palm species and temperature variables were likely linked to fewer palm species present in cooler foothills environments. An exception was *I. deltoidea*, which showed relatively high abundances in both lowlands and foothills though no arboreal palms were present > 1000 m.

Geographical distance was significantly related to floristic distance at the $P < 0.001$ level from simple Mantel comparisons with floristic data (Table 4). Geographical distance remained a significant factor controlling for elevation, but showed a loss of significance ($P > 0.05$) when the effects of elevation and soil clay or sand content were removed (Table 4). Elevation was the strongest factor related to floristic composition followed by clay content. Separate comparisons with palm species resulted in significant correlations with geographical distance controlling for elevation and clay, but showed a loss of significance controlling for Mg and elevation combined (Table 4). Mg concentrations were highly and significantly correlated with other soil cations, pH, and total acidity, to a lesser degree (Table 2). Elevation was also correlated with soil texture and temperature variation between the foothills and lowlands indicating important interrelationships among variables and species distributions. Geographical distance was not a significantly related to species abundance once controlling for stronger environmental gradients present.

TABLE 4. *Mantel correlation tests comparing environmental and floristic variability. Simple and Partial Mantel tests accounting for geographic distances are shown in parallel. Comparisons between floristic composition and log geographical distance is shown controlling for significant environmental factors in parentheses. Significance levels were determined from 999 matrix randomizations (*** P < 0.001, ** P < 0.01, * P < 0.05).*

	Trees and palms		Palms	
	Simple Mantel r	Partial Mantel r	Simple Mantel r	Partial Mantel r
Ca	0.05		0.20**	0.19**
K	0.02		0.07	
Mg	0.04		0.19**	0.18**
P	0.05		0.07	
Total acidity	0.06		0.20**	0.19**
pH	0.03		0.17**	0.16**
Organic matter	0.34***	0.31***	0.22***	0.20***
Sand	0.41***	0.35***	0.34***	0.28***
Silt	0.09		0.13*	0.13*
Clay	0.54***	0.50***	0.35***	0.31***
Elevation	0.54***	0.51***	0.29***	0.20***
Slope	0.14*	0.14*	0.10	
Mean annual temperature	0.48***	0.46***	0.32***	0.28***
Temperature seasonality	0.37***	0.36***	0.25***	0.23***
Min. monthly temperature	0.49***	0.47***	0.34***	0.31***
Annual precipitation	0.29***	0.26***	0.28***	0.23***
Precipitation seasonality	0.29***	0.26***	0.11**	−0.02
Min. monthly precipitation	0.19***	0.10*	0.10*	−0.02
Geo dist	0.28***			0.24***
Geo dist (Elev)	0.16***		(Elev)	0.10***
Geo dist (Elev + clay)	−0.03		(Elev + clay)	0.10*
Geo dist (Elev + sand)	−0.02		(Elev + Mg)	0.05

DISCUSSION

Variation in forest composition along environmental gradients for the study area has been reported from previous studies (Hartshorn & Peralta 1988, Lieberman *et al.* 1996) though without sufficient data for spatially explicit analyses of forest beta-diversity. Floristic patterns quantified by the present study were from a wide distribution of plots replicated along multiple gradients to the extent feasible. Turnover in species composition (beta-diversity) observed from ordination and correlogram plots showed strong spatial patterns that vary with both environmental and geographical distance. Our analyses identified significantly positive spatial autocorrelation for floristic composition and environmental factors up to 13 km distance. A steep decline in floristic and environmental similarity up to 4 km and significantly negative correlations after 40 km were quite similar to species turnover reported from Panamanian forest plots (Pyke *et al.* 2001, Condit *et al.* 2002).

These parallels are notable considering seasonal and intermittent drought (*e.g.*, El Niño events) occurs with greater severity across the Panama Canal Watershed in addition to complex geological and soil substrates found in this area (Pyke *et al.* 2001, Engelbrecht *et al.* 2007, John *et al.* 2007). Soil texture and climate variation with elevation differences and a decrease in rainfall with distance from the

Caribbean Coast in the present study area help explain similar floristic patterns after accounting for the effects of geographical distance. Turnover in tree species composition from *P. macroloba* dominated forest to the *Q. paraensis* floristic group correspond with a transition from continuously high rainfall to areas with seasonally lower precipitation in the lowlands. Bioclimatic data from interpolated climate surfaces greatly smoothes actual conditions across plots and may increase their importance relative to geographical factors with statistical comparisons. Nevertheless a clear trend of diminishing rainfall and increased seasonality is evident from the data obtained from Costa Rican and Nicaraguan climate stations.

Variation in soil chemical and physical properties measured from forest plots were comparable to values reported from other published studies for this region. The range of extractable cation and P concentrations was not substantially different from forest soil units analyzed at the La Selva Biological Station (Sollins *et al.* 1994). An exception was K concentrations that were low on average for our plots (0.08 cmol (+) / kg ± 0.04) compared to upland soil substrates analyzed from similar depths at La Selva (0.80 cmol (+) / kg ± 0.69) (Sollins *et al.* 1994). Grieve *et al.* (1990) found a corresponding increase in sand and organic matter with a gain in elevation and a decreasing trend for clay content from six forest sites sampled near our plots. The lack of a significant correlation

between elevation and soil pH, P, and extractable cations in our data was also in agreement with Grieve *et al.* (1990).

Factors influencing soil moisture and drainage are particularly important to forest composition in areas of high rainfall (Sollins 1998). Floristic variation for trees and palms, both together and with a separate matrix for palm species was significantly correlated with sand, clay and soil organic content. Foothills and lowland floristic groups observed along ordination axes and correlation comparisons confirm high species turnover with large differences in soil texture also reported from Amazonian rain forest studies (Ter Steege *et al.* 1993, Duivenvoorden 1995, Duque *et al.* 2002, Phillips *et al.* 2003). Lowland floristic groups on primarily clay soils showed less distinctive textural differences though an increase in sand and decrease clay content was observed for the *Q. paraensis* group (Fig. S1). A categorical comparison between plots from the two lowland floristic groups and a distance matrix from all soil variables resulted in a significant difference ($P < 0.05$) from statistical tests using Multi-response Permutation Procedures (Mielke 1984, McCune & Grace 2002).

Floristic variation with respect to soil chemical properties was compared primarily for low fertility Inceptisols and Ultisols, characteristic of remaining forest. From a land use perspective, the small number of plots on more nutrient rich alluvial soils reflects markedly reduced forest cover on these sites. Old-growth forest on more recently alluviated soils was rare in the study landscape having been cleared during colonization for agriculture or trees favored for lumber (*e.g.*, *Terminalia oblonga* (Ruiz & Pav.) Steud. and *Carapa guianensis* Aubl.) (Nuhn & Peréz 1967). Lack of a statistically significant trend between soil chemical factors and floristic variation (*e.g.*, trees and palms combined) was not surprising under conditions of low variation in soil chemical composition. Phillips *et al.* (2003) found that large difference in soil nutrient status was significantly related to trees species composition from forest plots in south-eastern Peru. Cation concentrations across a 10,000 km^2 landscape averaged 7.9 cmol (+) / kg versus 0.65 cmol (+) / kg for Ca, Mg, and K summarized by Holocene and Pleistocene aged soils respectively (Phillips *et al.* 2003). Average cation concentrations in the present study area (1.27 cmol (+)/kg) were indicative of more highly leached Pleistocene aged soils also deficient in phosphorous (see also Marrs *et al.* 1988, Grieve *et al.* 1990). Turnover in canopy tree species composition is unlikely to be strongly linked to small variations in soil chemical properties on *tierra firme* sites, as noted from studies of upland forest in the Columbian Amazon (Duivenvoorden 1995, Duque *et al.* 2002). However, more recent findings from John *et al.* (2007) indicate that soil nutrients strongly influence local-scale (< 1 km^2) distribution and niche differentiation for as many as one-third of tropical tree species in Panamanian, Columbian, and Ecuadorian rain forest plots.

Mid- to upper-canopy palms, on the other hand, showed a significant relationship with soil cations Mg and Ca and pH and total acidity. Our data suggest that soil physical properties and specific cations are important to palm species distribution. These results are in agreement with Clark *et al.* (1995) who found that palm species (*e.g.*, *E. precatoria*, *I. deltoidea*, and *S. exorrhiza*) were spatially structured according to meso-scale differences on soil types with varying chemical and textural composition. Poulsen *et al.* (2006) also found Mg and Ca concentrations were significantly correlated with palm distributions for a 1-ha plot studied in Amazonian Ecuador. Significant correlations for sand, clay and elevation and a lack of significance for K, P, pH, and slope from Poulsen *et al.* (2006) correspond surprisingly well with our results considering the wide difference in scales.

Geographical distance was not strongly related to tree and palm species abundance once controlling for statistically significant environmental variables. Soil and climate gradients quantified for the present study area can potentially mask the contribution of dispersal-assembly processes to species abundance patterns. Partial Mantel correlations were used to determine relationships between species and geographic distance by controlling the effect of spatially correlated environmental factors.

In contrast to these results, Ruokolainen & Vormisto (2000) report more generalized palm distribution patterns at the landscape-scale for three of the four palm species (*W. regia* excluded) on Amazonian plots with comparisons using summed cation concentrations (*i.e.*, Ca, Mg, K, and Na). However, species presence–absence data were used and no comparisons were made with soil textural conditions. In the present study area, *S. exorrhiza* and *W. regia* abundance decline substantially on increasingly sandy-loam soils > 300 m elevation while *I. deltiodea* and *E. precatoria* were abundant over much of the study area to 900 m. Vormisto *et al.* (2004b) also found a stronger relationship between geographic distance and palm species abundance than with soil and terrain characteristics for Peruvian and Ecuadorian rain forest plots. Forest plots from Vormisto *et al.* (2004b) occur at a somewhat larger spatial extent and show relatively low deviation in soil and climatic conditions in comparison with this study. Biogeographical factors and barriers to dispersal appear to exceed environmental controls over palm species abundance in these settings (see also Normand *et al.* 2006).

The length and steepness of gradients measured in addition to spatial extent likely influence results from ours and other studies occurring in differing geographic regions. Duque *et al.* (2002) noted that low environmental variation and weak beta-diversity or fewer species with restricted habitats in southwest Amazonia has led to different conclusions about principal factors controlling tropical plant composition. A stronger effect from soil factors on floristic composition opposed to geographic distance was observed in Columbian rain forest only when plots subject to flooding or more severe edaphic environments were included in analyses (Duque *et al.* 2002).

Once accounting for geographical distance with our analysis, complex physiographic conditions and changes in soil substrates across Caribbean lowland and foothills environments were significantly correlated with forest beta-diversity. From these comparisons, we find greater support for a niche-assembly hypothesis as the principal driver of forest beta-diversity in this landscape. Geographical distance and dispersal mechanisms undoubtedly play a role in tropical tree species distributions (Tuomisto *et al.* 2003a), but were less important after controlling for significant environmental variables in the study landscape. Pyke *et al.* (2001) also conclude that dispersal limitation is likely secondary to environmental drivers at the

landscape-scale. In contrast, recent analyses for Panamanian plots by Chust *et al.* (2006) showed stronger support for a dispersal hypothesis from correlation comparisons and model fitting. An explanation for differing conclusions is that geographical distance is possibly a better predictor of floristic patterns in the absence of data for important environmental factors such as underlying soil conditions and moisture gradients. A strong relationship between soil nutrient status and moisture availability have more recently been linked to tree species distributions at the local- and regional-scale in both Central and South America forest plots (Engelbrecht *et al.* 2007, John *et al.* 2007). Life-forms (*e.g.*, canopy trees vs. palms) may also differ in their response to the physical environment though detailed studies of individual species relationships with soil factors are needed to confirm differences noted here (see also Engelbrecht *et al.* 2007). Quantitative comparisons between soil and rain forest composition in neighboring Nicaragua or Costa Rica's Osa Peninsula where similar Amazonian centered tree and palm species coexist would also provide additional insight into principle factors driving forest beta-diversity.

Results from this study suggest that more detailed knowledge of soil and climate factors related to turnover in tree species composition will likely aid spatial models characterizing rain forest beta-diversity (see also Chust *et al.* 2006, Sesnie *et al.* 2008). Floristic variation within the biological corridor investigated with this study suggests that floristic patterns can vary over relatively short distances. This information is needed for natural resource planning and establishing conservation corridors in areas that contain floristic variation not currently represented within nationally protected areas.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

The following supporting information for this article is available online at: www.blackwell-synergy.com/loi/btp

FIGURE S1. Box plots of significant soil physical properties percent.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors.

Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

Austin, M. P. 2002. Spatial prediction of species distribution: An interface between ecological theory and statistical modeling. Ecol. Model. 157: 101–118.

Bouyoucos, G. J. 1936. Directions for making mechanical analysis of soils by the hydrometer method. Soil Sci. 42: 225–228.

Butterfield, R. P. 1994. The regional context: Land colonization and conservation in Sarapiquí. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). La Selva: Ecology and natural history of a Neotropical rain forest, pp. 299–306. University of Chicago Press, Chicago, Illinois.

Chust, G., J. Chave, R. Condit, S. Aguilar, S. Lao, and R. Pérez. 2006. Determinants and spatial modeling of tree ß-diversity in a tropical forest landscape in Panama. J. Veg. Sci. 17: 83–92.

Clark, D. A., D. B. Clark, R. Sandoval, and M. V. Castro. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology 76: 2581–2595.

Clark, D. B., M. W. Palmer, and D. A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rainforest trees. Ecology 80: 2662–2675.

Condit, R., N. Pitman, E. G. Leigh Jr., J. Chave, J. Terborgh, R. B. Foster, P. Núñez, S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. P. Hubbell. 2002. Beta-diversity in tropical forest trees. Science 295: 666–669.

DeFries, R., A. Hansen, A. C. Newton, and M. C. Hansen. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. Ecol. Appl. 15: 19–26.

Diaz Romeu, R., and A. Hunter. 1978. Metodología de muestreo de suelos, análisis químico de suelos, tejido vegetal e investigación en invernadero. Turrialba: Centro Agronómico Tropical de Investigación y Enseñanza, Costa Rica.

Duivenvoorden, J. F. 1995. Tree species composition and rain forest-environment relationships in the middle Caquetá area, Columbia NW Amazonia. Vegetation 120: 93–113.

Duque, A., M. Sánchez, J. Cavelier, and J. Duivenvoorden. 2002. Different floristic patterns of woody understorey and canopy plants in Columbian Amazonia. J. Trop. Ecol. 18: 499–525.

Dutilleul, P., P. Clifford, S. Richardson, and D. Hemon. 1993. Modifying the *t*-test for assessing the correlation between two spatial processes. Biometrics 49: 305–314.

Engelbrecht, B. M., L. S. Comita, R. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447: 80–82.

ESRI. 2005. ArcGIS software package v. 9.1. 380 New York Street Redlands, CA 92373-8100, http://www.esri.com/.

Faber-Langendoen, D., and A. H. Gentry. 1991. The structure and diversity of rain forests at Bajo Calima, Choco Region, Western Columbia. Biotropica 23: 2–11.

Franklin, J. 1995. Predictive vegetation mapping: Geographic modelling of biospatial patterns in relation to environmental gradients. Prog. Phys. Geog. 19: 474–499.

Gleason, H. A. 1927. Further views on the succession concept. Ecology 8: 299–326.

Grieve, I. C., J. Proctor, and S. A. Cousins. 1990. Soil variation with altitude on Volcan Barva, Costa Rica. Catena 17: 525–534.

Hartshorn, G. S. 1980. Neotropical forest dynamics. Biotropica 12: 23–30.

Hartshorn, G. S., and R. Peralta. 1988. Preliminary description of primary forest along the La Selva-Volcan Barva altitudinal transect, Costa Rica. *In* California Academy of Science Memoir No. 12, F. Almeda, and

C. M. Pringle (Eds.). Tropical rainforests: Diversity and conservation, pp. 281–295. California Academy of Science: Pacifica Division: American Association for the Advancement of Science, San Francisco, California.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25: 1965–1978.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey.

HUBBELL, S. P., R. B. FOSTER, S. T. O'BIEN, K. E. HARMS, R. CONDIT, B. WECHLER, S. J. WRIGHT, AND S. LOO DE LAO. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. Science 283: 554–557.

JOHN, R., J. W. DALLING, K. E. HARMS, J. B. YAVITT, R. F. STALLARD, M. MIRABELLO, S. P. HUBBELL, R. VALENCIA, H. NAVARRETE, M. VALLEJO, AND R. B. FOSTER. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proc. Natl. Acad. Sci. USA 104: 864–869.

JONES, M. M., H. TUOMISTO, D. B. CLARK, AND P. OLIVAS. 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. J. Ecol. 94: 181–195.

LEGENDRE, P., AND M. FORTIN. 1989. Spatial pattern and ecological analysis. Vegetation 80: 107–138.

LIEBERMAN, M., D. LIEBERMAN, G. S. HARTSHORN, AND R. PERALTA. 1985. Small-scale altitudinal variation in lowland wet tropical forest vegetation. J. Ecol. 73: 505–516.

LIEBERMAN, D., M. LIEBERMAN, R. PERALTA, AND G. S. HARTSHORN. 1996. Tropical forest structure and composition on a large scale altitudinal gradient in Costa Rica. J. Ecol. 84: 137–152.

MARRS, R. H., J. PROCTOR, A. HEANEY, AND M. D. MOUNTAINFORD. 1988. Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. J. Ecol. 76: 466–482.

MAYAUX, P., P. HOLMGREN, F. ACHARD, H. EVA, H. STIBIG, AND A. BRANTHOMME. 2005. Tropical forest cover change in the 1990's and options for future monitoring. Phil. Trans. Roy. Soc. B. 360: 373–384.

MCCUNE, B., AND M. J. MEFFORD. 1999. PC-ORD. Multivariate analysis of ecological data version 4. MjM Software Design, Gleneden Beach, Oregon.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MJM Software Design, Gleneden Beach, Oregon.

MIELKE, P. W. JR. 1984. Meterological applications of permutation techniques based on distance functions. In P. R. Krishnaiah and P. K. Sen (Eds.). Handbook of statistics, vol. 4, pp. 813–830. Elsevier Science Publishers, The Hague, The Netherlands.

NELSON, D. W., AND SOMMER, L. E. 1996. Total carbon, organic carbon and organic matter, pp. 961–977. Methods of soil analysis. Part 3, chemical methods, 3rd ed., SSSA Series: 5. Madison, WI.

NORMAND, S., J. VORMISTO, J. SVENNING, C. GRÁNDEZ, AND H. BALSLEV. 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. Plant Ecol. 186: 161–176.

NUHN, H., AND S. PÉREZ. 1967. Estudio geographico regional: Zona Atlantico norte de Costa Rica. Instituto de Tierras y Colonización, Programa de Asistencia Técnica del Gobierno de la Republica Federal de Alemania, San José, Costa Rica.

OLSEN, S. R., AND L. E. SOMMERS. 1982. Phosphorus. In A. L. Page, R. H. Miller, and D. R. Keeney (Eds.). Methods of soil analysis. Part 2. 2nd ed. Agron. Monogr. 9. pp. 403–427. ASA and SSSA, Madison, WI.

PHILLIPS, O. L., P. N. VARGAS, A. L. MONTEAGUDO, A. P. CRUZ, M. C. ZANS, W. G. SÁNCHEZ, M. YLI-HALLA, AND S. ROSE. 2003. Habitat association among Amazonian tree species: A landscape scale approach. J. Ecol. 91: 757–775.

POULSEN, A. D., H. TOUMISTO, AND H. BALSLEV. 2006. Edaphic and floristic variation within a 1-ha plot of lowland Amazonian rain forest. Biotropica 38: 468–478.

PYKE, C. R., R. CONDIT, S. AGUILAR, AND S. LAO. 2001. Floristic composition across a climatic gradient in a Neotropical lowland forest. J. Veg. Sci. 12: 553–566.

ROSENBURG, M. S. 2001. PASSAGE: pattern analysis, spatial statistics and geographic exegesis version 1.1. http://lsweb.la.asu.edu/rosenberg/Passage/.

RUOKOLAINEN, K., A. LINNA, AND H. TUOMISTO. 1997. Use of Melastomataceae and Pteridophytes for revealing phytogeographical patterns in Amazonian rain forest. J. Trop. Ecol. 13: 243–256.

RUOKOLAINEN, K., AND J. VORMISTO. 2000. The most widespread palms tend to be tall and habitat generalists. Basic Appl. Ecol. 1: 97–108.

RUOKOLAINEN, K., AND H. TUOMISTO. 2002. Beta-diversity in tropical forests. Sci. Tech. Comments 297: 1439a.

SCOTT, J. M., AND M. D. JENNINGS. 1998. Large-area mapping of biodiversity. Ann. Mo. Bot. Gard. 85: 34–47.

SESNIE, S. E., P. E. GESSLER, B. FINEGAN AND S. THESSLER. 2008. Integrating Landsat TM and SRTM-DEM derived variables with decision trees for habitat classification and change detection in complex Neotropical environments. Remote Sens. Environ. 112: 2145–2159.

SOIL SURVEY STAFF. 1975. Soil taxonomy. USDA Agriculture Handbook No. 436, U.S. Government Printing Office, Washington, DC.

SOLLINS, P., F. SANCHO, R. MATA, AND R. L. SANFORD. 1994. Soils and soil process research. In L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn (Eds.). La Selva: Ecology and natural history of a Neotropical rain forest, pp. 34–53, University of Chicago Press, Chicago, Illinois.

SOLLINS, P. 1998. Factors influencing species composition in tropical lowland rain forest: Does soil matter? Ecology 79: 23–30.

TER STEEGE, H., V. G. JETTEN, A. M. POLAK, AND M. J. A. WERGER. 1993. Tropical rain forest types and soil factors in a watershed area in Guyana. J. Veg. Sci. 4: 705–716.

TER STEEGE, H., C. A. PITMAN, O. L. PHILLIPS, J. CHAVE, D. SABATIER, A. DUQUE, J.-F. MOLINO, M.-F. PRÉVOST RS, H. CASTELLANOS, P. VON HILDERBRAND, AND R. VÀSQUEZ. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443: 444–447.

TUOMISTO, H., K. RUOKOLAINEN, R. KALLIOLA, A. LINNA, W. DANJOY, AND Z. RODRIGUEZ. 1995. Dissecting Amazonian biodiversity. Science 269: 63–66.

TUOMISTO, H., M. RUOKOLAINEN, AND M. YLI-HALLA. 2003a. Dispearsal, environment, and floristic variation of western Amazonian forests. Science 299: 241–244.

TUOMISTO, H., K. RUOKOLAINEN, M. AGUILAR, AND A. SARMIENTOS. 2003b. Floristic patterns along a 43-km long transect in an Amazonian rain forest. J. Ecol. 91: 743–756.

TUOMISTO, H., A. D. POULSEN, K. ROUKOLAINEN, R. C. MORAN, C. QUINTANA, J. CELI, AND G. CAÑAS. 2003c. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. Ecol. Appl. 13: 352–371.

VORMISTO, J., H. TUOMISTO, AND J. OKSANEN. 2004a. Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? J. Veg. Sci. 15: 485–494.

VORMISTO, J., J. SVENNING, P. HALL, AND H. BALSLEV. 2004b. Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazon basin. J. Ecol. 92: 577–588.

WAGNER, H. H., AND M.-J. FORTIN. 2005. Spatial analysis of landscapes: Concepts and statistics. Ecology 86: 1975–1987.

WATSON, V., S. CERVANTES, C. CASTRO, L. MORA, I. T. PORRAS, AND B. CORNEJO. 1998. Making space for better forestry: Policy that works for forests and people: Centro Cientifico Tropical and the International Institute for Environment and Development, No. 6 137p. San José, Costa Rica and London, UK.

WHITTAKER, R. H. 1967. Gradient analysis of vegetation. Bol. Rev. 42: 207–260.